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# DEVELOPMENT OF EARTHWORM BURROW SYSTEMS and the influence of earthworms on soil hydrology

*'But to ascertain the direction of many burrows was found too difficult and troublesome.'*

Charles Darwin (1881)

The formation of the vegetable mould through the action of worms with observations on their habits.

Thomas Nicolaas Ligthart

# DEVELOPMENT OF EARTHWORM BURROW SYSTEMS and the influence of earthworms on soil hydrology

Proefschrift
ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen
op gezag van de rector magnificus,
Dr. C.M. Karssen,
in het openbaar te verdedigen
op woensdag 17 april 1996
des namiddags te half twee in de Aula
van de Landbouwuniversiteit te Wageningen.

*Voor ma, je mocht ook dit niet meemaken.*

**Colofon**
Art director: Hans van Reemst.
Ontwerp cover: Hans van Reemst.
Lithografie cover: Hans Ruëdisuëli, Litho de Finne bv, Grou.
Druk: Grafisch bedrijf Ponsen & Looijen bv, Wageningen.

## Errata

**Stellingen**
14: In gebieden de recreatieve waarden ..... vervangen door: Indien in gebieden de recreatieve waarden .....

**Abstract**
The rate strongly increased up to an average 29.6 $m.y^{-1}$ ..... vervangen door: The rate strongly increased up to an average 29.3 $m.y^{-1}$ .....

**Curriculum Vitae**
..... Rapolano Terne vervangen door: Rapolano Terme .....

**1** De aanname van Brussaard en Faassen (1994) dat in afwezigheid van grondbewerking regenwormgangen gedurende vele jaren ongeschonden blijven bestaan, stemt niet overeen met de bevinding dat zelfs in onbeweid grasland regenwormen ruim 80% van de nabij het oppervlak gemaakte gangen weer opvullen.

*Brussaard, L. and Faassen, H.G. (1994) Effects of compaction on soil biota and soil biological processes. In: B.D. Soane and C. van Ouwerkerk (Eds.) Soil compaction in crop production. (Developments in agricultural engineering (11), Elsevier, Amsterdam, 662 p.*

*Dit proefschrift.*

**2** In de door A. Kretzschmar beschreven regenwormgangenstelsels kan het opvullen van gangen met regenwormuitwerpselen niet het belangrijkste proces zijn dat de afbraak van gangen bij het begin van het droge seizoen veroorzaakt.

*Kretzschmar, A. (1982) Description des galeries de vers de terres et variation saisonnière des résaux (observations en conditions naturelles). Rev. Écol. Biol. Sol* ***19****: 579-591.*

*Dit proefschrift.*

**3** Wanneer op de Ir. A.P. Minderhoudhoeve te Swifterbant bij de ingebruikname van perceel K22.7 enkele centimeters dieper was geploegd, was niet *Aporrectodea longa*, maar *A. caliginosa* de koloniserende soort geweest.

*Dit proefschrift.*

**4** Het hydrologisch functioneren van regenwormgangen wordt sterk bepaald door de waterdoorlatendheid van het macroporiënstelsel dat zij aansnijden.

*Bouma, J., Belmans, C.F.M. and Dekker, L.W. (1982) Water infiltration and redistribution in a silt loam subsoil with vertical worm channels. Soil Sci. Soc. Am. J.* ***46****: 917-921.*

*Urbánek, J. and Doležal, F. (1992) Review of some case studies on the abundance and on the hydraulic efficiency of earthworm channels in Czechoslovak soils with reference to the subsurface pipe drainage. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. Soil Biol. Biochem.* ***24 (12)****: 1563-1571.*

*Dit proefschrift.*

**5** Het wereldrecord voor de (lokale) verspreidingssnelheid van regenwormen werd tussen 1991 en 1994 gevestigd op de Ir. A.P. Minderhoudhoeve en bedroeg 29.3 m per jaar.

*Dit proefschrift.*

**6** Het begrip 'protective pore space' is te illustreren met een kat die op de vlucht voor een hondse belager onder een auto kruipt.

**7** De ambiance van het Groot Auditorium is aanzienlijk te verbeteren door de geschiedenis van de landbouw en haar relatie met de wetenschap in een imposante wandschildering te verbeelden.

**8** In landschappen of natuurgebieden waarbij de waarden sterk worden bepaald door relaties met de omgeving, zoals bij de Biebrza (Polen) en haar vallei het geval is, zal het niet betrekken van die omgeving bij maatregelen om de landschaps-/natuurwaarden te behouden uiteindelijk een tegengesteld effect sorteren.

*Wassen, M.J. (1995) Hydrology, water chemistry and nutrient accumulation in the Biebrza fens and floodplains (Poland). Wetlands Ecology and Management 3: 125-137.*

*Szkiruc, Z., Szulczewska, B., Burger, T., Jaroszewski, T., Glowacka, I., Matuszkiewicz, A. and Skalmowski, W. (1990) Biebrza Landscape Park. Outlines of the Physical Management Plan, National Foundation for Environmental Protection Poland. World Wildlife Fund for Nature. Warszawa.*

**9** Werkelijk duurzame landbouw is niet mogelijk wanneer landbouw en natuur op landschappelijke schaal zijn gescheiden.

*Risch, S.J., Andow, D. and Altieri, M.A. (1983) Agroecosystem diversity and pest control: data, tentative conclusions, and new research directions. Environmental Entomology 12: 625-629.*

**10** Om onderlinge samenwerking en interdisciplinariteit te waarborgen moeten AIO- en OIO-onderzoeken binnen een onderzoekschool zijn ingebed in goed gedefinieerde overkoepelende 'meta'-projecten.

**11** De glimlach van een baby is, in het bijzonder in doorwaakte nachten, een evolutionair adequate overlevingsstrategie van de mens.

**12** Het bestuur van de Landbouwuniversiteit had allereerst een prioriteitsstelling in aandachtsgebieden moeten vaststellen, alvorens de leerstoelendans werd uitgevoerd.

**13** Het door regenwormonderzoekers aanhalen van Darwin lijkt vaak te zijn ingegeven door het gevoel dat leken en veel landbouwkundigen dit soort onderzoek onderwaarderen.

**14** In gebieden de recreatieve waarden van een gebied mede worden bepaald door zijn agrarisch cultuurlandschap, dient een deel van de toeristenbelasting naar de beheerders - de boeren - te vloeien.

Stellingen behorend bij het proefschrift 'Development of earthworm burrow systems and the influence of earthworms on soil hydrology', Tom N. Ligthart, 17 april 1996.

Ligthart, Thomas Nicolaas

# DEVELOPMENT OF EARTHWORM BURROW SYSTEMS
## and the influence of earthworms on soil hydrology

## Abstract

Inoculation of earthworms can help to restore or ameliorate land qualities. Earthworms create burrows and alter the structure of the soil matrix, which influences the water infiltration, drainage, water retention and the aeration of the soil. The way and rate of the development of earthworm burrow systems are practically unknown, and form the core of this thesis.

When studying the relation earthworms - soil properties, correlations between earthworm activity and soil properties are commonly found, but cause and effect are hard to separate. This problem can be resolved in part by studying a chronosequence of earthworm burrow systems and associated earthworm-affected soil properties. Two of such chronosequences, which developed after inoculation of earthworms in pastures formerly without earthworms and covered 0 to 20.8 y of earthworm activity, were considered in this study.

In the most intensively studied chronosequence the average dispersal rate of the earthworms was $6.3\ \mathrm{m.y^{-1}}$ in the first seven years following the inoculation. The rate strongly increased up to an average $29.6\ \mathrm{m.y^{-1}}$ in the next three years. This accelerated dispersal is most likely related to a change in food supply.

To reveal the mode and rate of development of earthworm burrow systems, six of these systems were mapped three-dimensionally. Density and architecture of the burrow systems changed quickly and strongly responded to changes in the mass of the earthworm community. The burrow systems consisted of mainly vertical burrows, many of which were short (<6 cm) and only few of which reached lengths greater than 30 cm. Year-to-year variations, differences in burrow systems between the two chronosequences, and burrowing efficiency of the earthworms could be related to differences in earthworm activity.

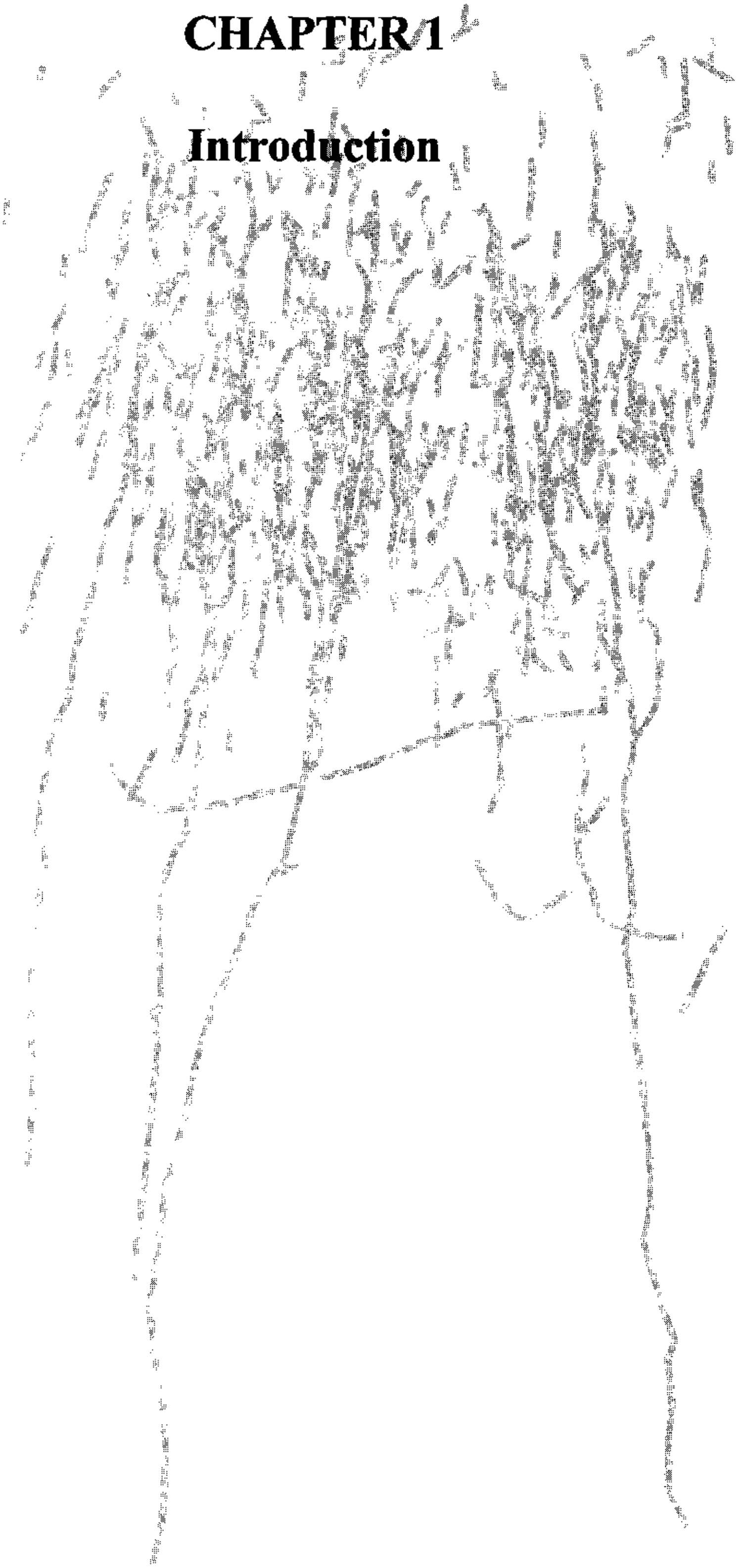
The highly dynamic nature of earthworm burrow systems indicated that both formation and destruction of burrow systems need to be considered. The destruction rate of earthworm burrows and its controlling factors were assessed by following the fate of artificial earthworm burrows in one of the pastures, and by thin section analysis of natural burrows. At and close to the soil surface trampling by cattle was the main cause of burrow destruction. At greater depth (22.5 cm) casting by earthworms was found to be the most important source of destruction.

Burrows increased hydraulic conductivities ($K$) of the fully water saturated soil and of the soil matrix close to saturation. The structure of the subsoil strongly influenced the $K$ of individual burrows. The change in structure of the topsoil by earthworm activity increased $K$ of the unsaturated soil matrix.

# CONTENTS

# CHAPTER 1

# Introduction



## Aims of the study 1.1

The main aim of the study presented in this thesis was to assess and explain the effects of earthworms on soil structure development, with emphasis on the development of earthworm burrow systems. The second aim was to assess and explain the effect of these soil-dwelling animals on the soil's hydraulic properties.

Earthworms play a crucial role in the restoration of farming land replaced after opencast mining (Scullion, 1994) and of cleaned, formerly contaminated, soil (Tamis and Udo de Haes, 1995). Inoculation of earthworms or stimulation of the community already present may help to reach 'sustainable agriculture' (e.g. Lee, 1985, Lee, 1992, Marinissen, 1992). One of the aspects of the amelioration of land qualities by earthworms is the formation of burrows. The rate of structural and functional development of earthworm burrow systems is virtually unknown, and this aspect forms the core of this thesis. As earthworms have the highest density in well-drained permanent pastures while tillage in arable land destroys burrows, the studies were confined to grassland.

A major dilemma in studying the relation earthworm activity - soil (hydraulic) properties is the often ignored 'chicken and egg' problem: correlations between soil properties and earthworm presence exist, but cannot be unravelled to separate cause from effect. In The Netherlands we are so fortunate to have large polders reclaimed from the 'IJsselmeer' in which earthworms were initially absent. Local inoculations of earthworms at various times in the past led to the formation of chronosequences of earthworm burrow systems and earthworm of affected soil properties. By studying such chronosequences, the 'chicken and egg' problem could, at least partly, be circumvented.

Before going into more detail of the study itself, I will discuss the relations between earthworms and the soil ecosystem in which they may play an important role. Following that discussion the impact of earthworms on the soil structure and on the soil hydraulic conductivity will be considered in more detail. Finally, the outlines of the study and of its resulting thesis are given.

## Earthworms and the soil ecosystem 1.2

Earthworms (Class Oligochaeta, Suborder Lumbricina) are muscular animals of up to 0.3 m long (*Lumbricus terrestris*). Most species live in subsurface soil horizons. Respiration takes place through the moist cuticle. Roughly two groups can be distinguished, on the base of their food source: litter consuming (detritivorous) and soil consuming (geophagous) species. A division into morpho-ecological groups (Bouché, 1977) is also often used: (a) epigeic earthworms which live in the litter layer or in animal faeces, (b) anecic earthworms that live in permanent burrows and feed on soil surface litter and (c) soil inhabiting endogeic earthworms that feed on soil containing organic material. Earthworms create burrows to feed, to relocate themselves and, in case of anecic species, to have a permanent 'home' in which they are more or less protected from adverse conditions.

In many soils earthworms are the dominant soil fauna, in terms of biomass and in terms of their ability to change the soil environment. The important position of earthworms in the soil ecosystem was recognized by great men as Aristotle and Charles Darwin, whose last book (1881) is a quite lyrical account on these subsurface dwellers.

Naturally, the abiotic and biotic state of the soil ecosystem influences the earthworm community. The soil moisture content and its regime are key factors determining the activity of individual earthworms and the composition of a community (Nordström and Rundgren, 1974, Nordström, 1975). Many species survive dry periods by going into diapause (also called quiescence or aestivation) in a specially prepared chamber. Soil texture has its impact on the earthworm community through its effects on soil structure and so the soil moisture economy. Temperature is another important factor. In the temperate region the optimum soil temperature for earthworms ranges from 10 to 15 °C. Kretzschmar (1982) took the ratio soil moisture content / soil temperature as the factor describing seasonal earthworm activity. The bulk density of the soil, or better the soil strength (at relevant pressure heads), determines the 'burrowability' of the soil (McKenzie and Dexter, 1988a and 1988b, Kretzschmar, 1991), though the relation between physical soil attributes and the ease with which earthworms create burrows is not always clear (Dexter, 1978, Rushton, 1986). Earthworms are also affected by the chemical state of the soil as described by pH, electrolyte concentration and $E_H$. Finally the quality and abundance of food source(s) determine composition and size of the earthworm community.

By incorporating organic material into the mineral soil and by mixing the soil earthworms alter structure, structure stability, moisture holding capacity, organic matter dynamics and chemical state of the soil to a large extent (e.g. Hoogerkamp et al., 1983, Knight et al., 1992, Tomlin et al., 1992, Marinissen, in press). Some soils are even classified by the strong alteration of the soil by earthworms as in case of Vermudolls (Buol et al., 1973). The nature and size of the effect of earthworms on soil properties depend on the composition and size of the earthworm community (e.g. Shaw and Pawluk, 1986).

The reader will find more details on the relation between earthworms and the soil ecosystem in the extensive work of Lee (1985), on which this review was largely based.

## Earthworms and soil structure 1.3

Earthworms influence soil structure by the formation of burrows and by the alteration of the non-burrow part of the pore system. With a few exceptions (Kretzschmar, 1978 & 1982, Kobel-Lamparski and Lamparski, 1987, Joschko et al. 1991, McKenzie and Dexter, 1993) little attention has been paid to the volume and the architecture of earthworm burrow systems. This lack of attention is due to the hidden nature of burrow systems and due to the effort it takes to study these systems in detail: 'But to ascertain the direction of many burrows was found too difficult and troublesome.', Darwin (1881). Nevertheless, an attempt is made in this thesis to characterize and explain the almost unknown development of earthworm burrow systems.

Earthworm burrow systems appeared to have an oblique to vertical main orientation and may be shallow (< 0.25 m depth) or extend to greater depths (>1 m) (Kretzschmar, 1982, McKenzie and Dexter, 1993). The systems may contain long burrows (up to 1 m) of the anecic species, though most burrows are short (2 - 6 mm). The diameter of burrows varied from 1 to over 10 mm, but was usually in the range of 2-5 mm, and this positions them in the class of large macropores.

Earthworms alter the soil structure of the soil matrix (e.g. Jeanson, 1964, Geyger, 1979, Stockdill, 1982, Hoogerkamp et al., 1983, Shaw and Pawluk, 1986, Kretzschmar, 1987, Knight et al. 1992), most probably changing size distribution, continuity and tortuosity of pores. Earthworms may increase the micro- to macroporosity of the soil (Hoogerkamp et al., 1983) although a marked reduction of macroporosity by earthworms has been reported (Stockdill, 1982).

The macropore system reflects a dynamic equilibrium between the formation and destruction of macropores (Beven and Germann, 1982). Compaction of the topsoil by grazing cattle may destroy macropores (including earthworm burrows) close to the surface (Beven and Germann, 1982). Earthworms themselves may destroy burrows too by filling them with casts (Kretzschmar, 1982), the extent to which they do so remains, however, unclear. Burrow systems may show seasonal variations (Kretzschmar, 1982, Monestiez et al., 1993) due to the formation of burrows in periods when the animals are active, followed by destruction of burrows before they go into aestivation.

Both the rate at which earthworm burrows are destroyed and the true importance of potential factors governing this rate are practically unknown. Therefor, two studies were performed to establish burrow destruction rates and the rate controlling factors.

## 1.4 Earthworms and soil hydraulic properties

White (1789) (cited in Graff and Makeschin (1979)) realized the importance of earthworm burrows for the infiltration of precipitation into the soil. In many later studies (e.g. Ehlers, 1975, Stockdill, 1982, Hoogerkamp et al., 1983, Edwards et al., 1992, Joschko et al., 1992) lumbricid earthworms are mentioned to considerably affect the soil hydraulic properties. When ponding occurs at the soil surface - which depends on a number of soil factors and rainfall characteristics - burrows may substantially increase the flux of water through the soil (Beven and Germann, 1982, Smettem, 1992, Booltink and Bouma, 1993). The connectivity of earthworm burrows with each other and with the non-burrow macropore system determines the efficiency of burrows in increasing the saturated hydraulic conductivity ($K_{sat}$) (Bouma et al., 1982, Urbánek and Doležal, 1992).

While many studies report an increase in infiltration rates due to earthworm activity, Lavelle et al. (in press) observed a tendency for $K_{sat}$ to decrease in the presence of the tropic (non-lumbricid) earthworm *Pontoscolex corethrurus*.

By altering the structure of the soil matrix, earthworms also change the hydraulic properties of the unsaturated matrix. Although the majority of studies on the influence of earthworms on soil hydraulic properties focus on the effect of burrows on $K_{sat}$, their effect on smaller pores, which will also affect soil hydrology, remains underexposed. This aspect forms therefor part of this study.

## 1.5 Outline of the study

The study was divided in partial studies each with its own objective(s):

1. Assessing the structural and functional development of earthworm burrow systems and the development of the earthworm community.
2. Assessing the factors involved in the destruction of earthworm burrows and the rates of destruction.
3. Establishing the effect of earthworm activity on soil hydraulic properties from full saturation down to an unsaturated soil matrix.
4. Investigation of the micromorphology of earthworm burrow walls and the consequences of their micromorphological properties for the hydraulic functionality of burrows.

The majority of these studies was based on one experimental site, a permanent pasture at the ir. A.P. Minderhoudhoeve (Swifterbant, The Netherlands), an experimental farm of the Wageningen Agricultural University. The study was a project funded by The Netherlands Integrated Soil Research Programme (Anonymous, 1989).

## Outline of the thesis 1.6

It was felt necessary to study earthworm burrow systems in three dimensions. To achieve 3D mapping of burrow systems a method based on serial sectioning was developed. This method and the accompanying specially designed apparatus are, together with some first results, described in chapter 2.

The final results of the 3D mapping of earthworm burrow systems are found in chapter 3 and 4. Chapter 3 focuses on the development of the architecture of burrow systems. In this chapter the development of the earthworm community following the inoculation of earthworms is also presented. Chapter 4 relates the density and structure of earthworm burrow systems to soil induced differences in earthworm activity.

As burrow systems reflect the result of both the formation and the destruction of burrows, the destruction rate of earthworm burrows and its determining factors were studied under field circumstances using two different approaches. Chapter 5 describes the use of artificial earthworm burrows whose fate was followed in a 4-month field experiment. Secondly, thin sections taken from a 7.3 year old chronosequence of burrow systems were studied to assess burrow destruction rates over a longer time span. The results of this study are found in chapter 6.

The development of the impact of earthworm activity on the soil's hydraulic properties is described in chapter 7. Finally, the findings from chapters 2 to 7 are synthesized and discussed in chapter 8.

## References

Beven, K. and Germann, P. (1982) Macropores and water flow in soils. *Water Resour. Res.* **18**, 1311-1325.

Booltink, H.W.G. and Bouma, J. (1993) Sensitivity analysis on processes affecting bypass flow. *Hydrological Processes* **7**, 33-43.

Bouché, M.B. (1977) Stratégies lombriciennes. In: U. Lohm and T. Persson (eds.) Soil ecosystems as components of ecosystems. *Biol. Bull. (Stockholm)* **25**, 122-132. (In French)

Bouma, J., Belmans, C.F.M. and Dekker, L.W. (1982) Water infiltration and redistribution in a silt loam subsoil with vertical worm channels. *Soil Sci. Soc. Am. J.* **46**, 917-921.

Buol, S.W., Hole, F.D. and McCracken, R.J. (1973) *Soil genesis and classification.* The Iowa State University Press, Ames, Iowa, USA. 360 pp.

Darwin, C. (1881) *The formation of the vegetable mould through the action of worms with observations on their habits.* Bookworm Publishing Co. (1976), Ontario, California, USA. 153 pp.

Dexter, A.R. (1978) Tunneling in soils by earthworms. *Soil Biol. Biochem.* **10**, 447-449.

Edwards, W.M., Shipitalo, M.J., Traina, S.J., Edwards, C.A. and Owens, L.B. (1992) Role of *Lumbricus terrestris* (L.) burrows on quality of infiltrating water. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24**, 1555-1561.

Ehlers, W. (1975) Observations on earthworm channels and infiltration on tilled and untilled loess soil. *Soil Science* **119**, 242-249.

Geyger, E.; (1979); Bodenstruktur und Regenwurm-Aktivität in einem Wiesenboden im Sölling; *Z. Pflanzenernähr. Bodenk.* **142**, 318 - 329. (In German)

Graff, O. and Makeschin, F. (1979) Der Einfluß der Fauna auf die Stoffverlagerung sowie die Homogenität und die Durchlässigkeit von Böden. *Z. Pflanzenernaehr. Bodenk.* **142**, 476-491. (In German)

Hoogerkamp, H., Rogaar, H. and Eijsackers, H.J.P. (1983) Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. In: Satchel, J.E. (ed.) *Earthworm ecology* Chapman and Hall, London, pp 85-105.

Jeanson, C. (1964) Micromorphologie et pédozoologie expérimentale. Contribution à l'étude sur plaques minces de grandes dimensions d'un sol artificiel structuré par les Lombricides. In: Jongerius, A. (ed.) *Soil Micromorphology.* Proc. 2nd Int. Working-meeting on Soil Micromorphology, Arnhem, The Netherlands, Sept. 22-25 1964. pp. 47-55. (In French)

Joschko, M., Söchtig, W. and Larink, O. (1992) Functional relationship between earthworm burrows and soil water movement in column experiments. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24**, 1545-1547.

Joschko, M., Graff, O., Müller, P.C., Kotzke, K., Lindner, P., Pretschner, D.P. and Larink, O. (1991) A non-destructive method for the morphological assessment of earthworm burrow systems in three dimensions by X-ray computed tomography. *Biol. Fert. Soils* **11**, 88-92.

Knight, D., Elliott, P.W., Anderson, J.M. and Scholefield, D. (1992) The role of earthworms in managed, permanent pastures in Devon, England. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24**, 1511-1517.

Kobel-Lamparski, A. and Lamparski, F. (1987) Burrow constructions during the development of *Lumbricus badensis* individuals. *Biol. Fert. Soils* **3**, 125-129.

Kretzschmar, A. (1982) Description des galeries de vers de terre et variation saisonnière des réseaux (observations en conditions naturelles). *Rev. Ecol. Biol. Sol* **19**, 579-591. (In French)

Kretzschmar, A. (1987) Caracterisation microscopique de l'activite de lombriciens endoges. In: Fedoroff, N., Bresson, L.M. and Courty, M.A. (Editors) *Micromorphologie des Sol - Soil Micromorphology*, Proc. VIIth Int. Working Meeting Soil Micromorph., Paris, July 1985, Association Française pour l'Étude du Sol, Plaisir, France. pp. 325-330. (In French)

Kretzschmar, A. (1991) Burrowing ability of the earthworm *Aporrectodea longa* limited by soil compaction and water potential. *Soil Biol. Biochem.* **11**, 48-51.

Lavelle, P., Pashani, B., Alegre, J. and Schaefer, R. (in press) Effects of inoculation of the earthworm *Pontoscolex corethrurus* in low input cropping systems of Peruvian Amazonian soil parameters and plant growth during six successive cropping seasons. *Soil Biol. Biochem.*

Lee, K.E. (1985) *Earthworms their ecology and relationships with soils and land use.* Academic Press Australia, Sydney. 411 pp.

Lee, K.E. (1992) Some trends and opportunities in earthworm research or: Darwin's children - the future of our discipline. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24**, 1765-1771.

Marinissen, J.C.Y. (1992) Population dynamics of earthworms in a silt loam soil under conventional and 'integrated' arable farming during two years with different weather patterns. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24**, 1647-1654.

Marinissen, J.C.Y. (in press) Earthworms and organic matter dynamics in macro-aggregates from differently managed arable fields. *Soil Biol. Biochem.*

McKenzie, B.M. and Dexter, A.R. (1988a) Axial pressures generated by the earthworm *Aporrectodea rosea*. *Biol. Fert. Soils* **5**, 323-327.

McKenzie, B.M. and Dexter, A.R. (1988b) Radial pressures generated by the earthworm *Aporrectodea rosea*. *Biol. Fert. Soils* **5**, 328-332.

McKenzie, B.M. and Dexter, A.R. (1993) Size and orientation of burrows made by the earthworms *Aporrectodea rosea* and *A. caliginosa*. *Geoderma* **56**, 233-241.

Monestiez, P., Kretzschmar, A. and Chadœuf, J. (1993) Modelling natural burrow systems in soil by fibre process: Monte-Carlo test on independence of fibre characteristics. *Acta Stereologia* **12(2)**, 237-242.

Nordström, S. (1975) Seasonal activity of lumbricids in southern Sweden. *Oikos* **26**, 307-315.

Nordström, S. and Rundgren, S. (1974) Environmental factors and lumbricid associations in southern Sweden. *Pedobiologia* **14**, 1-27.

Rushton, S.P. (1986) The effect of soil compaction on *Lumbricus terrestris* and its possible implications for populations on land reclaimed from open-cast coal mining. *Pedobiologia* **29**, 85-90.

Shaw, C. and Pawluk, S. (1986) The development of soil structure by *Octolasion tyrtaeum*, *Aporrectodea turgida* and *Lumbricus terrestris* in parent materials belong to different textural classes. *Pedobiologia* **29**, 327-339.

Smettem, K.R.J. (1992) The relation of earthworms to soil hydraulic properties. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24**, 1539-1543.

Stockdill, S.M.J. (1982) Effects of introduced earthworms on the productivity of New Zealand pastures. *Pedobiologia* **24**, 29-35.

Tomlin, A.D., McCabe, D. and Protz, R. (1992) Species composition and seasonal variation of earthworms and their effect on soil properties in Southern Ontario, Canada. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24**, 1451-1457.

Urbánek, J. and Doležal, F. (1992) Review of some case studies on the abundance and on the hydraulic efficiency of earthworm channels in Czechoslovak soils with reference to the subsurface pipe drainage. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24**, 1563-1571.

White, G. (1789) The natural history and antiquity of Selborne. *Letter XXXV*, 216-217, London.

# CHAPTER 2

# A method for the three-dimensional mapping of earthworm burrow systems

Ligthart, T.N., Peek, G.J.W.C. and Taber, E.J. (1993) A method for the three-dimensional mapping of earthworm burrow systems. *Geoderma* 57, 129-141.

## Abstract

To study the spatial structure of earthworm burrow systems a field method was developed to map these systems three-dimensionally. The method is based on serial sectioning of the soil. An important feature of the method is the use of the orientation of the burrows in order to reduce the number of layers needed for a reliable reconstruction of the burrow system. The burrow system is reconstructed from the measured data by using search windows of which the position and size depend on the orientation of each single burrow. An example of the three-dimensional structure of an earthworm burrow system made by *Aporrectodea longa* and *A. caliginosa* is given.

## Introduction 2.1

The influence of earthworm burrow systems on the soil air and soil water dynamics has been the topic of numerous studies e.g. Bouma et al. (1982), Hoogerkamp et al. (1983), Zachmann et al. (1987) and Edwards et al. (1990). In most of these studies the earthworm burrow system is described only in terms of burrow numbers per unit area, sometimes measured at several depths. The rough effects the earthworm burrow system has on the soil air and soil water dynamics as through the magnification of the saturated hydraulic conductivity or a higher air permeability compared with absence of the burrow system, can be established this way. A more detailed analysis of the influence of the burrow system on the soil water and air economies requires that its three-dimensional structure, and so its topology is known.

To achieve this it is necessary to map the burrow systems three-dimensionally. In this paper a field method for this mapping is presented. The method will be used in a future study on the influence of earthworm burrow systems on the soil water economy.

## Techniques 2.2

The three-dimensional imaging techniques that could be used for the three-dimensional mapping of earthworm burrow systems can be subdivided into two main groups: destructive and non-destructive techniques. Use of a non-destructive technique in the most strict sense leaves the burrow system in place and undisturbed and should not alter the behaviour of the earthworm population.

The most promising non-destructive three-dimensional imaging techniques are, at this moment, computer-assisted tomography also called X-ray computed tomography and magnetic resonance imaging. The latter which is also known as MRI or NMR provides information about the nuclei of atoms (Pykett, 1982). A three-dimensional data set is created containing this information. The application of this technique in soil science is still in an experimental phase. Also the high costs prevented it from being used by us to study the structure of earthworm burrow systems.

The other technique mentioned, computer-assisted tomography, is based on the scanning of a body with X-rays in several 'slices'. A three-dimensional data set of the X-ray attenuation coefficients is created, consisting of elements with a volume of for instance 2 cubic millimetres. Air filled pores have an attenuation which is considerably smaller than that of the surrounding matrix and so these pores can be extracted from the data set. Computer-assisted tomography has been used to study soil density (Jenssen and Heyerdahl, 1988), soil macropores of different origin (Warner and Nieber, 1988) and earthworm burrow systems (Joschko et al., 1991). Computer-assisted tomography has at the moment one main disadvantage, which is the very high expenses needed to obtain the data. Due to these costs it was not used by us to study the three dimensional structure of earthworm burrow systems.

The destructive techniques that can be used to determine the three-dimensional structure form two groups, excavation or sectioning techniques and casting techniques.

Casting techniques are based on filling earthworm or other burrows with a liquid that hardens after some time. The viscosity of the liquid determines the smallest pore size into which it can enter. Plaster of Paris (Bouma et al., 1982, Joschko, 1989), latex (Garner, 1953), polyester resin (Rogaar, 1974) and polyurethane foam (Kobel-Lamparski and Lamparski, 1987) have been used for this purpose. After the hardening of the liquid the soil around the cast is removed. Orientation, position and for instance diameter or volume can be measured directly at the casts or from depictions of them.

One important method which uses sections through a structure to gain three-dimensional information from this structure is stereology. Stereology is defined by Weibel (1979, p1) as 'a body of mathematical methods relating three-dimensional parameters defining the structure to two-dimensional measurements obtainable on sections of the structure'. Stereology has been applied to tubular structures (Baddeley and Averback, 1983; Cruz-Orive et al., 1985) resulting in estimations of the volume, surface and length densities of the structures. By using directional statistics Cruz-Orive et al. (1985) also gained information about the distribution of directions of an anisotropic tubular structure. Information about the degree of connectivity or continuity of the structure cannot be obtained by these stereological methods making a truthful reconstruction of the structure impossible. Other sectioning or excavation techniques can be used to assess this reconstruction needed to model for instance the influence of a burrow system on the flow of water inside the soil.

These techniques can be burrow-oriented or layer-oriented. In the burrow-oriented approach each single burrow is exposed bit by bit and at several points its coordinates are measured. The layer-oriented approach uses excavation in several parallel layers, of the exposed burrows the coordinates are measured. The direction of excavation can be horizontal (Kretzschmar, 1978) or vertical (Ehlers, 1973, Edwards et al., 1988). The mapping of the burrow system can be direct by recording the coordinates in situ or indirect by photographing or making drawings at first and measure the coordinates from these representations. Kretzschmar (1988) made a three-dimensional reconstruction of the earthworm burrow system by using a column of soil of 10 x 10 x 200 cm and destroying it little by little to expose and measure the coordinates of each burrow. Edwards et al. (1988) photographed horizontal surfaces with exposed earthworm burrows at four different depths and used image analysis techniques to recognize, count and describe the burrows. Ehlers (1973) used more closely spaced (between 2 and 20 cm) horizontal surfaces and counted the burrows which were divided into three diameter classes.

The reconstruction of the burrow system from layer by layer excavation is based on serial or sequentional sectioning, a technique mainly used for studying microstructures (DeHoff et al., 1972, Yanuka et al., 1984). Serial sectioning requires a series of closely spaced parallel sections through a structure, in order to reconstruct it three-dimensionally. The spacing between two successive layers depends on the scale of the structure to be studied (DeHoff et al., 1972). This scale may be described by the mean intercept of the phase of interest, lambda, in the case of an earthworm burrow system lambda can be translated into the mean width of intercepted burrows on a layer. DeHoff et al. (1972) recommend a spacing of 1/3 to 1/10 of lambda.

A preliminary test using several excavating and casting techniques in the field showed that these latter techniques (polyester resin and gypsum) do not give a reliable reproduction of the burrow system. The build-up of pressure inside a burrow by the invading liquid may cause a partial filling of the burrow. Using liquids with lower viscosity results in the enclosure of soil particles or aggregates thus obscuring burrows. Another disadvantage of casting is that it only reveals the burrows that are open to the surface, obstructed burrows or burrows with no contact with the surface cannot be found with this technique.

Excavating techniques combined with photography of the burrows showed that the burrows have to be marked before photographing them in order to recognize them properly on the images. Stereo photography does not request the measurement

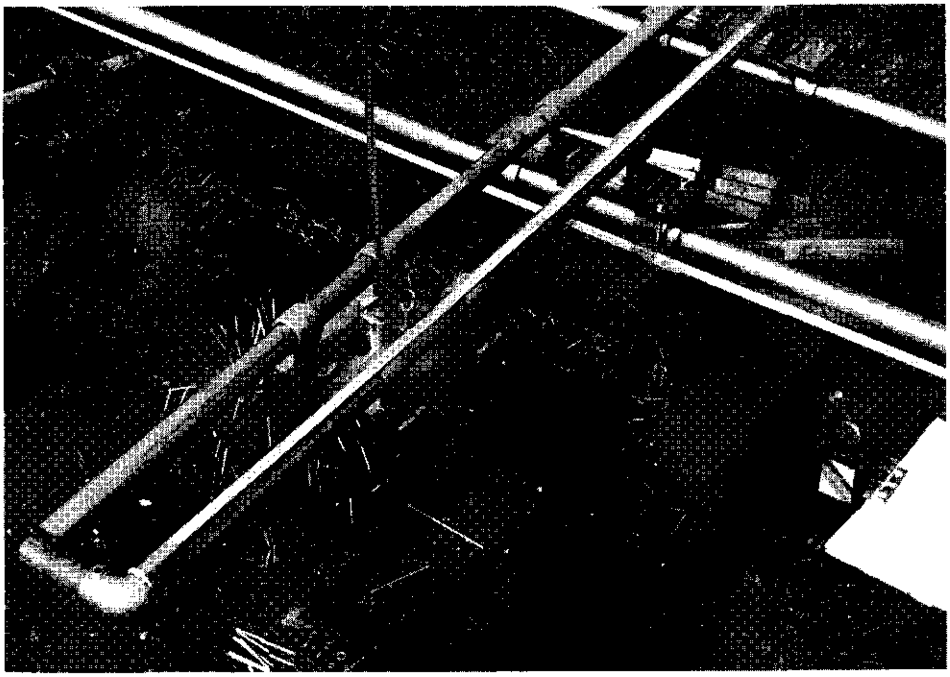


*Figure 2.1 Measuring apparatus with: in background support for x-position runner, from back to front x-position runner with mounted y- and z-position runners. The position is read from the attached measuring tapes.*

of the depth position(s) of the layers but this technique appeared to be too expensive. Among the excavating techniques we found the layer by layer approach combined with direct mapping to be the most practical one. Especially when working with large volumes and when collapsing of the soil column is probable. The method and procedure together with some of the first results are presented in the following.

## 2.3 Method

### 2.3.1 Introduction

Our method to map earthworm burrow systems three-dimensionally is based on serial sectioning. The recommendations of DeHoff et al. (1972) refer to isotropic networks, for oriented systems however a wider spacing can be used when the sections or layers are perpendicular to the orientation of the system. The reason for this is that horizontal sections have a much greater change of hitting a vertical element than vertical sections (Ringrose-Voase and Nortcliff, 1987). Translating DeHoff's rule of thumb on the spacing of sections (1/3 - 1/10 of lambda) to an earthworm burrow system with 3.5 mm as mean intercept results in a spacing of 1.2 to 0.35 mm. This would result in an impracticable number of layers for a 1 m high soil column. However, because of the vertical orientation of the earthworm burrow systems at the study site, a wider spacing could be used. Further increase of the spacing is obtained by using the orientation of each burrow in the reconstruction process thus greatly reducing the area in which to search for a matching burrow (see reconstruction procedure, 2.3.4). Wendt and Larink (1990) used a spacing of 1 cm to reconstruct earthworm burrows which had been formed in artificial soil cores. A spacing of the same magnitude has been used for our measurements.

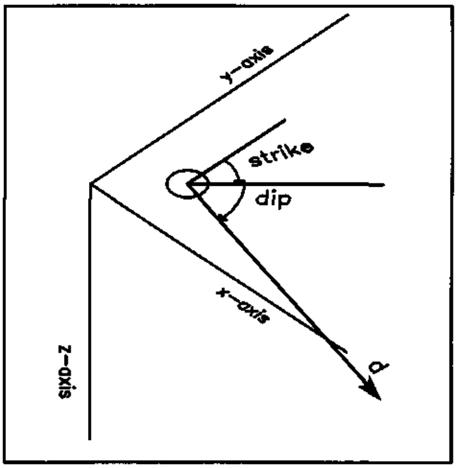


***Figure 2.2** Dip and strike for a burrow with direction d. The burrow is depicted as a horizontal circle.*

### Field site 2.3.2

In 1957 the polder Eastern Flevoland was reclaimed from the IJssel Lake, in the new soil no earthworms were present. In this polder earthworms were inoculated in 1983 at the Ir. A.P. Minderhoudhoeve, an experimental farm of the Wageningen Agricultural University, to study the effect of earthworm activity on the production rate of pastures. The earthworms were inoculated in two rows, separated 12 m apart, at one side of the plot. Individuals of the following species were placed under the turf: *Aporrectodea longa*, *A. caliginosa*, *Lumbricus terrestris* and *L. rubellus*.

Mapping of the burrow systems took place in August and September 1991 in this inoculated permanent pasture used for grazing and mowing situated at the ir. A.P. Minderhoudhoeve. The soil is a Calcaric Fluvisol with a loam texture. In the summer of 1991 the earthworms had spread *c.* 42.5 m into the plot. The burrow systems were mapped in four pits located between the point of inoculation and the point that had just been reached by the earthworms.

### Field procedure 2.3.3

At one side of a large pit of *c.* 2 x 2 x 1 m a square soil column of *c.* 0.7 x 0.7 m was maintained. Previously to the digging the surface of the column had been irri-

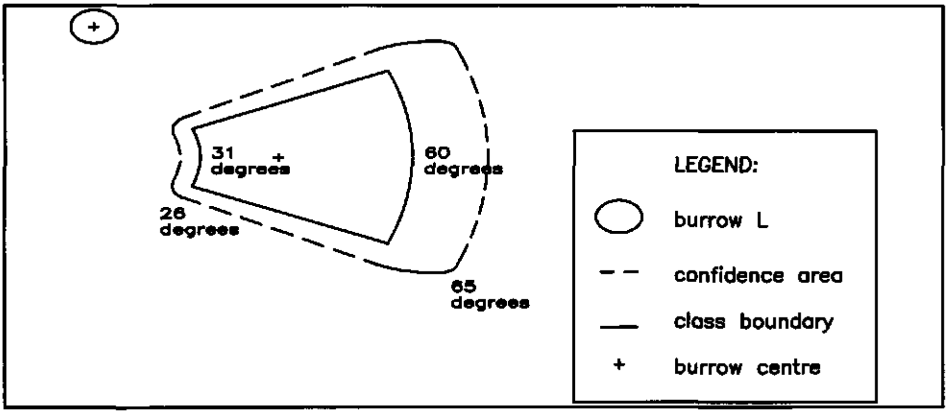


*Figure 2.3 The confidence area is based on the boundaries of the strike and dip class of a burrow. The direction of view makes an angle of 45° with the horizontal plane.*

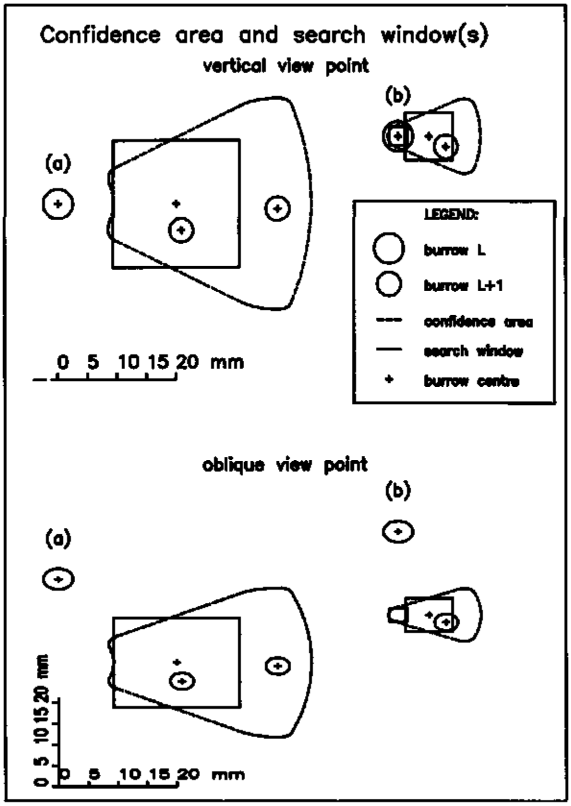


*Figure 2.4. (Top) Search window(s) and confidence area for a burrow with (a) a dip of 31-60° and b) a dip of 61-90°. The direction of view is perpendicular to the horizontal plane. (Bottom) Search window(s) and confidence area for a burrow with (a) a dip of 31-60 ° and (b) a dip of 61-90°. The direction of view makes an angle of 45° with the horizontal plane.*

gated with a methylene blue solution to stain burrows open to the surface. The column was excavated in successive horizontal layers ranging in thickness from 1 to 3 cm. After excavating of a surface with a sharpened stopping-knife the surface was brushed clean. Occasionally the soil was slightly smeared, causing the closure of burrows, or soil material was pushed into the burrows. By careful examination of the surface such burrows were spotted and re-opened. Burrows that were naturally filled e.g. by earthworm casts were not opened. On each exposed surface (measuring area 0.5 x 0.5 m) the coordinates of the open burrows equal to or greater than 2 mm were measured directly by a manually operated measuring apparatus (Fig. 2.1). Besides the coordinates the diameter, the presence of methylene blue, and the orientation were recorded. The coordinate and diameter were measured to the nearest mm. The orientation was de- scribed in terms of dip and strike (see Fig. 2.2), the dip being the angle with the horizontal plane was, following Kretzschmar (1982), divided into three classes: 0-30, 31-60 and 61-90°. The strike, the angle with the y-axis was recorded in 8 classes of 45° (N, NE, etc) a ninth class was added which represents burrows with a pure vertical orientation, thus having no strike. Dip and strike were estimated visually, in doubtful cases a compass or clinometer was used. Of horizontal burrow parts the end points and intermediate points where the burrow changed its direction were used. Particularities as e.g. branching of burrows, partial infilling, presence of earthworm were noted and were used in the manual reconstruction process.

### Reconstruction procedure 2.3.4

The reconstruction is based on the projection of the boundaries of the dip and strike classes of a burrow on layer L onto the layer L+1, starting with the top layer (Fig. 2.3). The area on layer L+1 in which to find a matching burrow for a certain burrow at layer L is called the confidence area. The size and shape of this area depend on the orientation of the burrow at layer L and of $\Delta z_L$, which is the distance between layers L and L+1. Estimation errors in the dip and strike occurring during the measurement or estimation are assumed to be ± 5° and are accounted for in the confidence area. The confidence area (Fig. 2.3) is created by adding to the sector that is formed by projecting the boundaries of the strike and dip classes on layer L+1 the projection of a cone with a width 10°. This cone reflects the estimation errors of ± 5°. For a burrow having a north eastern strike, that is between 22.5 and 67.5°, the confidence area lies between 17.5 and 72.5°. The boundaries of the dip class for a burrow with a dip of 31-60° become, by adding the uncertainty of ±5, 26 and 65°. Burrows that lie inside the confidence area and have, within a range of minus or

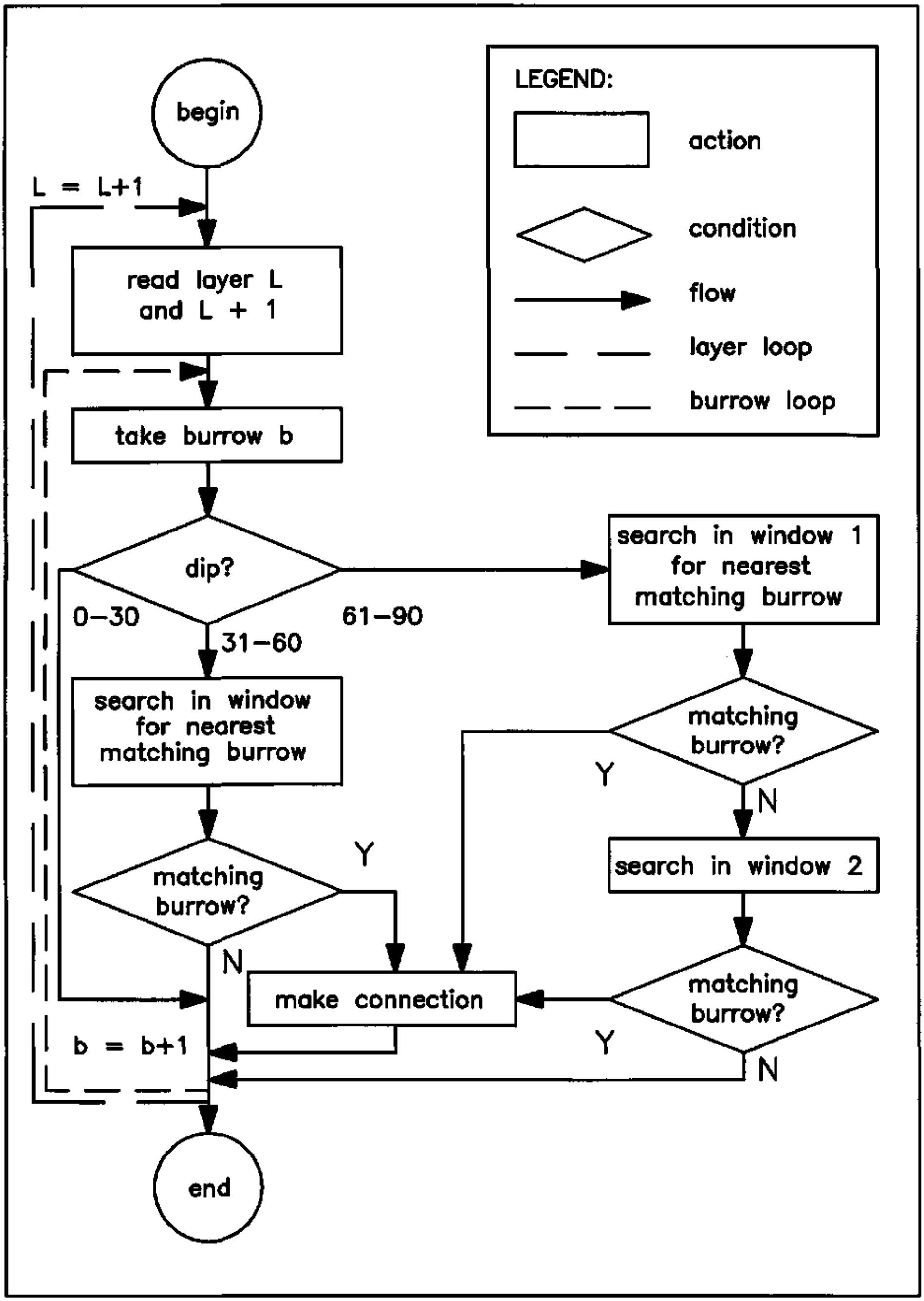


*Figure 2.5 Flow diagram of the search algorithm.*

plus 2 mm, the same diameter are called matching burrows (Fig. 2.4).

The search algorithm (Fig. 2.5) was implemented in the dBASE[1] command language. For reasons of programming efficiency the confidence areas are translated into square search windows. The size, shape, and the position of the midpoints $(x,y,z)'$ of these windows (Fig. 2.4) are calculated from the orientation of the burrow at layer L and from $\Delta z_L$ (see below). The midpoints of the search windows lay on the bisecting lines of each dip and strike class reflecting an estimation of the mean orientation per class.

In the case of the dip being close to 90° too few connections can be made with the window based on the bisecting lines (window 2), therefore a smaller window (window 1) is added in the search procedure. This window is based on the projected area of a cone with a width of 10°, reflecting the confidence area at a dip of 90°. The first search is made inside this small square window (window 1). If no connections can be made window 2 is used for searching.

The search window used for dips of 31 to 60° has an area which is 50% of that of the confidence area. In case of the dip being greater than 60° the area of the combined windows 1 and 2 is about 60% of that of the confidence area. Less than 10 % of the area of the squares is located outside the confidence area.

Dip = 61-90°:

search window 1:

$$\text{width} = 0.154 * \Delta z_L, \tag{2.1}$$

$$x' = x, \tag{2.2}$$

$$y' = y, \tag{2.3}$$

$$z' = z + \Delta z_L \tag{2.4}$$

search window 2:

$$\text{width} = 0.4 * \Delta z_L, \tag{2.5}$$

$$x' = x + (\tan(15) * \cos(\text{strike}) * \Delta z_L), \tag{2.6}$$

$$y' = y + (\tan(15) * \sin(\text{strike}) * \Delta z_L), \tag{2.7}$$

$$z' = z + \Delta z_L \tag{2.8}$$

Dip = 31-60°:

$$\text{width} = 1.07 * \Delta z_L, \tag{2.9}$$

$$x' = x + (\tan(45) * \cos(\text{strike}) * \Delta z_L), \tag{2.10}$$

$$y' = y + (\tan(45) * \sin(\text{strike}) * \Delta z_L), \tag{2.11}$$

$$z' = z + \Delta z_L \tag{2.12}$$

The dBASE programme only uses burrows with a dip greater than 30°. Automatic connections of horizontally oriented burrows are prone to errors in these connections because the search window can become very large.

After running of the dBASE programme the output file with data of the burrows and the connections between them was read into AutoCAD[2], a CAD package. The

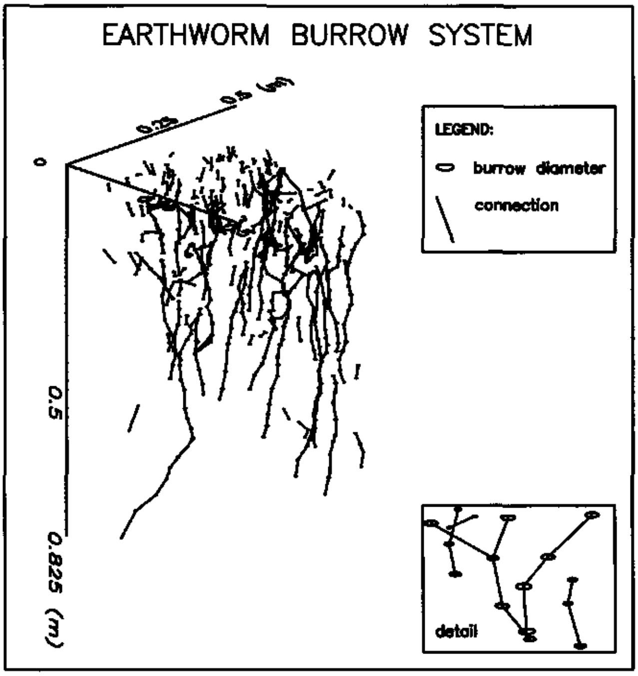


*Figure 2.6 Three-dimensional representation of earthworm burrow system. Only connected burrows are shown.*

burrows were displayed on screen as circles with diameters as measured. The connections between burrows are displayed as lines running between the centres of the burrows (Fig. 2.6). All the unconnected burrows were checked manually for the possibility to connect them with a burrow lying outside the window but inside the confidence area on layer L+1. If this proved to be possible a connection was made manually in AutoCAD. If not the search procedure was repeated manually using the layer L+2. The reason for using this layer is that in the field sometimes open burrows, stained by methylene blue, were missed and re-appeared at the next layer.

The automatic procedure only creates non-branching burrows. Branching burrows were created manually when these had been observed in the field.

## 2.4 Results

The first results of the method presented here are given as an example and do not represent a full analysis of the three-dimensional structure and topology of earthworm burrow systems. The results are based on the burrow system at 40 m from the inoculation site having an age of *c.* one year. This burrow system is created by

*Aporrectodea longa* and *A. caliginosa* with respectively abundances of 141.1 and 16.7 g/m2. To map the burrow system 41 layers were used, the mean distance between them was for the first ten layers 1.2 cm and for the total set 2.0 cm. The system is characterized by mainly vertically oriented burrows (Fig. 2.6). Only a small number of burrows have first order branches which are horizontal or directed upwards.

Of the burrows 60% could be connected with those on the layer below which means that they were at least continuous over the distance. Many of the deeper burrows are stained by methylene blue and are thus connected with the surface. However, it was not possible to connect all of them directly to the surface (see discussion).

## Discussion 2.5

A mean distance of 2 cm between horizontal layers used for serial sectioning appears to be applicable for describing vertically orientated earthworm burrow systems when used in combination with the measured orientation. This spacing far exceeds the one following from the rule of thumb on serial sectioning for isotropic systems (DeHoff et al., 1972), which for the here used earthworm burrow system calls for a spacing of 0.35 to 1.2 mm.

Due to the crumbly structure and the abundance of grass roots the preparation of the top layers is more difficult than for the deeper layers resulting in missed burrows. Probably these missed burrows are the cause of the inability to connect many of the more continuous burrows directly to the surface layers. Until now no reliable estimation can be made of the percentage of missed burrows in the top layers.

The results show that the developed apparatus and the described mapping method are suitable for assessment of the three-dimensional structure and topology of earthworm burrow systems in the field. A disadvantage is however that the method requires a fair amount of labour.

The use of the method could be extended to the study of other three-dimensional soil macrostructures as for instance cracks.

## References

Baddeley, A. and Averback, P. (1983) Stereology of tubular structures. *J. Microsc.* **131** (3) 323-340.

Bouma, J., Belmans, C.F.M. and Dekker, L.W. (1982) Water infiltration and redistribution in a Silt Loam subsoil with vertical worm channels. *Soil Sci. Soc. Am. J.* **46**, 917-921.

Cruz-Orive, L.M., Hoppeler, H., Mathieu, O. and Weibel, E.R. (1985) Stereological analysis of anisotropic structures using directional statistics. Applied Statistics **34** (1), 14-32.

DeHoff, R.T., Aigeltinger, E.H. and Craig, K.R. (1972) Experimental determination of the topological properties of three-dimensional microstructures. *J. Microscopy* **95**, 69-91.

Edwards, W.M., Norton, L.D. and Redmond, C.E. (1988) Characterizing macropores that affect infiltration into nontilled soil. *Soil Sci. Soc. Am. J.* **52**, 483-487.

Edwards, W.M., Shipitalo, M.J., Owens, L.B. and Norton, L.D. (1990) Effect of Lumbricus terrestris L. on hydrology of continuous no-till cornfields. *Geoderma* **46**, 73-84.

Ehlers, W. (1973) Observations on earthworm channels and infiltration on tilled and untilled loess soil. *Soil Science* **119**, 242-249.

Garner, M.G. (1953) The preparation of latex casts of soil cavities for the study of tunnelling activities of animals. *Science* **118**, 380-381.

Hoogerkamp, H., Rogaar, H. and Eijsackers, H.J.P. (1983) Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. In: Satchel, J.E. (Editor), *Earthworm ecology.*, pp 85-105, Chapman and Hall, London, 495 pp.

Jenssen, P.D. and Heyerdahl, P.H. (1988) Soil column descriptions from X-ray computed tomography density images. *Soil Science* **146** (2), 102-107.

Joschko, M. (1989) *Einfluss von Regenwürmern (Lumbricidae) auf verdichteten Boden - Modellversuche-.* Dissertation Technische Universität Carolo-Wilhelmina, Braunschweig.

Kobel-Lamparski, A. and Lamparski, F. (1987) Burrow constructions during the development of *Lumbricus badensis* individuals. *Biol. Fert. Soils* **3**, 125-129.

Kretzschmar, A. (1978) Quantification ecologique des galeries de lombriciens. Techniques et premieres estimations. *Pedobiologia* **18**, 31-38. (In French with English summary).

Kretzschmar, A. (1982) Description des galeries de vers de terre et variation saisonnière des réseaux (observations en conditions naturelles). *Rev. Écol. Biol. Sol* **19** (4), 579-591. (In French with English summary).

Kretzschmar, A. (1988) Structural parameters and functional patterns of simulated earthworm burrow systems. *Biol. Fert. Soils* 6, 252-261.

Pykett, I.L. (1982) NMR imaging in medicine. *Scient. Amer.* **246** (5), 54-64.

Ringrose-Voase, A.J. and Nortcliff, S. (1987) The application of stereology to the estimation of soil structural properties: a preview. In : Federoff, N. et al. (eds), *Soil Micromorphology*, Proc. Int. Workshop Meeting, 7th, Paris, july 1985, 81-88, L'association pour l'etude du Sol, Plaisir, France.

Rogaar, H. (1974) Polyester casts for the study of the pore structure in soils. *Neth J. agric. Sci.* **22**, 143-152.

Warner, G.S. and Nieber, J.L. (1988) *CT scanning of macropores in soil columns.* Paper Am. Soc. Agric. Eng., paper no. 88-2632, 13 pp.

Weibel, E.R. (1979) *Stereological Methods*. Vol. I, Practical methods for biological morphometry. Academic Press Inc. Ltd., London, Great Britain, 415 pp.

Wendt, K. and Larink, O. (1990) Computer-aided analysis of earthworm burrows from sectioned soil columns. *Pedobiologia* **34** (4), 221-225.

Yanuka, M., Dullien, F.A.L. and Elrick, D.E. (1984) Serial sectioning and digitization of porous media for two- and three-dimensional analysis and reconstruction. *J. Microscopy* **135** (2), 159-168

Zachmann, J.E., Linden D.R. and Clapp, C.E. (1987) Macroporous infiltration as affected by earthworms, tillage, and residue. *Soil Sci. Soc. Am. J.* **51**, 1580-1586.

1. dBase is a trademark of Ashton-Tate Inc.
2. AutoCAD is a trademark of Autodesk Inc.

# CHAPTER 3

# Evolution of earthworm burrow systems after inoculation of lumbricid earthworms in a pasture in The Netherlands

Ligthart, T.N. and Peek, G.J.C.W. (in press) Evolution of earthworm burrow systems after inoculation of lumbricid earthworms in a pasture in the Netherlands. *Soil Biol. Biochem.*

## Abstract

In 1983 an earthworm-free pasture was inoculated with four earthworm species. The earthworms dispersed with an average velocity of 6.8 m.y$^{-1}$. In 1991 four burrow systems, ranging in age from 0.6 to 7.3 y, were mapped three-dimensionally to establish the development of these systems.

*Aporrectodea longa* was the fastest colonizer, *Lumbricus terrestris* dispersed slowly. The abundance of earthworms peaked at 4.1 years after which it dropped to a lower level. The density of the burrow systems followed a similar pattern. The net burrow creation rate reached a maximum of 110 m.m$^{-2}$.y$^{-1}$ between 0.6 and 0.9 years. The burrow systems had a highly vertical orientation which increased with age. The density of branched burrows relative to the total system has its maximum in the youngest system and declines with age. The burrow systems continued to deepen after the maximum density had been reached.

## Introduction

Most earthworm species create tubular soil pores (burrows) by ingesting and pushing aside soil material (Lee, 1985). Burrows are formed for three main reasons. More or less permanent burrows are formed as shelter for unfavourable environmental conditions (Edwards and Lofty, 1977; Lee, 1985) by anecique species such as *Lumbricus terrestris* and *L. badensis,* which feed mostly on organic material on the soil surface. More ephemeral burrows are created by consumption of soil material by geophagous species. Finally, burrows are created by earthworms in search of sites with better food supply, or more favourable moisture content and temperature. However, burrows created for feeding may also be used to move to a more favourable site.

The burrow systems of earthworms have been mainly described in terms of number of burrows per unit area ranging from several tens to hundreds per m$^2$ (Ehlers, 1975; Edwards et al., 1988). Casting techniques (Garner, 1953; Kobel-Lamparski and Lamparski, 1987; Joschko et al., 1989) and excavation techniques (Kretzschmar, 1982, 1988; McKenzie and Dexter, 1993) have been used to study burrow systems in detail. Kretzschmar (1982) studied the seasonal variations in burrow systems mainly created by anecique earthworms.

The evolution of earthworm burrow systems after colonization of a site has been studied only in terms of burrow density at a certain depth (Hoogerkamp et al., 1983). In our research this evolution is studied in more detail by using a chronosequence of earthworm burrow systems, formed by inoculated earthworms dispersing into an initially earthworm-free pasture.

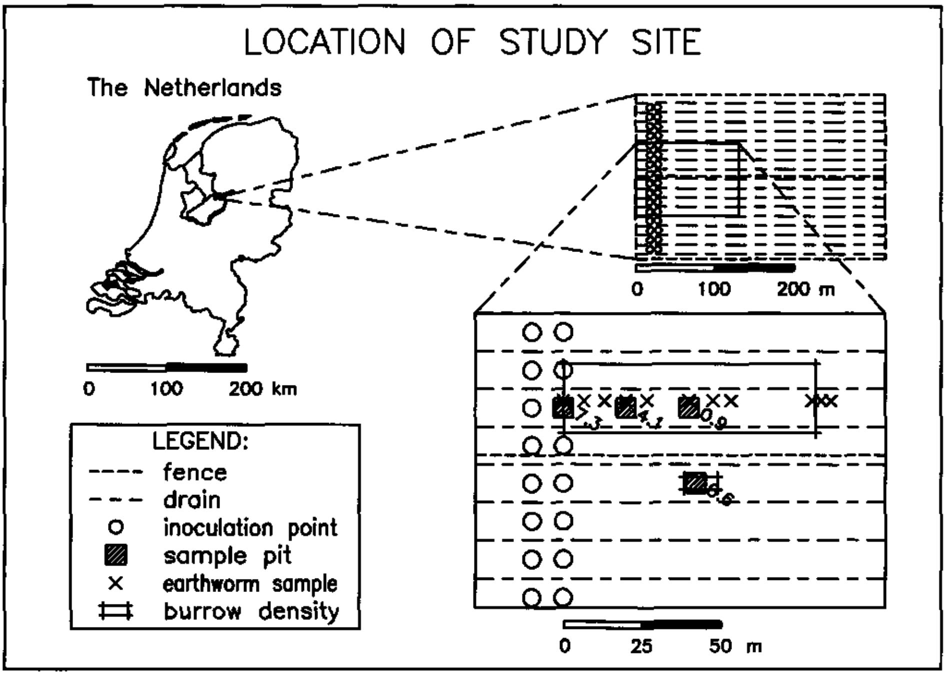


*Figure 3.1* *Location and layout of study site with inoculation points and sample points of burrow systems, earthworms and burrow density. Figure at sample pit gives age of burrow system.*

## 3.2 Method and materials

### 3.2.1 Field site

The study site is a nonirrigated pasture at the ir. A.P. Minderhoudhoeve farm (Wageningen Agricultural University) in the polder Oostelijk Flevoland, The Netherlands (Fig. 3.1). In this polder earthworms were absent at the time of reclamation. The climate is humid temperate with a warm summer (Cfb, Köppen). The soil is a Calcaric Fluvisol (FAO, 1990) with a silt loam texture in the upper 70 cm and sandy loam below 70 cm.

Grass was sown in the autumn of 1981, after the parcel had been used as arable land. In October and November 1983 earthworms were inoculated in this earthworm-free pasture from thirty-two inoculation points on ridges (12 m wide, 12 cm high) between the drains at the south-west side of the parcel (Fig. 3.1) (Ma, 1991, pers. comm.). At each point 250 individuals per species were placed under the sod: *Aporrectodea caliginosa* (60% adult, 40% sub adult), *Aporrectodea longa* (12% adult, 88% sub adult), *Lumbricus rubellus* (84% adult, 16% sub adult), *Lumbricus terrestris* (72% adult, 28% sub adult).

From the relation between the colonized area and time after inoculation found by

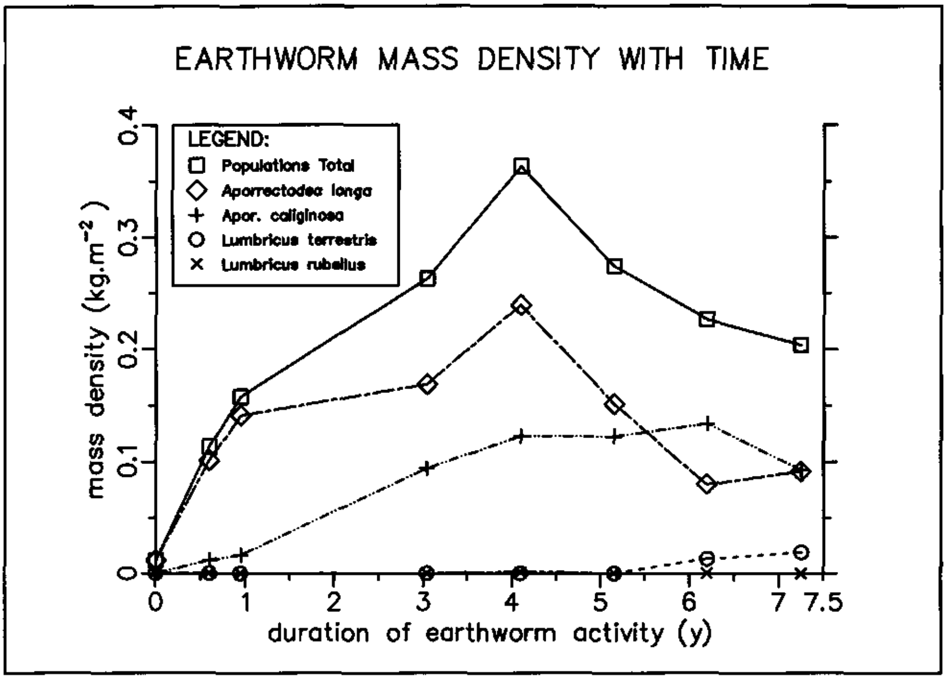


*Figure 3.2 Mass density (fresh weight, kg.m$^{-2}$) of earthworm populations based on sample line, August - September 1991. Duration of earthworm activity was estimated assuming a constant dispersion rate (see 3.3.1).*

Hoogerkamp et al. (1983) at a comparable site and with the same species, we estimated a lag phase (Stockdill, 1982) of 0.5 year after which colonization by the earthworms started.

Outside the colonized area a 3 cm thick root mat (O horizon) occurred at the soil surface. In 1991 this root mat had been completely consumed by the earthworms over a distance of nearly 20 m from the inoculation points.

### Quantification of earthworm populations 3.2.2

In August-September, 1991 earthworms were collected by handsorting at eleven points (Fig. 3.1, 3.2) on the ridge where the burrow systems were mapped. The sampled volume at each point was 0.3 x 0.3 x 0.3 m = 0.027 m$^3$. A large part (80%) of the community was in quiescence during sampling. Adding a formalin solution at the bottom of the sample pit yielded in general no additional earthworms. Individuals of deep burrowing species present below 0.3 m depth will thus not have been collected, leading to an underestimation of these species.

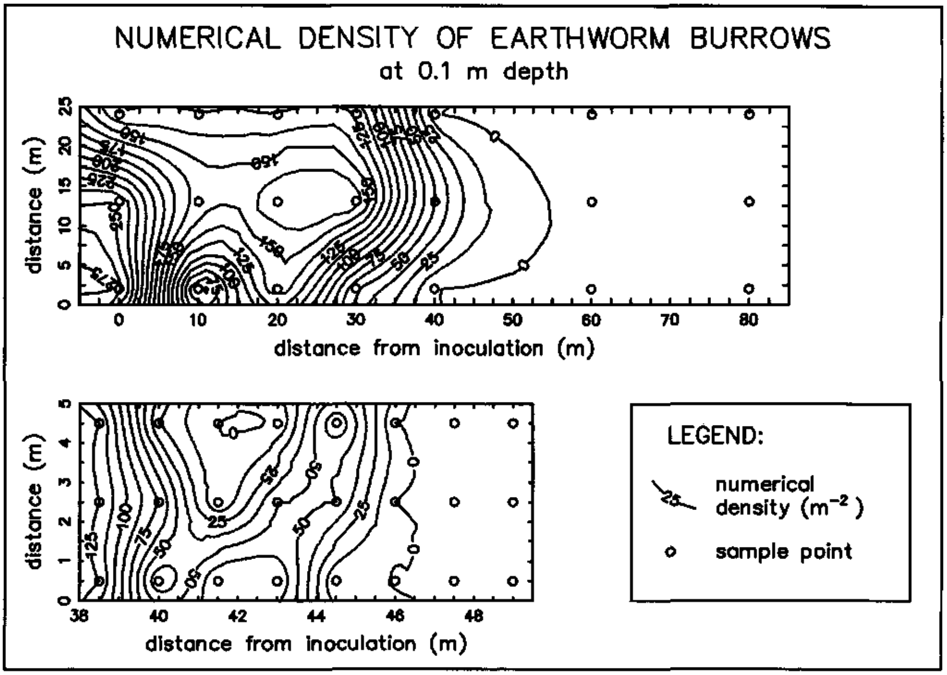


***Figure 3.3** Numerical density ($m^{-2}$) of earthworm burrows ≥2 mm. Top map: situation of June 1991. Bottom map: situation in the front zone, August 1991. Isolines, Equidistance 12.5 $m^{-2}$. For locations see Fig. 3.1.*

### 3.2.3 Mapping and reconstruction of burrow systems

The burrow systems were mapped in the period of August-September, 1991, 7.75 years after inoculation. The areal distribution of burrows was determined by counting open burrows on areas of 0.04 $m^2$ at 10 cm depth. The results are shown in contour plots (Fig. 3.3) obtained by kriging (Davis, 1986). Inside the dispersion area four mapping pits were chosen (Fig. 3.1). Because a large part of the earthworm community was during mapping in quiescence, the systems may all be considered 'frozen' in the same state. The pits were mapped in a random order to reduce time-related artifacts.

The burrow systems were mapped by recording the position, orientation and diameter of the open burrows with a diameter ≥ 2 mm on successively deeper horizontal layers spaced 1.5 to 2 cm apart (Table 3.1). The mean spacing was calculated by weighing the distances between layers by the number of open burrows on each layer. The earthworm burrow systems were reconstructed from these data as described by Ligthart et al. (1993). Empty root channels were distinguished from earthworm burrows by remnants of the root cortex. Crane-fly (Tipulidae) larvae

*Table 3.1 Parameters of the mapped burrow systems in relation with their age.*

| | age of burrow system (y) | | | |
|---|---|---|---|---|
| | 0.6 | 0.9 | 4.1 | 7.3 |
| distance from inoculation (m) | 42.2 | 40.0 | 20.0 | 0.0 |
| total burrow points | 177 | 900 | 2154 | 1659 |
| connected burrow points | 120 | 575 | 1552 | 975 |
| ratio connected/total[1] | 0.68 | 0.64 | 0.72 | 0.59 |
| correlation (r) ratio[1] with depth[2] | 0.942* | 0.512* | 0.652** | 0.757** |
| mean layer distance (m) | 0.015 | 0.016 | 0.017 | 0.021 |
| mean burrow diameter[3] (mm) | 4.6 ± 1.6 | 4.3 ± 1.4 | 3.4 ± 1.2 | 3.3 ± 1.5 |
| maximum depth[3] (m) | 0.546 | 0.825 | 0.726 | 0.907 |

[1]Ratio between connected points and total points. [2]The 2-tailed significance is given by: ** 0.001, * 0.01. [3]Based on individual burrows.

burrows were also excluded from the reconstruction.

To assure a representative sampling of the burrow system (Kretzschmar, 1987; Bouma, 1990) a 0.5 by 0.5 m area was sampled to a depth below which no more burrows were found. High labour intensity precluded replicated excavations. However, replicated (n=3) measurements of numerical burrow density on a 0.3 by 0.3 m horizontal section at depths of 5, 10 and 15 cm within the chronosequence showed that variability was rather low (standard deviation 19% of the mean), except in the front zone (Fig. 3.3) where the standard deviation was 94% of the mean (see Ch. 4).

The following definitions concerning the burrow system are used in this text:

**Burrow point**: point at which an open earthworm burrow was dissected by a mapping layer or a point at which an intersected (near) horizontal open burrow changed direction.

**Burrow segment**: section of an earthworm burrow which connects two burrow points. These burrow points are called connected burrow points.

**Burrow**: tubular void in the soil matrix which consists of one or more burrow segments.

The approximate ages of the burrow systems (Table 3.1) have been calculated assuming a constant colonization rate of 6.3 m.y$^{-1}$.

### Structure parameters of burrow system 3.2.4

The development of earthworm burrow systems was described using parameters related to the structure of these systems. The declination, the angle with the horizontal plane, of a burrow is calculated by using it's first and last position.

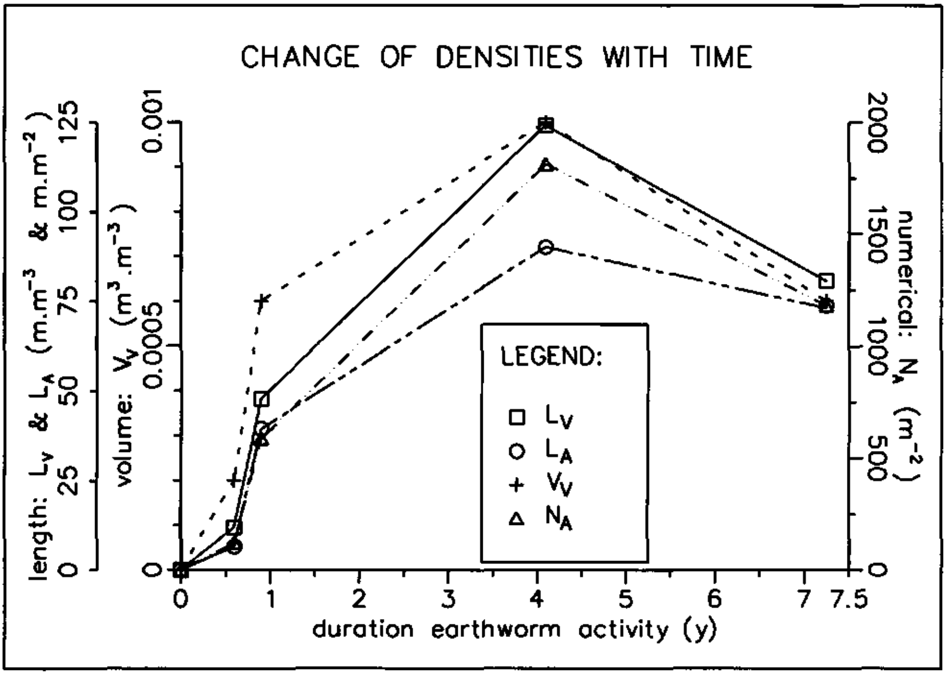


*Figure 3.4 Development of earthworm burrow system densities with increasing duration of earthworm activity.*

The following parameters were distinguished (cf Weibel (1979)):

-maximum depth of system, $z_{max}$ (m)

-volume of the system V,

$$V = z_{max} * A \quad (m^3) \qquad (3.1)$$

-mean burrow length (m),

-numerical density of burrows $N_A$,

$$N_A = \sum_{b=1}^{b} \frac{1}{A} \quad (m^{-2}) \qquad (3.2)$$

-depth of maximum numerical density (m),

-ratio connected/total number of burrow points,

-length density of burrows $L_A$ and $L_V$,

$$L_A = \sum_{b=1}^{b} \frac{l}{A} \quad (m.m^{-2}) \qquad (3.3)$$

$$L_V = \sum_{b=1}^{b} \frac{l}{V} \quad (m.m^{-3}) \qquad (3.4)$$

-volume density of burrows $V_V$,

$$V_V = \sum_{b=1}^{b} \frac{v}{V} \quad (m^3.m^{-3}) \qquad (3.5)$$

-numerical densities of branched burrows $N_{Nb}$ and $N_{Ab}$,

$$N_{Nb} = \sum_{b_b=1}^{b_b} \frac{1}{N} \quad (.) \qquad (3.6)$$

$$N_{Ab} = \sum_{b_b=1}^{b_b} \frac{1}{A} \quad (m^{-2}) \qquad (3.7)$$

-length densities of branched burrows $L_{Lb}$ and $L_{Ab}$,

$$L_{Lb} = \sum_{b_b=1}^{b_b} \frac{l_b}{L} \quad (m.m^{-1}) \qquad (3.8)$$

$$L_{Ab} = \sum_{b_b=1}^{b_b} \frac{l_b}{A} \quad (m.m^{-2}) \qquad (3.9)$$

-mean burrow declination (°),
-mean burrow diameter (m),
where:
N,b= number of burrows, L= length (m), A= area ($m^2$), V= volume ($m^3$), l= length of burrow b (m), v= volume of burrow b ($m^3$), $_b$ = index for branched burrows.

## Results 3.3

### Development of earthworm community 3.3.1

Three of the four inoculated species established a population (Fig. 3.2). Of *Lumbricus rubellus* only one juvenile individual was collected. *Aporrectodea longa* is the main species in the front zone, and may be characterized as a colonizer. *Aporrectodea caliginosa* had a slower development. *L. terrestris* obviously spread very slowly, but may have been underestimated because only earthworms to a depth of 30 cm were collected. Two morphological types of *Aporrectodea caliginosa, sensu strictu* and *nocturna* (Sims and Gerard, 1985) were present in approximately equal numbers. *Allolobophora chlorotica* was present in low numbers at some spots in the pasture and is regarded as noise. *A. chlorotica* was, however, not found at the sample pits.

At the time of mapping, 7.25 years after the lag phase, earthworms had migrated approximately 45 to 46 m (Fig. 3.3). One individual *A. longa*, however, reached a distance of 48 m. Apparently the colonization front was not sharp, but was a 6 m wide zone with low burrow numbers and marked variability.

Taking 46 m for the outer limit of the front zone and 7.25 y earthworm activity, the colonization velocity or dispersion rate of the earthworm community was estimated at 6.3 $m.y^{-1}$. The rate for *L. terrestris* was estimated at 1.4 $m.y^{-1}$. Maximum earthworm density (Fig. 3.4) was observed at 20 m from the nearest inoculation row.

### Evolution of the burrow systems 3.3.2

The youngest burrow system was inside the front zone, and probably started developing in spring of 1991. The burrow system of 0.9 y was located just outside the inner margin of the front zone. The oldest burrow system was close to an inoculation point.

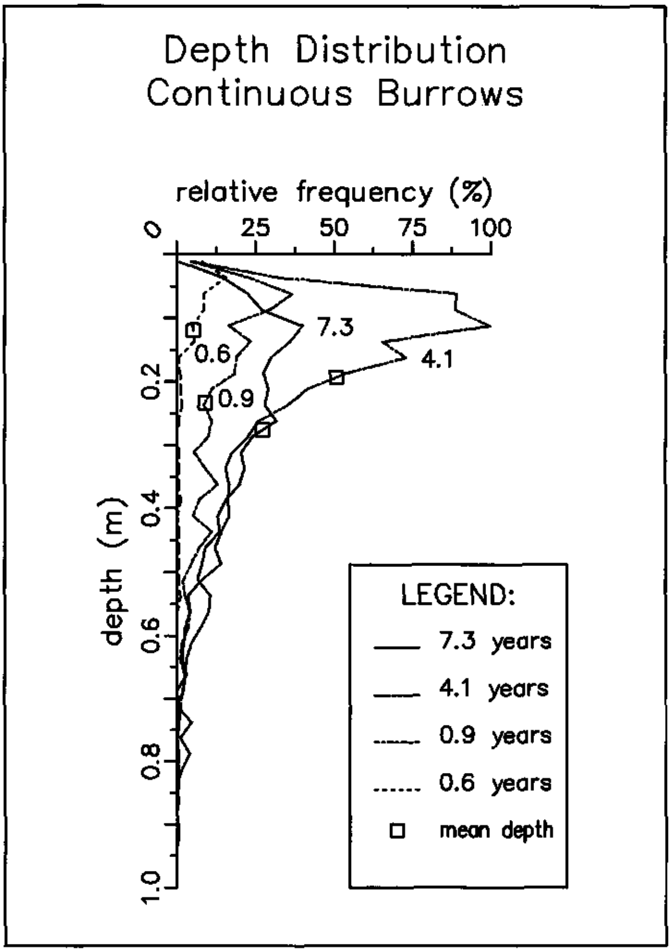


***Figure 3.5*** *Distribution of connected burrow points per depth class of 25 mm for the four burrow systems.*

***Table 3.2*** *The correlation ($r^2$) between burrow system parameters and earthworm population parameters.*

| | population parameter | | |
|---|---|---|---|
| burrow system parameter | biomass | number | ind. mass |
| numerical density $N_A$ | 0.94** | 0.92** | 0.76 |
| length density $L_A$ | 0.95** | 0.88* | 0.76 |

2-tailed significance: * ≤ 0.05, ** ≤ 0.01

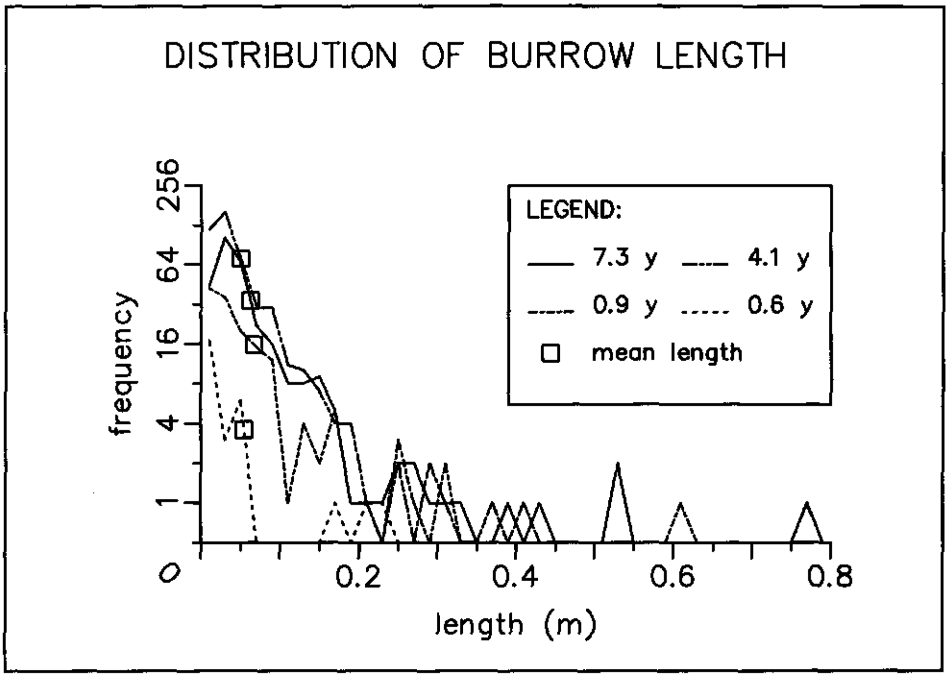


*Figure 3.6 Distribution of burrow length per length class of 20 mm in the four burrow systems.*

Between 59 to 72% of the burrow points could be connected (Table 3.1), so approximately one-third of a burrow system consisted of burrow fragments shorter than the average layer distance. The portion of connected burrows points increased with depth.

In the first 4.1 years the density of the systems ($N_A$, $L_A$, $L_V$ and $V_V$ ) increased sharply with time (Fig. 3.4) and decreased later. The number of continuous burrows varied with depth (Fig. 3.5) in a similar manner for all four systems: it rapidly increased with depth to a maximum and declines further down. The depth of maximum burrow density increased with time (Table 3.2). Below depth of maximum density the number of continuous burrows increased with age, so the system deepened with age. The mean depth of the burrow system (Fig. 3.5) seemed to increase with time, the 4.1 year old system did not obey this trend.

The distribution of lengths of individual burrows within a burrow system (Fig. 3.6) was characterized by a long right tail. The mean length of the burrows did not show a clear trend with age of the burrow system. Individual burrows (Fig. 3.7 and 3.8) had a strong vertical orientation which increases with age of the burrow system.

greatest part of the fieldwork. Kretzschmar (1982) observed a decline of the number of burrows in the superficial layer (0-20 cm) in dry periods.

## 3.5 Conclusions

Length and numerical density of earthworm burrow systems very quickly respond to the development of the mass of the earthworm community. The decrease in the earthworm biomass after 4.1 year is probably related to the disappearance of the root mat after that time. A fast response of the burrow system density to a lower earthworm density implies that the destruction rate of burrows is high.

Over a longer time span the system the deepens because of a lower destruction rates at greater depths.

The increased verticality and decreased proportion of branched burrows, thus minimizing the size of the territory, indicates an increased competition between earthworms.

To better understand the development of these burrow systems, the destruction rate of burrows in relation to burrow depth needs to be assessed.

## Acknowledgements

This study was part of a project funded by the Netherlands Integrated Soil Research Programme. The discussion with Dr. A. Kretzschmar about an earlier manuscript is highly appreciated by the authors. Valuable suggestions for improvement of this manuscript were also given by Prof. dr. ir. N. van Breemen en Dr. ir. R. Miedema. Staff and personnel of the Ir. A.P. Minderhoudhoeve gave valuable assistance during the field work.

## References

Blackwell, P.S., Green, T.W., and Mason, W.K. (1990) Responses of Biopore Channels from Roots to Compression by Vertical Stresses. *Soil Science Society of America Journal* **54,** 1088-1091.

Bolton, P.J. and Phillipson, J. (1976) Burrowing, feeding, egestion and energy budgets of *Allolobophora rosea* (Savigny) (Lumbricidae). *Oecologia* (Berlin) **23,** 225-245.

Bouma, J. (1990) Using morphometric expressions for macropores to improve soil physical analyses of field soils. *Geoderma* **46,** 3-11.

Davis, J.C. (1986) *Statistics and data analysis in geology* (2nd ed.) John Wiley & Sons, New York.

Edwards, C.A. and Lofty J.R. (1977) *Biology of earthworms* (2nd ed.) Chapman and Hall, London.

Edwards, W.M., Norton, L.D. and Redmond, C.E. (1988) Characterizing macropores that affect infiltration into nontilled soil. *Soil Science Society of America Journal* **52,** 483-487.

Ehlers, W. (1973) Observations on earthworm channels and infiltration on tilled and untilled loess soil. *Soil Science* **119,** 242-249.

FAO (1990) *Soil map of the world, revised legend (reprinted).* Food and Agricultural Organization of the United Nations, UNESCO, International Soil Reference and Information Service FAO World Soils Resources Report 60, Rome.

Garner, M.G., (1953) The preparation of latex casts of soil cavities for the study of tunnelling activities of animals. *Science* **118,** 380-381.

Gregory, K.J. and Walling, D.E. (1979) *Drainage basin form and process. A geomorphological approach.* Edward Arnold (Publishers) Ltd., London.

Hoogerkamp, H., Rogaar, H. and Eijsackers, H.J.P. (1983) Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. In *Earthworm ecology: From Darwin to Vermiculture.* (J.E. Satchell, Ed.), pp 85-105. Chapman and Hall, London.

Joschko, M., Diestel, H. and Larink, O. (1989) Assessment of earthworm burrowing efficiency in compacted soil with a combination of morphological and soil physical measurements. *Biology and Fertility of Soils* **3,** 125-129.

Kobel-Lamparski, A. and Lamparski, F. (1987) Burrow constructions during the development of *Lumbricus badensis* individuals. *Biology and Fertility of Soils* **3,** 125-129.

Kretzschmar, A. (1982) Description des galeries de vers de terre et variation saisonnière des réseaux (observations en conditions naturelles). *Revue d'Ecologie et Biologie du Sol* **19,** 579-591.

Kretzschmar, A. (1987) Soil partitioning effect of an earthworm burrow system. *Biology and Fertility of Soils* **3,** 121-124.

Kretzschmar, A. (1988) Structural parameters and functional patterns of simulated earthworm burrow systems. *Biology and Fertility of Soils* **6,** 252-261.

Lee, K.E. (1985) *Earthworms, Their Ecology and Relationships with Soils and Land Use.* Academic Press Australia, Sydney.

Ligthart, T.N., Peek, G.J.W.C. and Taber, E.J. (1993) A method for the three-dimensional mapping of earthworm burrow systems. *Geoderma* **57,** 129-141.

McKenzie, B.M. and Dexter, A.R. (1993) Size and orientation of burrows made by the earthworms *Aporrectodea rosea* and *A. caliginosa. Geoderma* **56,** 233-241.

Sims, R.W. and Gerard, B.M. (1985) Earthworms. In *Keys and notes for the identification and study of the species. Synopses of the British Fauna (New Series)* (D.M. Kermack and R.S.K. Barnes, Eds.), pp 1-171, No. 31. The Linnean Society of London & The Estuarine and Brackish-Water Sciences Association, London.

Stockdill, S.M.J. (1982) Effects of introduced earthworms on the productivity of New Zealand pastures. *Pedobiologia* **24,** 29-35.

Van den Berg, J.A. and Ullersma, P. (1991) Stability status of a macropore channel under transient conditions of ponded to non-ponded infiltration. In *Hydrological Basis of Ecologically Sound Management of Soil and Groundwater.* Proceedings of the Vienna Symposium, august 1991. (H.P. Nachtnebel and H. Kovar, Eds.), pp 163-172, IAHS Publication No. 202, International Association of Hydrological Sciences.

Weibel, E.R. (1979) *Stereological Methods.* Vol. I, Practical methods for biological morphometry. Academic Press Inc. Ltd., London.

# CHAPTER 4

# Density of earthworm burrow systems in permanent pastures in relation to earthworm mass density and earthworm activity

Ligthart, T.N. and Van Breemen, N. Density of earthworm burrow systems in permanent pastures in relation to earthworm mass density and earthworm activity. *Soil Biol. Biochem.* (submitted)

## Abstract

In 1992 earthworm burrow systems were mapped three-dimensionally at two sites (APM & IVVO) in The Netherlands differing in earthworm density (APM: 168.9 kg.m$^{-2}$, IVVO: 464.7 kg.m$^{-2}$) and duration of earthworm activity (APM: 8.3 y, IVVO: 20.3 y). The systems had developed in formerly earthworm-free permanent pastures after inoculation of earthworms (*Aporrectodea caliginosa*, *A. longa*, *Lumbricus rubellus* and *L. terrestris*). Earthworm burrow systems had been mapped previously at APM in 1991.

Replicated measurements of burrow density were made with a simple 2D method in 1992 to assess the variability of the 3D mapped systems. The mapped burrow systems are considered representative for depths ≥ 10 cm, as standard deviations in burrow density were low in the 2D measurements.

The high earthworm mass density at IVVO resulted in high burrow system density. Burrow system density at APM increased markedly between 1991 and 1992, even though earthworm mass density slightly decreased. Burrow system density was highly correlated with earthworm biomass density, but apparent burrowing efficiency (burrow density per unit earthworm mass density) increased two to three times between 1991 and 1992. This increase in burrowing efficiency explained the higher burrow system density at APM in 1992.

Calculated soil-moisture contents and mean monthly temperature were used to predict earthworm activity. The increase in burrowing efficiency could be related to a difference in earthworm activity between 1991 and 1992. The IVVO site appeared to have a more favourable soil-moisture regime than APM, allowing earthworms to be active for long periods, which most likely explained the high earthworm mass density.

## Introduction 4.1

In the polder Oostelijk Flevoland, The Netherlands (Fig. 4.1) earthworms were absent directly after reclamation from an inland sea in 1957. By experimental inoculation of earthworms at some sites, chronosequences of earthworm burrow systems developed. Ligthart et al. (1993) designed a method for a three-dimensional (3D) mapping of these burrow systems. At one of those sites (APM) four earthworm burrow systems, ranging in age from 0.6 to 7.3 y, were mapped in 1991 to follow their development (Ligthart and Peek, subm.). The burrow densities were highly correlated (R = 0.97) with the earthworm biomass density.

Much higher earthworm mass densities were observed by Stein et al. (1992)

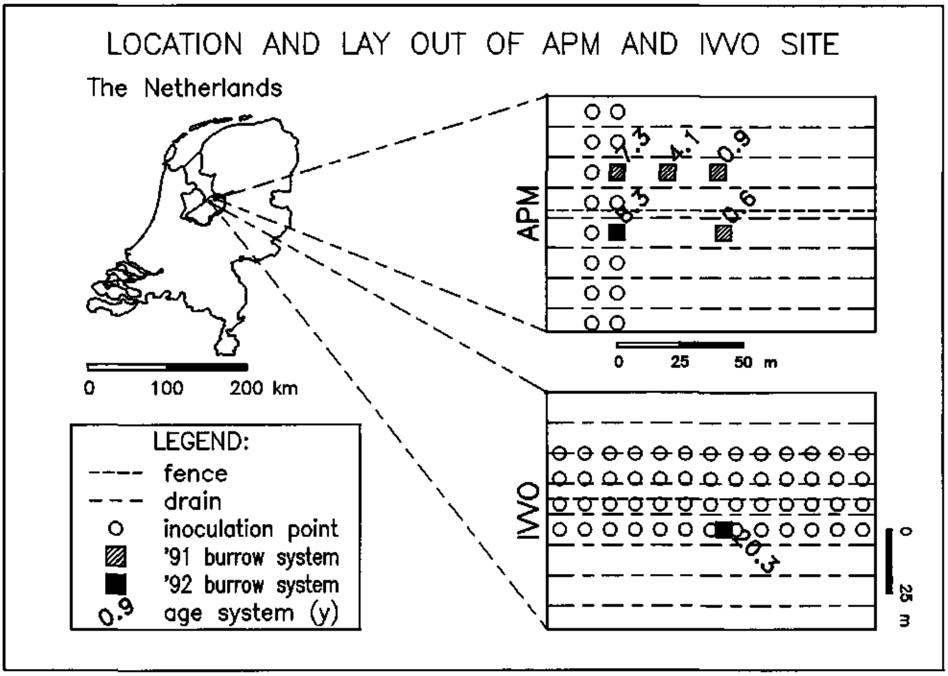


*Figure 4.1 Location and lay out of study sites in the polder Oostelijk Flevoland with inoculation points and sample points of burrow systems.*

at another pasture in the same polder (IVVO), with management similar to APM, but a longer history of earthworm activity. We hypothesized that (1) differences in earthworm density were related to either differences in soil or in development stage (age) of earthworm community, and (2) higher earthworm density would be reflected by a more extensive burrow system. To test those two hypotheses, we mapped one burrow system at IVVO and one at APM in 1992.

Large labour requirement precluded replicated 3D mapping of burrow systems. A quick and simple method determining the burrow density at different depths was used in addition to the 3D mapping to estimate the representativity of the mapped burrow systems.

## 4.2 Method and materials

### 4.2.1 Field sites

The first study site was a non-irrigated pasture at the Wageningen Agricultural University experimental farm 'ir. A.P. Minderhoudhoeve' (APM) at Swifterbant (Fig. 4.1). The soil was a Calcaric Fluvisol (FAO, 1990a) with a silt loam texture in the upper 70 cm and sandy loam texture below 70 cm. The parcel had been ploughed after reclamation up to 35 cm depth. Below the plough layer the top of the undisturbed stratified sediment was an approximately 5 cm thick sand layer (Cg1 horizon) (Fig. 4.2).

Grass was sown on the parcel in the autumn of 1981, after it had been used as arable land. In October and November 1983 earthworms (*Aporrectodea caliginosa*, *Aporrectodea longa*, *Lumbricus rubellus* and *Lumbricus terrestris*) were inoculated in two arrays of points at the south-west side of the parcel (Fig. 4.1) (Ma, 1991, pers. comm.).

The second site was located at the DLO-Institute for Animal Science and Health (IVVO) at Lelystad, 7 km SW of APM (Fig. 4.1). The Calcaric Fluvisol (silt loam texture) lacked the sand layer at 35 cm depth (Fig. 4.2) found at APM, but its sedimentary make-up was otherwise similar with that of APM. Grass was sown in the spring of 1971 and in the end of 1971 earthworms were inoculated (Hoogerkamp and Donker, 1979). The inoculated species were the same as at APM, but *L. rubellus* and *A. caliginosa* dominated.

The land at both sites was used for sheep / cattle grazing and fodder production.

### Sampling of earthworm communities 4.2.2

Earthworms were collected by handsorting at APM in August 1992 and at IVVO in September 1992. The sample pits (0.3 x 0.3 x 0.3 m) were taken close to each burrow system sample pit. The collected earthworms were stored for one day in water before weighing. Individuals of deep burrowing species, though present below 0.3 m depth, could not be to collected by adding of a formalin solution at the bottom of the sample pit. Those species have thus been underestimated in the results.

Fresh weight of active earthworm populations (with filled alimentary canal) was divided by 1.1 to be comparable with fresh weight of populations in diapause (empty alimentary canal), based on a 10% mass contribution of the contents of the alimentary canal (Lee, 1985, Sims and Gerard, 1985).

### Mapping and reconstruction of burrow systems 4.2.3

The burrow systems were mapped by recording the position, orientation, diameter and methylene blue staining (+ or -) of open burrows (called burrow points) with a diameter ≥ 2 mm on successive deeper horizontal layers spaced 1.5 to 2 cm apart (Ligthart et al., 1993). Sprinkling the soil surface plus vegetation with 0.05 $m^3.m^{-2}$ methylene blue solution (0.1 %) stained the burrows connected to the surface. The burrow system at APM was mapped in August 1992, 8.8 years after inoculation, using

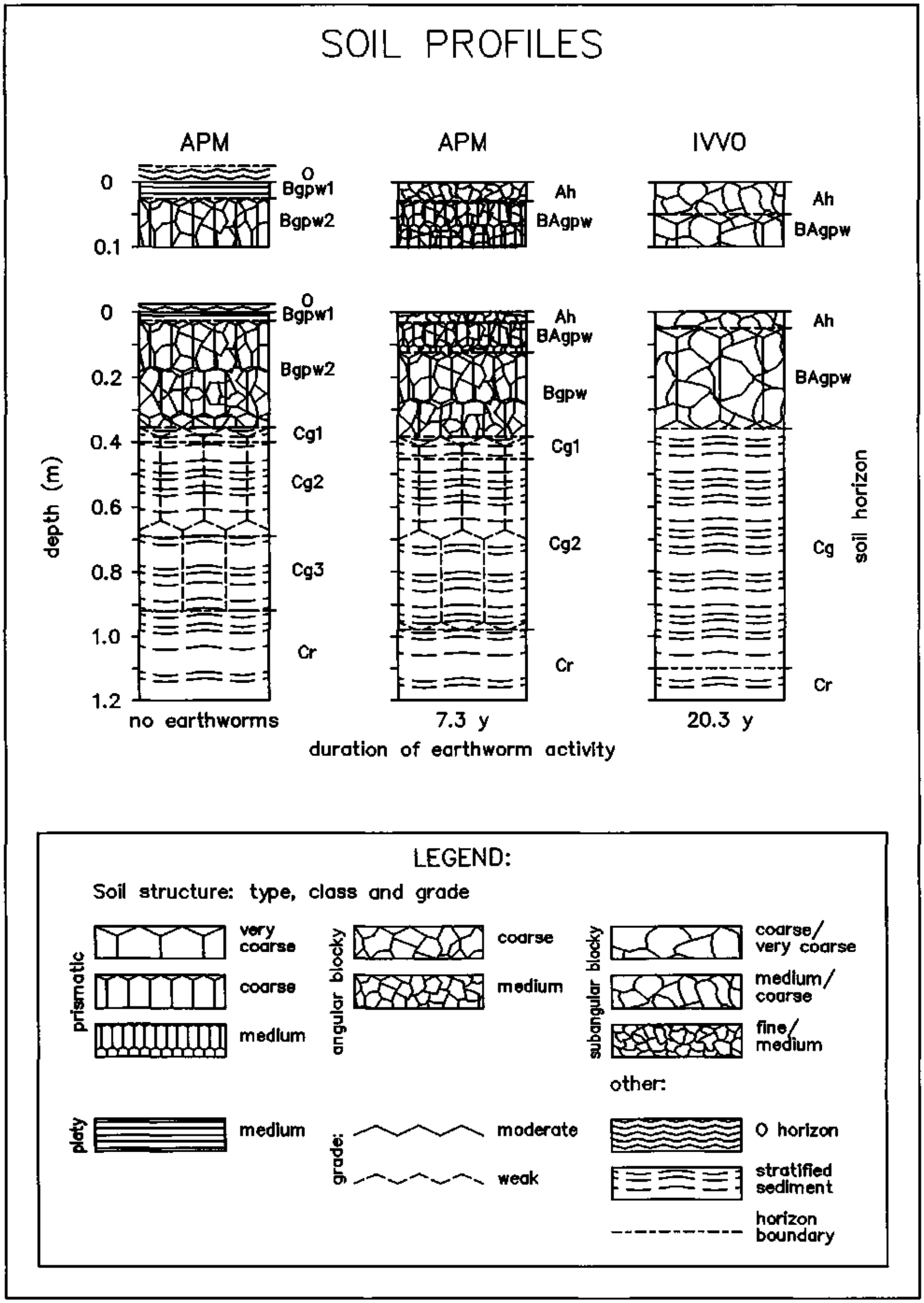


*Figure 4.2 Profiles of soil horizons (FAO, 1990a) and soil structure (FAO, 1990b) at the APM site and the IVVO site with increasing duration of earthworm activity. Data of the APM profiles were obtained in 1991, the IVVO data in 1992.*

layers of 0.5 x 0.5 m. At IVVO the system was mapped in August-September 1992, 20.8 y after inoculation. The surface mapped at IVVO was smaller (0.35 x 0.35 m) than at APM, as a reconnaissance showed very high burrow densities. With the burrow point data the burrow systems were reconstructed three-dimensionally.

Two small modifications were made to the original reconstruction method (Ligthart et al., 1993) to improve reconstruction. First, burrow points that were connected to the surface could not be joined with those that were not. In few occasions field observation showed the connection nevertheless, it was then also made in the reconstruction. Second, actual angles between points were used to connect burrow points rather than search windows, connections closest to the class means (of declination and azimuth) were used. These two modifications may have slightly decreased the number of connections compared to the original method. Details of the calculation of the several densities of a burrow system can be found in Chapter 3.

### Variability of burrow density 4.2.4

Large labour requirement precluded replicated 3D mapping of burrow systems. To assess the variability in burrow system density, open burrows were counted on replicated (n=3) horizontal areas (0.3 by 0.3 m) at depths of 5, 10, 15 and 35 cm. Five different ages were chosen at APM, and two at IVVO. The burrow point density $N_{Ap}$ ($m^{-2}$) established with this 2-dimensional method will exceed the burrow density in the 3D burrow systems, as small burrow remnants, which would be excluded in the 3D mapping, are included in these 2D data. The 2D data were used to evaluate the significance of differences in numerical burrow system density ($N_A$) between the 3D systems.

### Duration of earthworm activity 4.2.5

From the relation between the colonized area and time after inoculation found by Hoogerkamp et al. (1983) at an experiment comparable to that at APM, we estimated a lag phase of 0.5 year between inoculation and the start of colonization. A lag phase of 0.5 y was also assumed at the IVVO site. Next, the duration of earthworm activity at points at a given distance from the point of inoculation was calculated by using the mean earthworm dispersion rate and the position of the colonization front. In 1991, 7.3 years after dispersal of earthworms, the earthworms at APM had spread 46 m, giving a mean dispersion rate of 6.3 $m.y^{-1}$ (Ligthart and Peek, in press). However, one year later the front had moved to 72 m resulting in a much higher dispersion rate (28.3 $m.y^{-1}$) in 1992 (Ch. 8). At IVVO earthworms had spread 96 m (based on the burrow density at 5 cm depth) in 11.5 years (Blom, 1986), giving

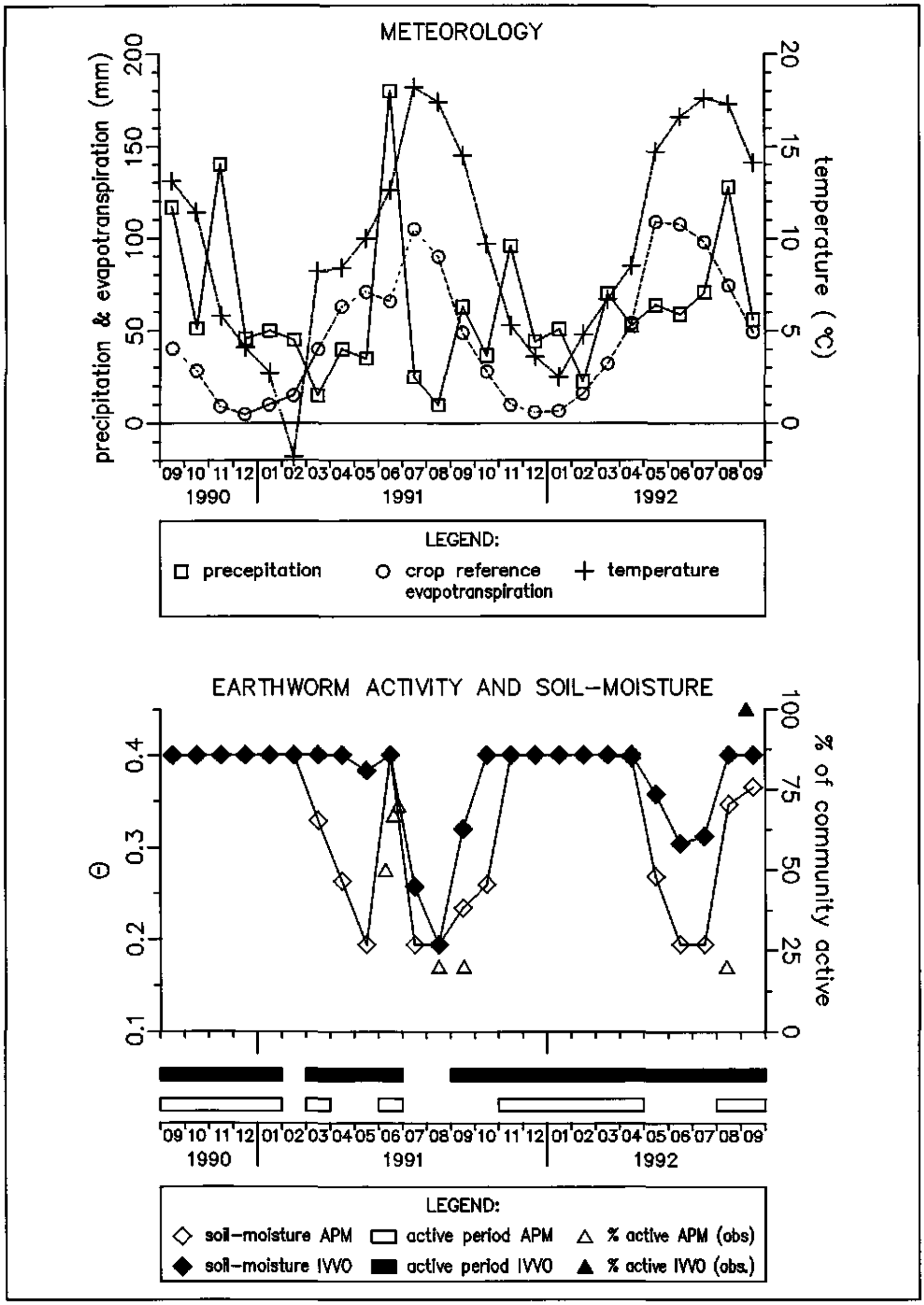


*Figure 4.3 Calculated active periods and observed earthworm activity at APM and IVVO for September 1990 through September 1992 in relation with mean monthly precipitation, temperature and calculated soil-moisture status. Meteorologic data are from the national weather station at Lelystad.*

a mean dispersion rate of 8.3 m.y$^{-1}$. By March 1990 the earthworms had completely invaded the parcels. Stein et al. (1992) estimated the hypothetical front, based on the extrapolation of the burrow density at 10 cm, at 216 m, the dispersion rate beyond 96 m thus became 18.5 m.y$^{-1}$.

### Seasonal activity of earthworm community 4.2.6

The activity of earthworms is hampered by low soil temperature and drought (Nordström and Rundgren, 1974, Nordström, 1975, Kretzschmar, 1982, Lee, 1985). Under the Dutch climate they are seasonally active, with maximum activity in spring and autumn. The soil-moisture budget for the upper 35 cm of both sites was estimated with the monthly precipitation and crop reference evapotranspiration data from the national weather station Lelystad for the period of September 1990 - September 1992 (Fig. 4.3). The difference in precipitation and crop reference evapotranspiration was added to the soil-moisture storage. Field capacity (pF 2.0) was assumed to be the maximum soil moisture content (APM, $\Theta = 0.40$ m$^3$.m$^{-3}$) on a monthly basis, while the lower limit was at pF 5.0 (APM, $\Theta = 0.19$ m$^3$.m$^{-3}$). For IVVO the soil moisture limits found for APM were used. Capillary rise from the groundwater at ± 60 to 120 cm depth was hindered at APM due to the sand layer at 35-40 cm (Fig. 4.2), the upward flux towards the topsoil was thus assumed to be negligible. A constant upward flux to the topsoil of 30 mm per month was presumed at IVVO (Wösten et al., 1987).

Earthworms were assumed to be inactive at pF $\geq 3.5$, equivalent to $\Theta \leq 0.29$ m$^3$.m$^{-3}$, and at a mean monthly temperature below 2 °C (Nordström, 1975). When soil temperature and soil-moisture content were above these limits, the earthworm community was considered to be active. Occasional observations of the percentage of the community not in diapause (active) at APM were made in June, August and September 1991 and in August 1992 (Fig. 4.3).

## Results 4.3

### Earthworm community 4.3.1

In both 1991 (Ligthart and Peek, in press) and 1992 the community at APM was largely (80%) in diapause at time of sampling, when the soil was dry (pF > 3.5) from 0 to 35 cm. The topsoil at IVVO, in contrast, was moist (pF ≈ 2) at the time of sampling, and earthworms were fully active. *Aporrectodea caliginosa* and *A. longa* were in 1992 the dominant species in the oldest part of the chronosequences (Fig. 4.4) Earthworm biomass at the point of inoculation was at APM slightly lower in 1992 than in 1991. Earthworm biomass at IVVO was much higher than at APM with total mass density of *A. longa* plus *A. caliginosa* exceeding 0.45 kg.m$^{-2}$.

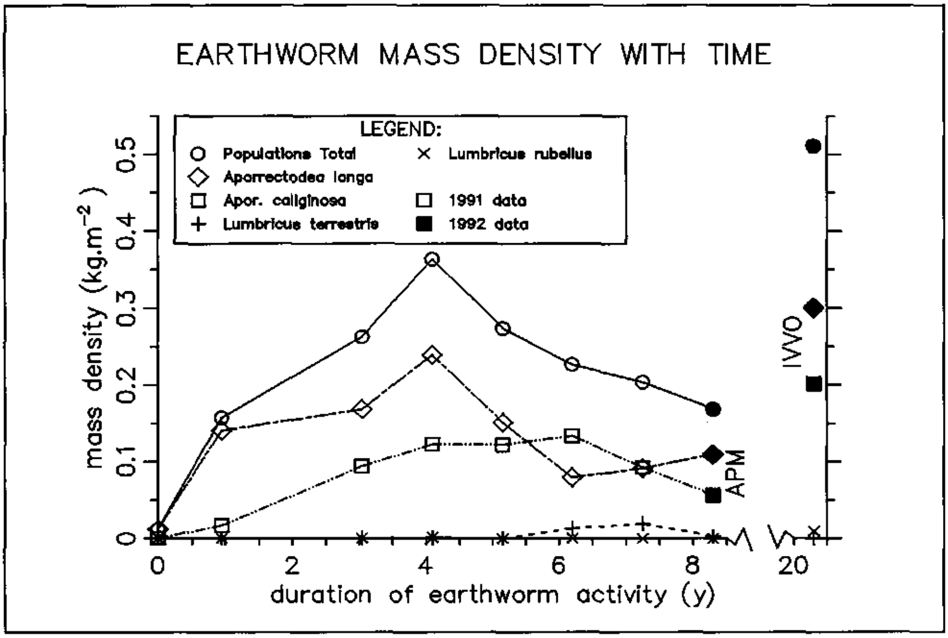


*Figure 4.4 Earthworm fresh mass density (kg.m$^{-2}$) in relation with duration (y) of earthworm activity for APM (1991 and 1992) and IVVO (1992).*

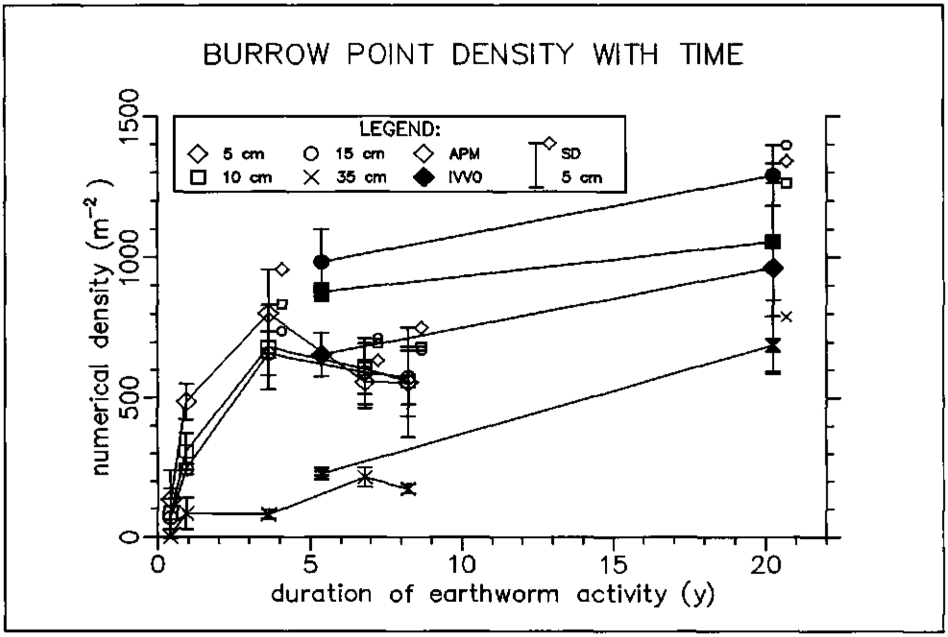


*Figure 4.5 Numerical burrow point densities (n=3) at depths of 5, 10, 15 and 35 cm at APM and IVVO with duration of earthworm activity. Bars indicate standard deviation. Data collected in 1992.*

### Seasonal activity of earthworm community 4.3.2

At APM site the (computed) active periods (Fig. 4.3) were frequently interrupted, first by low temperature in February 1991 and by an early drought in April-May 1991. Between November 1991 and April 1992 the earthworms were continuously active for six months. Low soil-moisture ($\Theta \leq 0.29$ $m^3.m^{-3}$) in May-July 1992 discontinued earthworm activity.

Soil moisture allowed more continuous earthworm activity at IVVO and active periods persisted longer. Contrary to APM, at IVVO earthworms could be continuously active from September 1991 to September 1992.

### Variability of burrow density 4.3.3

The variability in burrow point density $N_{A_p}$ of the burrow systems of 5.4 year and older at APM and IVVO were low at depths greater than 5 cm, with the SD ≈20% of mean burrow point density (Table 4.1). The two oldest APM systems (6.8 and 8.2 y) never differed significantly ($\leq 0.05$) in mean density at the same depth. The burrow point density at IVVO increased with age (Fig. 4.5). The IVVO site had at 5.4 year structurally higher densities at 10 and 15 cm depth than APM at the same age (Fig. 4.5). The oldest system (20.3 y) at IVVO had significantly higher densities at all depths than the oldest system (8.3) at APM.

### Comparison of burrow systems 4.3.4

The 8.3 y old APM burrow system (Fig. 4.6) was dominated by relatively short, vertical burrows in the upper 40 cm. Below 40 cm a few long vertical burrows continued. The 20.3 y system at IVVO consisted of a shallow upper part (up to 7 cm) with many horizontal burrows underlain by a thin (± 5 cm) zone with fewer burrows, abundant vertical burrows occurred between ± 10 cm and 40 cm depth (Fig. 4.7). Relatively few burrows continued to greater depths. The two systems (APM, 8.3 y and IVVO 20.3 y) differed in burrow declination, but not in mean burrow length (Table 4.2).

At APM the number of burrows increased rapidly with depth to a maximum and gradually decreased further down (Fig. 4.8). The IVVO system, by contrast, had two clear maxima, at 4 and 20 cm depth.

The burrow system densities $L_A$ ($m.m^{-2}$) and $N_A$ ($m^{-2}$) (Fig. 4.9) were strongly positively correlated (1-sided sign. $\leq 0.05$) with the mass density of the earthworms in 1991. The slopes of numerical ($N_A$) and length ($L_A$) densities against biomass for 1992 (APM and IVVO) (Fig. 4.9) all exceeded those for 1991 at APM. The densities of the system at IVVO (20.3) were three to four times higher than those of the oldest

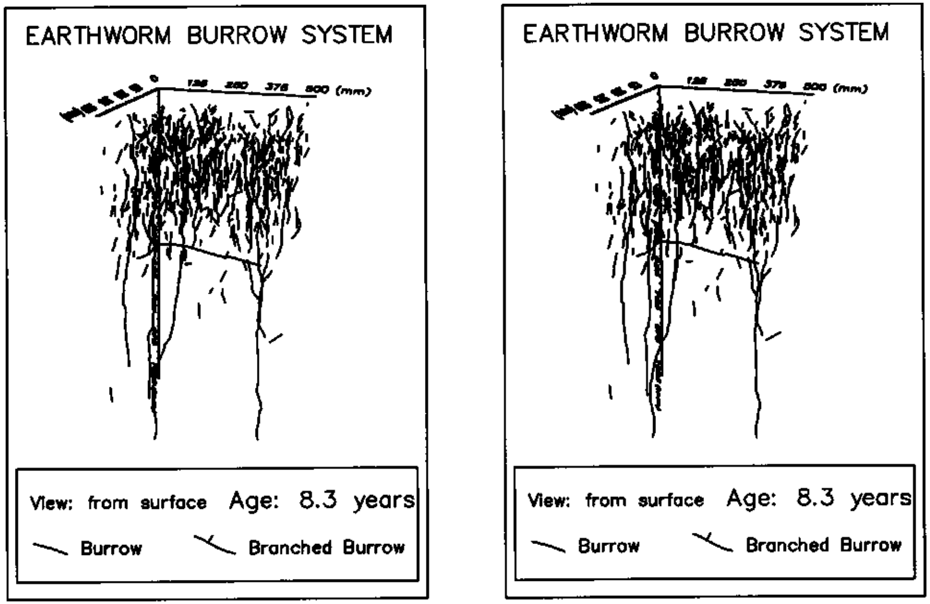


***Figure 4.6*** *Stereoscopic image of earthworm burrow system (APM) at 8.3 y of earthworm activity seen from the surface at an angle of 20 ° with the surface. For stereoscopic view a stereoscope has to be used.*

***Table 4.1*** *Mean and SD (expressed in percentage of mean) of burrow point density $N_{Ap}$ ($m^{-2}$) for the two locations at three selected durations of earthworm activity. Data were collected in 1992. Letters denotes significant groups within a row at the two-sided ≤ 0.05 level (Norusis, 1992).*

| Location | APM | | | | IVVO | | | |
|---|---|---|---|---|---|---|---|---|
| Activity (y) | 6.8 | | 8.2 | | 5.4 | | 20.3 | |
| Depth (cm) | mean | SD | mean | SD | mean | SD | mean | SD |
| 5 | 555.6**a** | 14 | 555.6**a** | 35 | 655.6**a** | 12 | 963.0**b** | 38 |
| 10 | 603.7**a** | 15 | 559.3**a** | 22 | 877.8**b** | 4 | 1055.6**b** | 20 |
| 15 | 588.9**a** | 21 | 574.0**a** | 17 | 983.3**b** | 12 | 1288.9**c** | 8 |
| 35 | 214.8**a** | 17 | 174.1**a** | 1 | 227.8**a** | 3 | 688.9**b** | 15 |

system (8.3 y) at APM. Site or age appeared to have no effect on the relation earthworm mass - burrow density in the 1992 data.

## Discussion 4.4

At time of sampling the topsoil was dry at APM, in agreement with the calculated soil-moisture content (Fig. 4.3). The estimation of earthworm activity for June and July '91 (APM) is supported by the occasional observations of activity. Monthly climatic data and calculated soil-moisture contents provided a reasonable estimation of the true earthworm activity. Earthworms could be active longer with less interruptions at IVVO than at APM, mainly because at IVVO the topsoil dries out less as capillary rise recharges soil-moisture. The favourable soil-moisture conditions at IVVO most likely caused the high earthworm mass density (0.46 $kg.m^{-2}$). High earthworm mass density (>0.5 $kg.m^{-2}$) was reported earlier by Stein et al. (1992) at the point of inoculation in 1990.

The 3D mapped burrow systems were considered representative at depths ≥ 10 cm, as the variability was low in the replicated 2D density measurements. (Table 4.1).

The 3D mappings at APM at an inoculation point yielded clearly higher burrow densities in 1992 ($N_A$: 2056 $m^{-2}$, $L_A$: 94.4 $m.m^{-2}$) than in 1991 ($N_A$: 1180 $m^{-2}$, $L_A$: 73.1 $m.m^{-2}$), while earthworm biomass was lower in 1992 (168.9 $kg.m^{-2}$ vs 203.8 $kg.m^{-2}$). Higher burrow densities could be due to (1) further development of the burrow system with time, (2) differences in earthworm biomass or (3) year to year variation in burrow density resulting from differences in earthworm activity. Greater age of the burrow

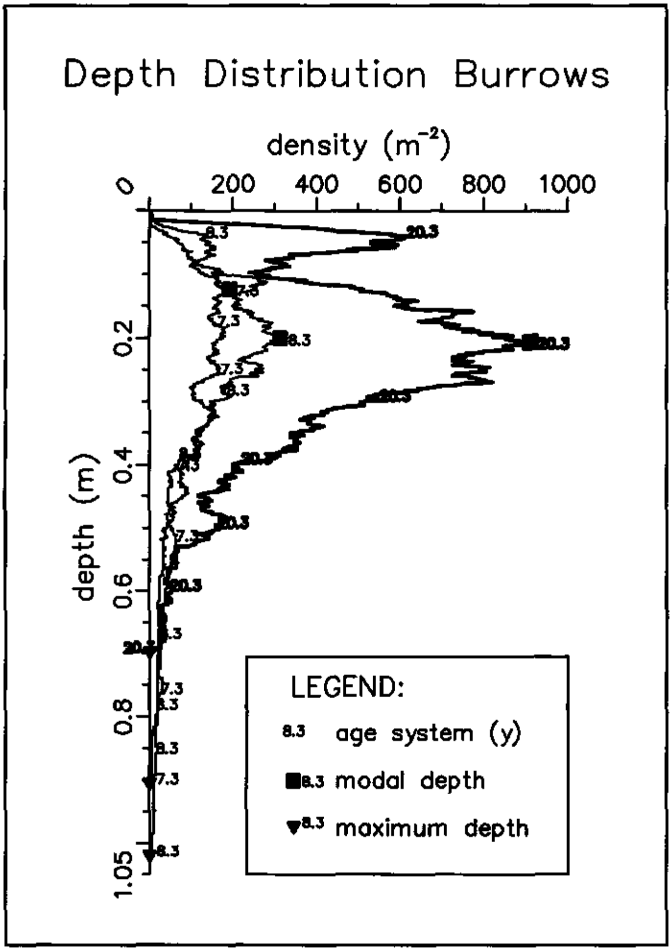


*Figure 4.8 Distribution of numerical burrow density $N_A$ ($m^{-2}$) with depth (m) for the 7.3 y (1991) and 8.3 y (1992) burrow systems at APM and the 20.3 y the IVVO system.*

Burrow densities $N_A$ and $L_A$ from the 3D data were related to earthworm biomass (R = 1.00) in 1992, without evidence for age/site effects; however the number of observations is very limited. Therefor, an effect of extended seasonal activity on 3D burrow density can not completely be excluded. The very high earthworm mass density at IVVO (0.465 kg.m$^{-2}$ vs APM: 0.169 kg.m$^{-2}$) will be the main reason for the IVVO system differing so greatly from the 8.3 y APM system.

The IVVO system (Fig. 4.7) had a superficial part of the system (0-7 cm) with common horizontal burrows, which was not found in the other systems. It is possible that the presence of such a superficial part is related to the active state of the earthworm community at the time of mapping. Earthworms are known to destroy

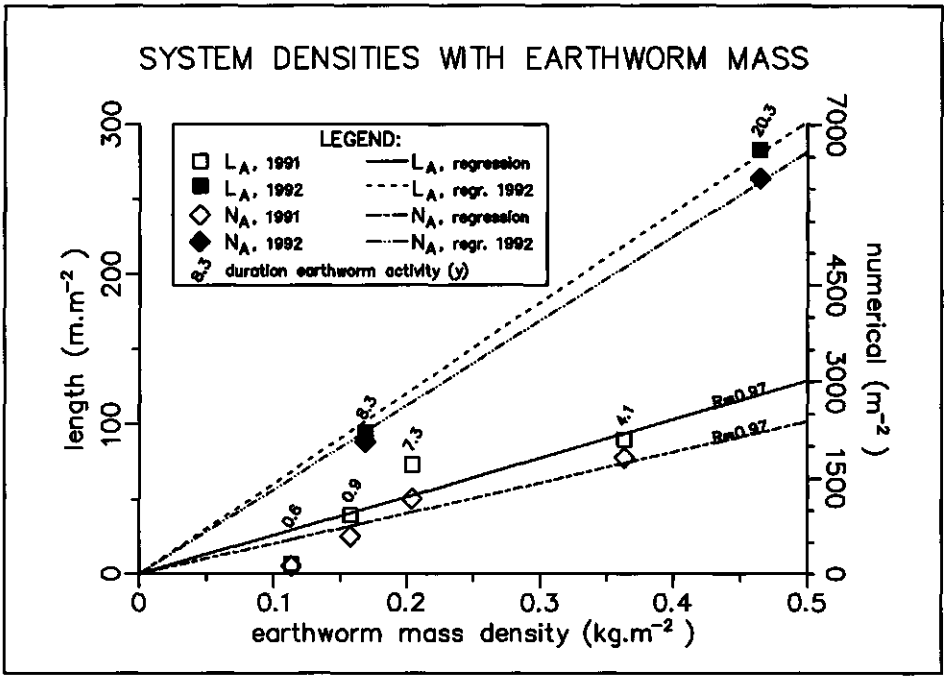


*Figure 4.9 Correlation of burrow system densities $N_A$ ($m^{-2}$) and $L_A$ ($m.m^{-2}$) with fresh earthworm mass density ($kg.m^{-2}$) in 1991 (APM) and in 1992 (APM and IVVO). The regression lines were forced through the origin.*

their superficial burrows before going into aestivation (summer quiescence) (Kretzschmar, 1982, Monestiez et al., 1993). At IVVO the animals may not yet have destroyed these burrows. Kretzschmar (1982) assumed that aestivation leads to a low mean burrow length, because of the destruction of burrows. In that case the IVVO system would have a higher mean burrow length than APM (1992), which is not so (Table 4.2). The mean burrow length calculated from Table II of Kretzschmar (1982) shows, however, no relation with seasonal earthworm activity, as is the case for the 1992 burrow systems. The mean burrow length is thus apparently independent of seasonal earthworm activity.

## Conclusions 4.5

The 3D mapped burrow systems are representative at depths ≥ 10 cm, as the variability was low in the replicated 2D density measurements.

Earthworm activity calculated from monthly climatic and calculated soil-moisture data is a reasonable estimator of the true activity. A sand layer at 35 cm in the APM soil hindered capillary rise of groundwater, which had an important effect on soil-moisture contents and so on earthworm activity. High earthworm mass density at IVVO is most likely related to the more favourable soil-moisture regime, which allows long active periods.

Three hypotheses were formulated to explain the increase in burrow density at APM from 1991 (7.3 y) to 1992 (8.3 y): (1) further development with age of the system, (2) effect of earthworm biomass and (3) increased burrowing efficiency of earthworms. Increased age could not explain the difference in burrow density, as the 2D data on burrow point density did not change between 6.8 and 8.2 year. Earthworm biomass was lower in 1992 than in 1991, and could not explain increased burrow density. Burrowing activity had indeed increased in 1992, indicated by the steeper slope of burrow density to earthworm density. The increased burrowing efficiency in 1992 is most likely due to differences in weather, which caused a shorter and interrupted active period of the earthworms in 1991.

As hypothesized, the much higher earthworm mass density at IVVO resulted in higher density of the earthworm burrow system. In the very limited 1992 data set no effects of age or site could be detected in the relation between burrow density and earthworm biomass.

The high correlation of $N_A$ and $L_A$ with earthworm biomass makes earthworm biomass a robust predictor of burrow system density. The relation between biomass and burrow density can change, however, markedly from year to year due to changes in earthworm activity. The comparison between burrow systems mapped in the same season, but in different years, must thus be made with great prudence.

The superficial part with high burrow density of the burrow system at IVVO is probably related to the active state of the earthworm community at the time of mapping.

## Acknowledgements

Mrs. A. van Liere assisted in the acquisition and entry of the huge amount of data needed to map the burrow systems. J.C.Y. Marinissen and R. Miedema gave valuable comments on an earlier version of the manuscript. The study was part of a project funded by the Netherlands Integrated Soil Research Programme.

## References

Blom, J.H.C. (1986) *De invloed van regenwormactiviteit op de bodemprofielontwikkeling en de verdeling van koolstof, stikstof, fosfaat en calciumcarbonaat in het bodemprofiel onder grasland in Oostelijk Flevoland.* Unpublished MSc report SCR-635, Dept. Soil Sc. & Geol., Agric. Univ. Wageningen. (in Dutch).

FAO (1990a) *Soil map of the world, revised legend (reprinted).* Food and Agricultural Organization of the United Nations, UNESCO, International Soil Reference and Information Service FAO World Soils Resources Report 60, Rome.

FAO (1990b) *Guidelines for Soil Description.* (3rd ed.) Food and Agricultural Organization of the United Nations, International Soil Reference and Information Service, Rome.

Hoogerkamp, M. and Donker, W. (1979) *Aanleg van blijvend grasland op de bedrijven van instellingen voor landbouwkundig onderzoek nabij Lelystad.* Internal Report CABO, Wageningen and IVVO, Lelystad. 48 pp (in Dutch).

Hoogerkamp, H., Rogaar, H. and Eijsackers, H.J.P. (1983) Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. In: Satchel, J.E. (ed.) *Earthworm ecology* Chapman and Hall, London, 495 pp.

Kretzschmar, A. (1982) Description des galeries de vers de terre et variation saisonnière des réseaux (observations en conditions naturelles). *Rev. Ecol. Biol. Sol* **19** (4), 579-591. (in French)

Lee, K.E. (1985) *Earthworms their ecology and relationships with soils and land use.* Academic Press Australia, Sydney.

Ligthart, T.N., Peek, G.J.W.C. and Taber, E.J. (1993) A method for the three-dimensional mapping of earthworm burrow systems. *Geoderma* **57**, 129-141.

Ligthart, T.N. and Peek, G.J.C.W. (submitted) Evolution of earthworm burrow systems after inoculation of lumbricid earthworms in a pasture in the Netherlands. *Soil Biol. Biochem.*

Monestiez, P., Kretzschmar, A. and Chadœuf, J. (1993) Modelling natural burrow systems in soil by fibre process: Monte-Carlo test on independence of fibre characteristics. *Acta Stereologia* **12(2)**, 237-242.

Nordström, S. (1975) Seasonal activity of lumbricids in southern Sweden. *Oikos* **26**, 307-315.

Nordström, S. and Rundgren, S. (1974) Environmental factors and lumbricid associations in southern Sweden. *Pedobiologia* **14**, 1-27.

Norusis, M.J. (1992) *SPSS/PC+ Advanced Statistics version 5.0.* SPSS, Chicago. 481 pp.

Sims, R.W. and Gerard, B.M. (1985) *Earthworms.* Synopses of the British Fauna, no. 31. E.J. Brill/Dr. W. Backhuys, London. 171 pp.

Stein, A., Bekker, R.M., Blom, J.H.C. and Rogaar H. (1992) Spatial variability of earthworm populations in a permanent polder grassland. *Biol. Fertil. Soils* **14**, 260-266.

Wösten, J.H.M., Bannink, M.H. and Beuving, J. (1987) *Waterretentie- en doorlatendheidskarakteristieken van boven- en ondergronden in Nederland: de Staringreeks.* ICW-report 18 / STIBOKA-report 1932, Wageningen. 75 pp. (in Dutch)

# CHAPTER 5

# Modes and rates of destruction of artificial earthworm burrows in an intensively used pasture

Ligthart, T.N., Miedema, R. and Van Breemen, N. Modes and rates of destruction of artificial earthworm burrows in an intensively used pasture. *Soil Biol. Biochem.* (submitted)

## Abstract

Earthworm burrow systems are in a dynamic equilibrium, being affected by both formation and destruction of burrows. This study deals with the rate at which earthworm burrows are destroyed and with the main factors determining their destruction. The fate of artificial earthworm burrows was followed in a pasture in The Netherlands. In the trampling experiment, newly made artificial burrows were exposed to trampling by cattle equal to the trampling during one year. In the monitoring experiment, with the pasture in use for grazing and fodder production, the artificial burrows were sampled two and four months after they were made. The presence of burrows and their functionality, in terms of drainage ability, were estimated visually. Both experiments were carried out in a part of the pasture with nine years of earthworm activity and in a part where earthworms were lacking.

In the trampling experiment, trampling destroyed the burrows with destruction rates that diminished with depth of the burrow. Earthworm activity had a small positive effect on the burrow presence. Trampling by cattle was most probably also the main cause of burrow destruction in the monitoring experiment. The strong effect of trampling makes the burrow destruction an event-driven process. Earthworms had a small, time-dependent, effect on the burrow destruction, and could increase as well as decrease burrow destruction.

At a depth of 0-5 cm calculated burrow presence after one year was 11% of its initial value. Burrow presence was reduced to 89% at 25-30 cm depth after one year. The functionality of the artificial burrows was in the presence of earthworms after one year 4% of the initial value, without earthworms 31%.

## 5.1 Introduction

Numerous studies (e.g. Bouma et al., 1982, Hoogerkamp et al., 1983, Edwards et al., 1988) show that earthworm burrows can be important for the drainage and aeration of the soil. The efficiency of the burrows for drainage and aeration depends greatly on the connectivity of the burrows with the soil surface. This efficiency, further called functionality, is strongly reduced by closing of burrows. A limited number of species, such as the anecic *Lumbricus terrestris*, maintain their burrows, most other species, like the endogeic *Aporrectodea caliginosa,* create more ephemeral burrows (Lee, 1985).

Burrows can be destroyed by (1) infilling, (2) compression and (3) collapse. Infilling can take place by earthworms casting excrements into an existing burrow (Lee, 1985). During a rainstorm, sediment-loaded water can flow into the burrow, followed by deposition of sediment in the burrow. Roots can enter burrows and clog them. Forces resulting from trafficking by machinery and trampling by livestock (Blackwell et al., 1990) and forces created inside the soil by swelling/ shrinking cycles and freezing/thawing cycles (Buol et al., 1973) may cause compression of a burrow. The collapse of a burrow arises from the seepage force generated by the flow of water during draining of a burrow and the surrounding soil (Van den Berg and Ullersma, 1991). Destruction of an earthworm burrow is here defined as the partly or fully closing/infilling of an originally completely open burrow.

Among the factors which probably affect the sensitivity of a burrow to destruction are: (1) burrow declination, (2) depth of burrow, (3) burrow diameter, (4) soil strength and (5) soil structure stability. Livestock and traffic exert mainly vertical forces (Gill and Vandenberg, 1968) at the soil surface, resulting within the soil in mainly vertical stresses. Therefore the declination of the burrow, the angle with the horizontal, will affect its life span: vertical burrows will be less compressed than oblique or horizontal burrows (Horn, 1986, Blackwell et al., 1990; Bohne, 1991). Bolling and Söhne (1982) show that traffic, associated with pulling loads, may cause mainly horizontal stresses in the superficial soil layers, whilst the stresses become more vertical with depth. In such case vertical burrows near the surface may be the most susceptible to compression. We assumed that in general vertical burrows will have a longer life-span than oblique or horizontal ones.

Effects of earthworm activity such as the development of well homogenized soil horizons (Ah) (Hoogerkamp et al., 1983) or the mixing of particles from the soil surface into the soil (Tomlin et al., 1992) are strongest near the surface and decrease with depth. Destruction of burrows by earthworms will thus decrease in intensity with depth. The magnitude of forces exerted by livestock and traffic (Bolling and Söhne, 1982) on the soil diminishes with depth. The chance of burrows being blocked by roots will depend on the root density, grass species have maximum density in the top 20 cm, below the density gradually decreases (Schuurman, 1973). We expected burrow destruction to decrease with depth, as do the aforementioned processes.

The ability of a burrow to withstand forces is related to the soil strength (Gill and Vandenberg, 1968), here defined as the force which the soil can withstand without deforming. This soil property depends among others of the soil water potential, the structure stability and the volume of mesopores and macropores. Earthworms influence soil strength and structure stability (Marinissen and Dexter, 1990, Marinissen, 1994). Earthworms create a topsoil that has a more loose, granular structure than one without earthworms (Hoogerkamp et al., 1983). Due to the looser structure, forces applied onto the soil surface (such as trampling by livestock) will lead to a relative stronger soil compaction (Lee, 1959). However, in general aggregate stability increases due to earthworm activity, which would reduce the chance of the

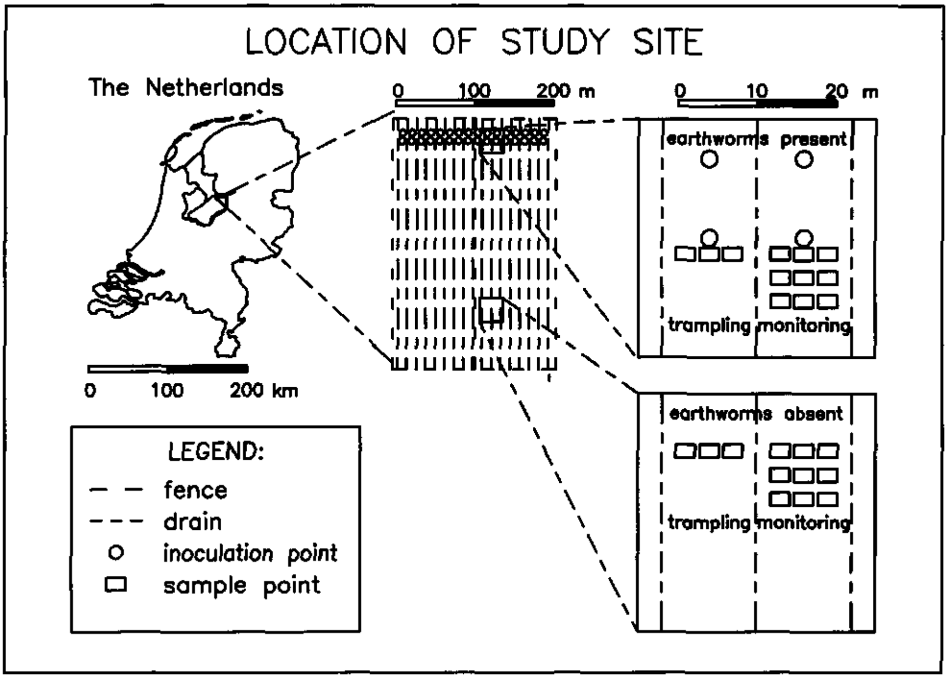


*Figure 5.1 Location of the study site with earthworm inoculation points (1983) and sample points (1993).*

burrow wall being disrupted by water flow or the infilling of a burrow with detached soil particles. The influence of earthworms on burrow destruction by affecting soil properties will be called an indirect effect of earthworms. The destruction of burrows by earthworms due to casting into burrows is a direct effect.

We developed a field experiment, using artificial burrows in a pasture soil, to test a number of hypotheses: (1) trampling by livestock destroys earthworm burrows, (2) earthworms destroy burrows by casting into burrows, (3) the destruction rate of burrows diminishes with depth, (4) oblique burrows have a higher destruction rate than vertical burrows and (5) alteration of the soil (structure, strength, etc.) by earthworms affects destruction rates.

## Method and materials 5.2

### Field site 5.2.1

The study site (Fig. 5.1) was a non-irrigated permanent pasture at the experimental farm 'ir. A.P. Minderhoudhoeve' in the polder Oostelijk Flevoland, The Netherlands. Earthworms were absent in this polder as it had been reclaimed from an

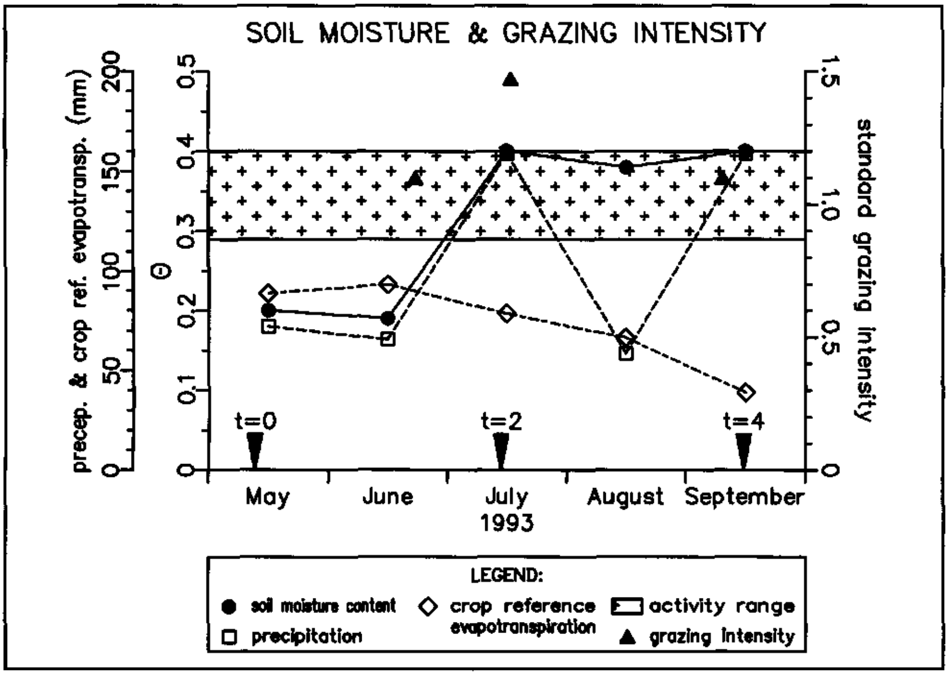


*Figure 5.3 Mean monthly precipitation and crop reference evapotranspiration (national weather station Lelystad), calculated monthly soil-moisture content (Θ) and observed grazing intensity (standard=100 cow.day$^{-1}$.ha$^{-1}$) during the monitoring experiment. The shaded area gives the soil-moisture range which allows earthworm activity.*

cm were in the zone in which burrow density increased with age of the burrow system (Ligthart and Peek, in press). Two burrow declinations (60 and 90° with the horizontal) were used to analyze the effect on the destruction rate (Fig. 5.2).

To study the effects of trampling by livestock on burrows while excluding direct effects of earthworms, the trampling experiment was designed. On 7 June 1993, the day after creating the artificial burrows, the trampling of one grazing season (five grazing events) was simulated by driving 43 heifers 26 times over sample points with and without earthworms present (Fig. 5.1). The trampling simulation method has been designed to quickly assess the impact of a known trampling intensity (Beuving et al., 1989). To ensure that the burrows would be sensitive to deformation, the soil was irrigated prior to the trampling to a mean moisture content in the upper 15 centimetres of 0.34 $m^3.m^{-3}$ (pF 2.9). The reference sample points were used as non-trampling points. No direct earthworm effect can occur as insufficient time will be available for significant casting during the two days the trampling experiment lasted.

The monitoring experiment was performed to monitor the (direct) destruction of burrows by earthworms (casting into burrows) over a longer time span. Two sampling times (2 and 4 months) were used. During the experiment the pasture was in normal use for grazing and fodder production, traffic/trampling and other destructive processes will thus also have destroyed burrows. Grazing intensity relative to the standard grazing event (100 cow.day.ha$^{-1}$) was recorded (Fig. 5.3). Knowledge of the indirect effects by earthworms from the trampling experiment can be used to estimate the direct earthworm effect in the monitoring experiment.

In both experiments 10 burrows per sample point were drilled for each of the 2 declination classes. This gave a maximum density of ± 300 artificial burrows per m$^2$ which is in the same order of maximum density ($N_A$ 340 m$^{-2}$) in the natural systems (Ligthart and Peek, in press). We assume that the small increase in total pore volume (± 1.5%) did not affect destruction rates.

Per time - earthworm activity combination (6 in total) and per trampling intensity - earthworm activity combination (in total 4) 3 replicate sample points were used, yielding 240 sample cores per combination. These sample cores are considered to be independent. At t=0 and earthworms present only 2 replicate sample points were available.

### Seasonal activity of earthworm community 5.2.4

Under the Dutch climate earthworms may become inactive due to summer droughts. Earthworms were assumed to be inactive at pF $\geq$ 3.5 (Nordström, 1975), equivalent to $\Theta \leq 0.29$ m$^3$.m$^{-3}$ at the study site. The soil-moisture budget for the upper 35 cm during the experiment was estimated by adding the difference in monthly precipitation and crop reference evapotranspiration (national weather station Lelystad) to the soil-moisture storage (Fig. 5.3). The initial soil-moisture content was assumed to be at its maximum (pF 2.0, $\Theta = 0.40$ m$^3$.m$^{-3}$) in January. The lower limit of soil-moisture was set at pF 5.0 ($\Theta = 0.19$ m$^3$.m$^{-3}$). Capillary rise from the groundwater at ± 1 m depth was hindered, the upward flux towards the topsoil was assumed to be negligible. The calculated soil-moisture content was used as an indication of soil strength, which depends greatly on the soil water potential.

## Results & discussion 5.3

### Biases in reference samples 5.3.1

The burrow presence and functionality for the reference or control sample points (Fig. 5.4) showed some small, but significant ($p \leq 0.05$), effects of earthworm activity level and declination of the burrow (Table 5.1). The burrow presence and

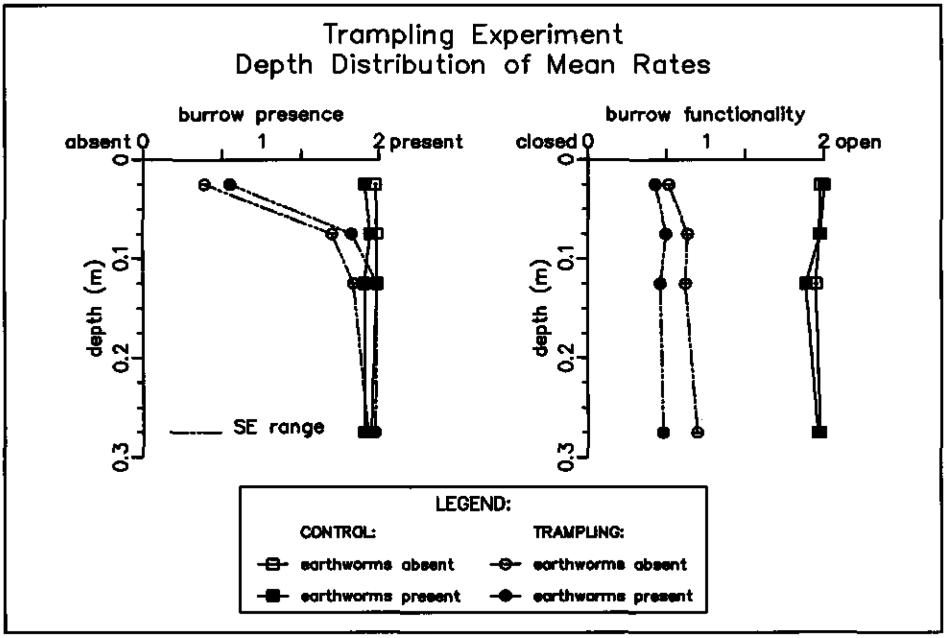


*Figure 5.4 Distribution of mean burrow presence and mean burrow functionality with depth in the control sites and the trampling sites. Data for declination 90 ° and 60 ° have been combined. Bars indicate standard error of mean.*

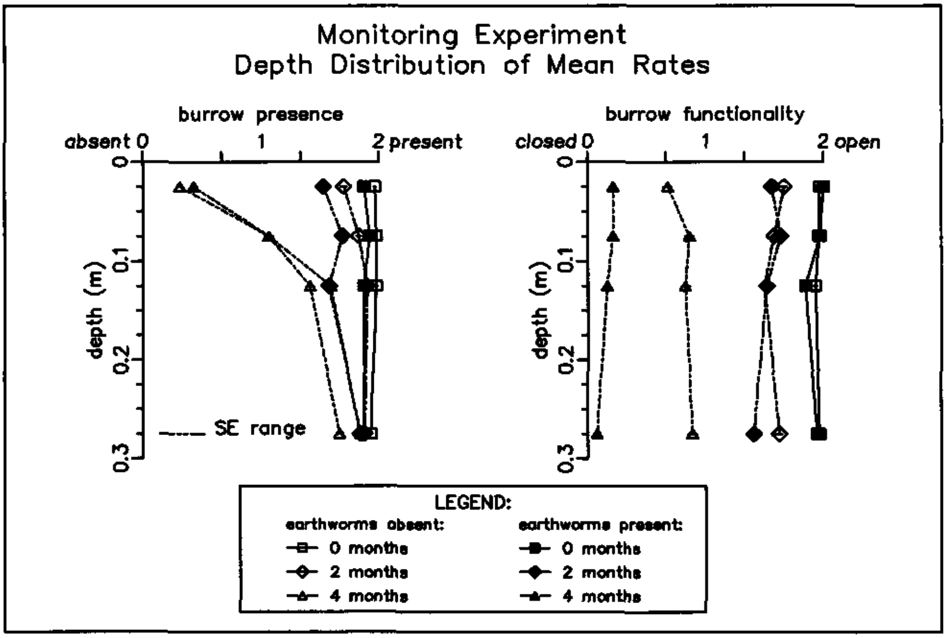


*Figure 5.5 Distribution of mean burrow presence and mean burrow functionality with depth at the start of the monitoring experiment (0 months) and after 2 and 4 months. Data for declination 90 ° and 60 ° have been combined. Bars indicate standard error of mean.*

*Table 5.1 Factors having a significant effect on the presence or functionality of burrows in the reference samples. The significance (p) is given by: ** $p \leq 0.01$, * $p \leq 0.05$. ($R^2$(presence)=0.04, $R^2$(functionality)=0.01, n=398). Results of ANOVA analysis (Norusis, 1986).*

| Factor | F & significance | |
|---|---|---|
| | presence | functionality |
| declination | **9.3 | |
| earthworms | *6.3 | |
| declination by earthworms | | *4.8 |

functionality should have their maximum value (2) directly after drilling (t=0), deviations must be ascribed to artifacts of drilling or sampling method. R Square for the significant effects (Table 5.1) was for both presence (0.04) as for functionality (0.01) very small. Treatment effects in the experiments (Fig. 5.4 and 5.5, Table 5.2 and 5.3) had considerably higher R Squares (≥0.39), and can therefore be interpreted as real treatment effects.

### Trampling experiment 5.3.2

Effects (Table 5.2) were highly significant even at relatively small values of F due to the high number of cases (n=825), the limit for significance was therefore set at p = 0.01.

Trampling was the only destructive force in this experiment, as other processes (destruction by earthworms, shrinking/swelling, etc.) could not play a role in the short time span of the experiment. Trampling reduced the burrow presence, especially in the upper 5 cm (Fig. 5.4). The effect of trampling strongly diminished with depth and became very small below 10 cm. Soil strength apparently increased by earthworm activity, as the destruction of burrows was highest at the sample points with no earthworm activity. Inclined burrows (Fig. 5.6) were more sensitive to trampling than vertical ones, which demonstrates that trampling indeed resulted in mainly vertical forces in the soil. Trampling probably destroyed the burrows mainly by compression, in some cases smeared soil was pressed into the burrows.

Trampling was the only factor that affected the burrow functionality (Table 5.2). Burrow functionality was evidently determined at the soil surface, as a depth effect was absent (p = 0.650). Earthworms had no significant (p = 0.026) effect.

Soil characteristics near the surface will influence to which degree functionality is affected by trampling. The burrow presence, on the other hand, is influenced by processes inside the soil and therefore by bulk soil characteristics.

***Table 5.2** Factors having a significant effect on the presence or functionality of burrows in the trampling experiment. The significance (p) is given by: *** $p \leq 0.0001$, ** $p \leq 0.001$, * $p \leq 0.01$. ($R^2$(presence)=0.45, $R^2$(functionality)=0.43, n=825).*

| Factor | F & significance | |
|---|---|---|
| | presence | functionality |
| trampling | ***164.8 | ***650.6 |
| depth | ***100.7 | |
| depth by trampling | ***100.3 | |
| earthworms by trampling | ***15.1 | |
| declination | **12.9 | |

***Table 5.3** Factors having a significant effect on the presence or functionality of burrows in the monitoring experiment. The significance (p) is given by: *** $p \leq 0.0001$, ** $p \leq 0.001$, * $p \leq 0.01$. ($R^2$(presence)=0.39, $R^2$(functionality)=0.48, n=1318).*

| Factor | F & significance | |
|---|---|---|
| | presence | functionality |
| time | ***200.6 | ***555.6 |
| depth | ***51.6 | |
| depth by time | ***35.7 | |
| declination | ***30.2 | **6.8 |
| earthworms | | ***41.6 |
| time by earthworms | **7.5 | ***30.9 |
| declination by depth by time | ***5.3 | |
| declination by depth | **4.2 | |

### 5.3.3 Monitoring experiment

Burrow presence and functionality decreased strongest between 2 and 4 months (Fig. 5.5); time was the most important factor explaining the burrow presence and functionality (Table 5.3). The strong decrease between 2 and 4 months may be explained by (1) higher grazing intensity at a higher soil-moisture content, (2) increased earthworm activity due to favourable soil-moisture conditions and (3) higher precipitation (Fig. 5.3). At high soil-moisture contents soil strength will be limited, increasing the susceptibility of burrows to trampling. Soil-moisture contents below the limit of $\Theta = 0.29\ m^3.m^{-3}$ restrained earthworm activity during the first period, reducing the change of infilling of burrows. No indications for sedimentation inside burrows were found.

The strongest decrease of burrow presence was near the surface, as in the tram-

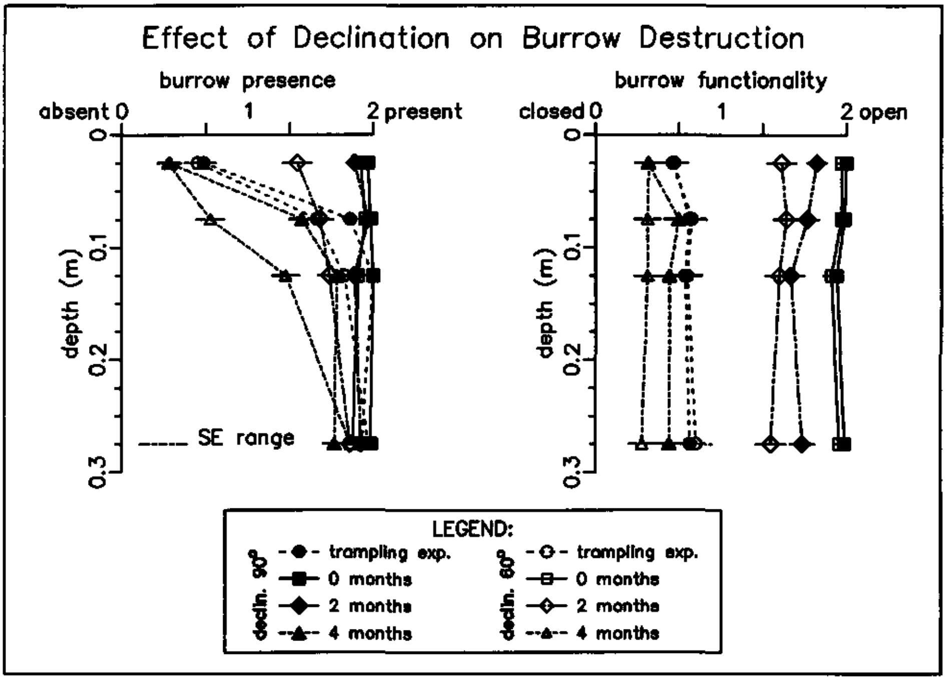


*Figure 5.6 Effect of declination (90 ° and 60 °) on burrow presence and burrow functionality in both the trampling and monitoring experiment. Data for earthworms absent and present have been combined. Bars indicate standard error of mean.*

pling experiment. Clearly, destructive processes and/or susceptibility to destruction are greatest near the soil surface. The profiles of burrow presence against depth at 4 months (Fig. 5.5) had roughly the same form as those in the trampling experiment (Fig. 5.4). Together with vertical burrows appearing the most stable (Fig. 5.6) this strongly implies that vertical stresses related to trampling are the main destructive process.

The effect of earthworm activity on burrow presence was small and varied with time (Fig. 5.5). Between 0 and 2 months the presence of earthworms lowered burrow presence, while between 2 and 4 months they had no apparent effect. The high grazing intensity at high Θ is thus the cause of the large reduction in burrow presence between 2 and 4 months. The expected increase in earthworm activity (Fig. 5.3) was confirmed though: casting inside the artificial burrows was most common between 2 and 4 months. This destruction by earthworms was probably counteracted by the indirect earthworms effects (soil properties), which, as seen in the trampling experiment, reduce the effect of trampling. The duration (4 months) of the experiment may also have been too short to allow significant casting.

burrows are the most stable, as trampling results mainly in vertically orientated forces in the soil.

Earthworm burrows that are not maintained, can only contribute a relatively short period to the drainage and aeration of the soil due to high destruction rates (48 % of functionality lost per event).

## Acknowledgements

The discussion with participants of the discussion group 4 of the C.T. De Wit Graduate School Production Ecology is highly appreciated by the authors. Staff and personnel of the Ir. A.P. Minderhoudhoeve gave valuable assistance during the field experiments. This study was part of a project funded by the Netherlands Integrated Soil Research Programme.

## References

Beuving, J., Oostindïe, K. and Vellinga, Th. (1989) Vertrappingsverliezen door onvoldoende draagkracht van veengrasland. *Rapport 8*, Staring Centrum, Wageningen.

Blackwell, P.S., Green, T.W., and Mason, W.K. (1990) Responses of Biopore Channels from Roots to Compression by Vertical Stresses. *Soil Sci. Soc. Am. J.* **54**, 1088-1091.

Bohne, H. (1991) Stabilität des Bodengefüges unter Einfluss der Bodennutzung -Voraus-setzungen, Anforderungen, Möglichkeiten-. In: *Bodennutzung und Bodenfruchtbarkeit, Band 2. Bodengefüge*, Berichte über Landwirtschaft: Sonderheft **204**, 43-54.

Bolling, I. and Söhne W. (1982) Der Bodendruck schwerer Ackerschlepper und Fahrzeuge. *Landtechnik* 37 (2), 54-57.

Bouma, J., Belmans, C.F.M. and Dekker, L.W. (1982) Water infiltration and redistribution in a Silt Loam subsoil with vertical worm channels. *Soil Sci. Soc. Am. J.* **46**, 917-921.

Buol, S.W., Hole, F.D. and McCracken, R.J. (1973) *Soil Genesis and Classification.* The Iowa State University Press, Ames, Iowa, USA, 360 p.

Edwards, W.M., Norton, L.D., Redmond, C.E. (1988) Characterizing macropores that affect infiltration into nontilled soil. *Soil Sci. Soc. Am. J.* **52** (2), 483-487.

FAO (1990) *Soil map of the world, revised legend (reprinted).* Food and Agricultural Organization of the United Nations, UNESCO, International Soil Reference and Information Service FAO World Soils Resources Report 60, Rome.

Gill, W.R. and VandenBerg, G.E. (1967) *Soil dynamics in tillage and traction.* Agric. Handbook USDA, no. 316, USDA, Washington, USA, 511 p.

Hoogerkamp, H., Rogaar, H. and Eijsackers, H.J.P. (1983) Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. In: Satchel, J.E. (Editor), *Earthworm ecology.* Chapman and Hall, London, 495 pp.

Horn, R. (1986) Auswirkung unterschiedliger Bodenbearbeitung auf die mechanische Belastbarkeit von Ackerböden. *Z. Pflanzenernaehr. Bodenk.* **149**, 9-18.

Lee, K.E. (1959) The earthworm fauna of New Zealand. *N.Z. dept. Sci. Industr. Res. Bull.* **130**

Lee, K.E. (1985) *Earthworms their ecology and relationships with soils and land use.* Academic Press Australia, Sydney.

Ligthart, T.N. and Peek G.J.W.C. (in press) Evolution of earthworm burrow systems after inoculation of lumbricid earthworms in a pasture in the Netherlands. *Soil Biol. Biochem.*

Marinissen, J.C.Y. (1994) Earthworm populations and stability of soil structure in a silt loam soil of a recently reclaimed polder in The Netherlands. *Agriculture, Ecosystems and Environment* **51**, 75-87.

Marinissen, J.C.Y. and Dexter, A.R. (1990) Mechanisms of stabilization of earthworm casts and artificial casts. *Biol. Fertil. Soils* **9**, 163-167.

Nordström, S. (1975) Seasonal activity of lumbricids in southern Sweden. *Oikos* **26**, 307-315.

Norisus, M.J. (1986) *SPSS/PC+ Advanced Statistics.*

Schuurman, J.J. (1973) *Overzicht van de resultaten van het bewortelingsonderzoek bij grassen en op grasland aan het Instituut voor Bodemvruchtbaarheid.* Report **10-1973**, Instituut voor Bodemvruchtbaarheid, Haren, The Netherlands, 39 pp. (Dutch)

## Abstract

Earthworm burrow systems are dynamic systems; active earthworms are forming burrows, while other burrows are being destroyed. Thin sections, made from soil samples taken at 2.5 and 22.5 cm depth in a chronosequence (0 to 7.3 y) of burrow systems, were studied to assess the processes responsible for the destruction of earthworm burrows and to estimate the rates of these processes. As far as we know this is the first time a study was made to identify and quantify the long range mechanisms destroying earthworm burrows in a field situation.

Destruction rates of earthworm burrows, expressed in numbers per unit area per year, were found to be depth-dependent. Near the soil surface at 2.5 cm the rate (1172 ± 401 $m^{-2}.y^{-1}$) was 6 times higher than at 22.5 cm (193 ± 55 $m^{-2}.y^{-1}$). Destruction of earthworm burrows appeared primarily caused (>70%) by earthworms casting excrements into burrows. Burrows closed by compression could not be recognized in thin sections, so actual destruction rates will exceed these values as compression of burrows certainly will have occurred.

To obtain the best possible estimation of the burrow destruction rate, the rates found here were combined with the rates found for an experiment with artificial burrows (Ligthart, T.N., Miedema, R. and Van Breemen, N., submitted. *Modes and rates of destruction of artificial earthworm burrows in an intensively used pasture.* Soil Biol. Biochem.). It than appeared that near the surface, at 2.5 cm depth, trampling by cattle became with time an important process destroying earthworm burrows. At greater depth (22.5 cm) casting by earthworms (>60%) remained the most important source of destruction.

## Introduction

6.1

In the climate of Western Europe earthworms are seasonally active, with maximum activity in spring and autumn (Nordström, 1975, Lee 1985). Earthworm burrow systems also show a seasonal variation. Burrows are formed when the soil is moist and not frozen, while earthworms actively close burrows throughout the whole system by filling them with casts at the onset of the dry season (Kretzschmar, 1982). So, earthworm burrow systems are dynamic systems in which burrows are formed and destroyed.

Rates and mechanisms of burrow destruction systems have been assessed by Ligthart et al. (submitt.) in field experiments using artificial earthworm burrows (Ch. 5). These artificial earthworm burrows were destroyed mainly by trampling by cattle in the intensively grazed permanent pasture. Casting by earthworms was a

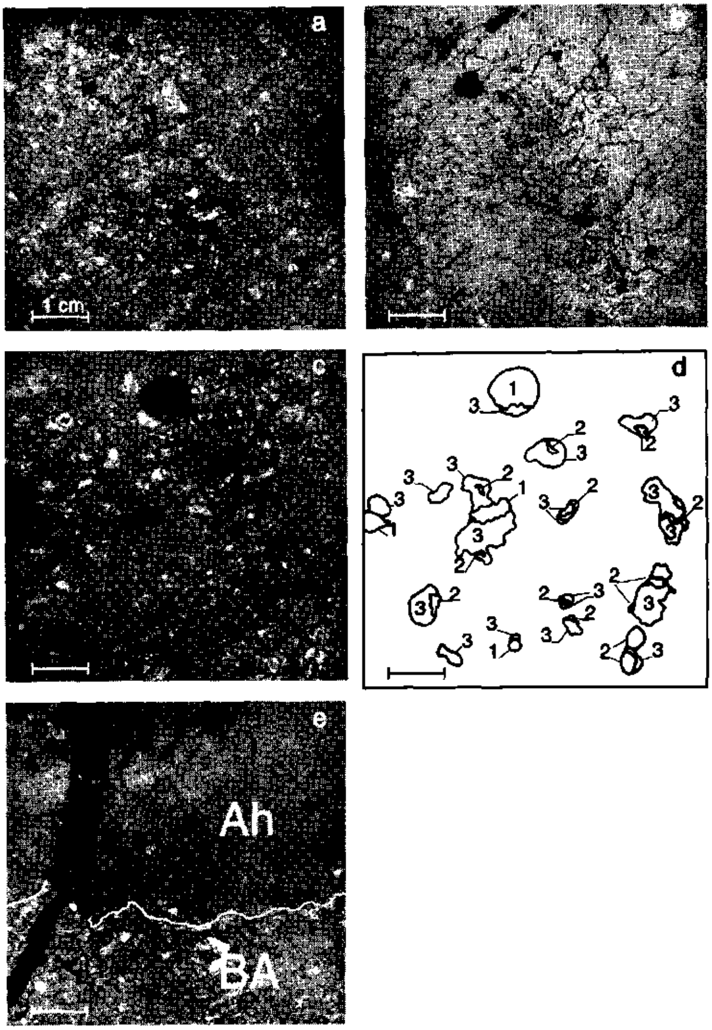


***Figure 6.1** Examples of photograms of thin sections (voids are black, matrix grey to white), bars indicate 1 cm. **a)** Soil at 2.5 cm depth without earthworm activity, **b)** soil at 2.5 cm depth with 7.3 y of earthworm activity, approx. 75% of area influenced, **c)** soil at 2.5 cm depth with 4.1 y of earthworm activity, matrix outside casts resembles that of soil without earthworm activity, **d)** interpretation of thin section c: 1. B○, open burrow, 2. B⊗, partly closed burrow, 3. 'Cast', **e)** vertical thin section (0-7.5 cm) at 7.3 y of earthworm activity showing developing Ah horizon.*

experiment lasted. Schrader (1993) found in a cuvette study that earthworms (partly) fill approximately 30 to 60% of their burrows with casts. Destruction of artificial burrows strongly decreased with increasing depth, because both forces from trampling diminish (Ligthart et al., submitt.) and earthworm activity itself decrease with depth (Tomlin et al., 1992).

A chronosequence of earthworm burrow systems, ranging in age from 0 to 7.3 y (Ligthart and Peek, in press), offered the possibility to study the modes of burrow destruction and their rates over a time span of several years. For this purpose soil thin sections were studied micromorphologically to characterize and quantify the destructive mechanisms. Earthworm casts and burrows have been studied before using micromorphological analysis (FitzPatrick, 1984, Kretzschmar, 1987 and Babel and Kretzschmar, 1994). As far as we know this is the first time a study was made to identify and quantify the long range mechanisms destroying earthworm burrows in a field situation.

## Methods and materials 6.2

### Field site 6.2.1

The study site is a non-irrigated pasture at the Wageningen Agricultural University experimental farm 'ir. A.P. Minderhoudhoeve' at Swifterbant. The soil is a Calcaric Fluvisol (FAO, 1990) with a silt loam texture in the upper 70 cm. After reclamation from the 'IJsselmeer' lake in 1957, the land was ploughed down to 35 cm depth and used as tilled arable land till 1981. Afterwards, grass was sown and the parcel was used for grazing of cattle/sheep and fodder production. In October and November 1983 earthworms (*Aporrectodea caliginosa*, *Aporrectodea longa*, *Lumbricus rubellus* and *Lumbricus terrestris*) were inoculated at one side of the parcel. After a lag time of approximately 0.5 year earthworms started to spread into the parcel at a rate of 6.3 $m.y^{-1}$ (Ligthart and Peek, in press).

At the time of sampling, in August-September 1991, a chronosequence of earthworm burrow systems was present, ranging in age from 0 y at the colonization front to 7.3 y at the inoculation point. During the sampling period the soil was dry, causing the earthworms to be largely (80%) in quiescence. The burrow systems consisted mainly of short ephemeral vertical burrows of *A. caliginosa* and *A. longa*. Long continuous and permanent burrows of *A. longa* and *L. terrestris* were scarce in the systems (Ligthart and Peek, in press).

***Table 6.1** Mean area per m² (expressed as %) and standard deviation (n=3) of 1. open burrows, 2. partly closed burrows, 3. 'Cast', 4. 'Infilling' and 5. total destroyed burrow area at 2.5 and 22.5 cm depth with duration of earthworm activity (y).*

| | **2.5 cm** | | | | | **22.5 cm** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | duration of earthworm activity (y) | | | | | duration of earthworm activity (y) | | | | |
| Unit | 0.0 | 0.6 | 0.9 | 4.1 | [a]7.3 | 0.0 | 0.6 | 0.9 | 4.1 | 7.3 |
| 1. B○, open burrow | 0.00 ± 0.00 | 0.22 ± 0.34 | 2.17 ± 1.83 | 1.29 ± 1.09 | 0.85 ± 0.69 | 0.00 ± 0.00 | 0.12 ± 0.20 | 0.11 ± 0.19 | 0.26 ± 0.27 | 1.11 ± 1.30 |
| 2. B⊗, partly closed b. | 0.00 ± 0.00 | 0.38 ± 0.66 | 0.36 ± 0.35 | 1.08 ± 0.49 | ND | 0.00 ± 0.00 | 0.02 ± 0.00 | 0.12 ± 0.08 | 0.11 ± 0.10 | 0.22 ± 0.15 |
| 3. 'Cast' | 0.00 ± 0.00 | 0.25 ± 0.43 | 2.75 ± 2.36 | 4.22 ± 2.80 | ND | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.57 ± 0.61 | 0.06 ± 0.08 | 1.49 ± 0.38 |
| 4. 'Infilling' | 0.00 ± 0.00 | 0.38 ± 0.65 | 0.22 ± 0.30 | 0.06 ± 0.07 | ND | 0.00 ± 0.00 | 0.00 ± 0.01 | 0.16 ± 0.25 | 0.01 ± 0.02 | 0.13 ± 0.06 |
| 5. 'Destroyed' (2+3+4) | 0.00 ± 0.00 | 1.01 ± 1.75 | 3.34 ± 2.96 | 5.36 ± 2.89 | ND | 0.00 ± 0.00 | 0.02 ± 0.03 | 0.86 ± 0.66 | 0.18 ± 0.20 | 1.84 ± 0.57 |

[a] At a depth of 2.5 cm and 7.3 y of earthworm activity units 2. partly closed burrows, 3. 'Cast' and 4. 'Infilling' were not traced separately.

***Table 6.2** Mean area ($m^2$) of open burrows not cut by the edges of the thin sections at 2.5 cm and at 22.5 cm depth.*

| | **2.5 cm** | | | **22.5 cm** | | |
|---|---|---|---|---|---|---|
| | Mean | Std. Dev. | n | Mean | Std. Dev. | n |
| B○, individual area | [a]1.01 E-05 | 1.37 E-05 | 58 | 1.02 E-05 | 1.44 E-05 | 19 |

B○, open burrow. [a]Earthworm activity of 7.3 y included.

## Destroyed burrows on thin sections 6.2.2

Horizontally oriented thin sections, perpendicular to the main orientation of the burrows, of 7.5 by 7.5 cm were prepared from undisturbed soil samples (Miedema et al., 1974) taken triplicate at 2.5 and 22.5 cm depth at four earthworm burrow systems of 0.6 to 7.3 y old (Ligthart and Peek, in press) and at a point not yet reached by the earthworms (0 y). The outlines of open burrows (B○), the pore space of partly closed burrows (B⊗), excremental infillings made by earthworm (Cast) and infillings of an other nature associated with burrows (Infilling) were traced on photographic enlargements (2x) of the thin sections (Fig. 6.1d). Burrows were recognized by their tubular character and smooth walls, with diameters exceeding 1 mm and lack of root cortex at the pore wall. Pores of other origin, but modified and apparently used by earthworms as burrows were also classified as burrows. 'Cast' was recognized by: (a) crescent or bow like deposition patterns (FitzPatrick, 1984), (b) having a mammilated shape (Bullock et al., 1985), (c) mixing of sand grains and finer material, (d) absence of fragments with sedimentary layering and (e) contrast with surrounding matrix, i.e. due to enrichment in organic material relative to matrix. Casts are not always enriched in organic material, but casts low in organic material with a dense mineral fabric do exist (Kretzschmar, 1987) and they occurred in some of the samples. 'Infilling' (a) did not have 'cast' properties and (b) consisted of more or less stratified accumulation of matrix material (unsorted textural pedofeatures, Bullock et al., 1985). The tracings were digitized and the areas of the classified units were calculated as a percentage of the total area of each thin section (average 46.1 cm$^2$). The total area of destroyed burrows (Destroyed) was found by summing the areas of partly closed burrows (B⊗), 'Cast' and 'Infilling' (Table 6.1).

The average area of an open burrow was estimated by dividing the total area of open burrows not cut by the sides of the thin section by their number (Table 6.2). To avoid overestimation of the numerical density (numbers per unit area, $N_A$) of open burrows 'B○' (Table 6.3), this value was assessed in the thin section by using the 'forbidden line' principle (Weibel, 1979); burrows touching the left edge, bottom edge, or the downward and leftward projection of these edges were not recorded.

***Table 6.3*** *Mean numerical density $N_A$ ($m^{-2}$) with standard deviation (n=3) of: 1. open burrows, units 2., 3., 4., 5. (standardized as average open burrow) and 6. the ratio between destroyed burrows and total number of burrows per unit area at 2.5 and 22.5 cm depth with duration of earthworm activity (y).*

| | **2.5 cm** | | | | | **22.5 cm** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | duration of earthworm activity (y) | | | | | duration of earthworm activity (y) | | | | |
| Unit | 0.0 | 0.6 | 0.9 | 4.1 | [a]7.3 | 0.0 | 0.6 | 0.9 | 4.1 | 7.3 |
| 1. B○, open burrow | 0 ± 0 | 145 ± 250 | 1374 ± 1113 | 868 ± 651 | 1735 ± 1208 | 0 ± 0 | 217 ± 376 | 72 ± 125 | 362 ± 331 | 795 ± 546 |
| 2. B⊗, part. closed burrow | 0 ± 0 | 380 ± 657 | 360 ± 348 | 1073 ± 489 | ND | 0 ± 0 | 16 ± 28 | 121 ± 76 | 105 ± 99 | 219 ± 150 |
| 3. 'Cast' | 0 ± 0 | 248 ± 429 | 2723 ± 2341 | 4175 ± 2769 | ND | 0 ± 0 | 0 ± 0 | 562 ± 601 | 59 ± 78 | 1464 ± 371 |
| 4. 'Infilling' | 0 ± 0 | 373 ± 646 | 221 ± 294 | 59 ± 71 | ND | 0 ± 0 | 3 ± 6 | 154 ± 241 | 13 ± 23 | 127 ± 61 |
| 5. 'Destroyed' (2+3+4) | 0 ± 0 | 1000 ± 1732 | 3304 ± 2932 | 5310 ± 2861 | ND | 0 ± 0 | 20 ± 34 | 840 ± 647 | 180 ± 198 | 1804 ± 557 |
| 6. 'DestRatio' (5:(1+5)) | [b]ND | 0.87 ± 0.00 | 0.68 ± 0.06 | 0.86 ± 0.10 | ND | [b]ND | 0.50 ± 0.71 | 0.95 ± 0.08 | 0.33 ± 0.21 | 0.70 ± 0.22 |

[a] At a depth of 2.5 cm and 7.3 y of earthworm activity partly closed burrows, 'Cast' and 'Infilling' were not traced separately.[b] 'DestRatio' not determined as total burrow area was zero.

## Results and discussion 6.3

Earthworm activity lead to the formation of a granular mull-like Ah horizon (Stockdill, 1982, Hoogerkamp et al., 1983 and Lee, 1985) at the study site, probably by accumulation of casts deposited at the surface. After 7.3 years of earthworm activity this horizon consisted almost completely of (reworked) earthworm casts and extended beyond 2.5 cm (Fig. 6.1e). The area of the horizontal thin sections in this Ah consisted for more than 70% of earthworm casts with diffuse boundaries (Fig. 6.1b), which made it impossible to trace partly closed burrows (B⊗), individual casts and infillings separately. The data from 2.5 cm depth at 7.3 y were therefore excluded from further analysis.

By dividing the surface areas of the units 'B⊗', 'Cast', 'Infilling' and 'Destroyed' by the mean area of an individual open burrow at that depth (Table 6.2) they were expressed in the number of average burrows per unit area (Table 6.3). The parameter 'DestRatio' expressed the number of destroyed burrows per unit area (Destroyed) as a fraction of the total number of burrows per unit area (B○ + Destroyed), with values between 0 (no destruction) and 1 (complete destruction).

Numerical densities of 'B⊗', 'Cast' and 'Destroyed' (Table 6.4) were significantly ($p \leq 0.01$) larger at 2.5 than at 22.5 cm (Table 6.3). The density of open burrows (B○) also increased with depth ($p \leq 0.05$). The numerical density of infilled burrows (Infilling) and 'DestRatio' showed no significant relation with depth of the sample.

Except for 'Infilling' and 'DestRatio' all units increased significantly with time (Tables 6.4 and 6.5). The increase of 'B⊗', 'Cast' and 'Destroyed' was depth-dependent, as shown by the interaction between time and depth. The strongest increase with time, as indicated by the regression coefficient '$\beta$', was found at 2.5 cm depth (Table 6.5).

The ratio of the density of destroyed burrows to the total burrow density (DestRatio) was independent of time at both depths. When burrow systems are in dynamic equilibrium, with only a seasonal fluctuation in the number of open burrows, 'DestRatio' would gradually increase with time, as destroyed burrows accumulate. The lack of such an increase in 'DestRatio' found here, must be attributed to the fact that the burrow systems are still developing with time.

Earthworms casting excrements into burrows appeared to be the main cause of burrow closure (Table 6.3 and 6.5). At both depths more than 70% of the destruction (Destroyed) was accounted for by casting (Cast). Near the surface at 2.5 cm the casting rate (958 ± 340 m$^{-2}$.y$^{-1}$) was 6 times higher than at 22.5 cm (159 ± 44 m$^{-2}$.y$^{-1}$). The importance of casting is still underestimated as only the casts themselves are included in the calculated rates. If the pore space of burrows (B⊗) partly closed by casts would be included, the rate of destruction due to casting of earthworms would become even higher.

***Table 6.4** Significance of the explanation of the variance of the numerical density $N_A$ ($m^{-2}$) of: open burrows 'B○', destroyed burrows (B⊗, 'Cast', 'Infilling') and 'DestRatio' by: 1. the duration of earthworm activity (Time), 2. depth of sample (Depth) and 3. the interaction between Time and Depth. The significance of the total explained variance is also given (n=27).*

| | *'B○' | 'B⊗' | 'Cast' | 'Infilling' | 'Destroyed' | 'DestRatio' |
|---|---|---|---|---|---|---|
| 1. Time | **0.020** | **0.013** | **0.037** | 0.663 | **0.033** | 0.708 |
| 2. Depth | **0.041** | **0.004** | **0.008** | 0.255 | **0.004** | 0.317 |
| 3. Time * Depth | 0.710 | **0.012** | **0.018** | 0.682 | **0.018** | 0.097 |
| 4. Explained | **0.034** | **0.001** | **0.004** | 0.714 | **0.003** | 0.362 |

*Duration of earthworm activity of 7.3 y included (n=30). **Significance** ≤ 0.05, **significance** ≤ 0.01.

Ligthart et al. (submitt.) found in a 4 months experiment, held at the same site, that compression of artificial burrows by trampling of cattle was the main cause of burrow destruction, while earthworms contributed only to a small extent to burrow destruction. The greater importance of casting found in this study may be due to: (a) the timing and relative short duration of the earlier experiment, (b) preferential casting by earthworms into their own burrows or (c) failure to recognize compressed burrows in thin sections. The experiment of Ligthart et al. (submitt.) started in June when earthworms were inactive as a result of dry soil conditions. Earthworms became active in the second period and probably formed new burrows by consumption of soil. This soil had to be deposited elsewhere; indeed casting onto the surface and into the artificial burrows was occasionally observed. Main destruction of burrows by casting takes place before the onset of the dry period when earthworms actively close their burrows (Kretzschmar, 1982). That earthworms were already inactive at start of the experiment by Ligthart et al. (submitt.) may have contributed to the lack of casting into the artificial burrows. The structure of the soil matrix not affected by earthworm activity (Fig. 6.1a) is the result of annual ploughing up to 1981 of lacustrine/marine sediments, followed by settling and merging of the soil clods and reduction of tillage voids after the parcel became permanent grassland. Outside the destroyed burrows the soil structure (Fig. 6.1c) resembled that of the soil not influenced by earthworms (Fig. 6.1a). Because the former tillage voids could not be recognized any more in thin sections, the same probably holds for former burrows destroyed by compression.

Failing to recognize compressed burrows with thin section analysis gives an underestimation of the true destruction rate of burrows. Ligthart et al. (submitt.) also underestimated the destruction rate because: (a) burrow destruction by earthworms casting into burrows was limited during their experiment, (b) partly closed

***Table 6.5** Regression coefficients $\alpha$ and $\beta$ (with standard error) of the equation $N = \alpha + \beta^{*}t$ and correlation coefficient (R) for the regression of the numerical density $N_A$ of: open burrows B○, 'B⊗', 'Cast', 'Infilling', 'Destroyed' (standardized as number of average open burrows) and 'DestRatio' with duration of earthworm activity (y).*

| | 2.5 cm | | | 22.5 cm | | |
|---|---|---|---|---|---|---|
| | $\alpha$ ($m^{-2}$) | $\beta$ ($m^{-2}.y^{-1}$) | R | $\alpha$ ($m^{-2}$) | $\beta$ ($m^{-2}.y^{-1}$) | R |
| 1. 'B○' | 355 ± 301 | 182 ± 78 | $0.54^{*}$ | 34 ± 108 | 99 ± 29 | $0.70^{**}$ |
| 2. 'B⊗' | 120 ± 157 | 238 ± 74 | $0.71^{**}$ | 27 ± 31 | 25 ± 8 | $0.65^{**}$ |
| 3. 'Cast' | 445 ± 721 | 958 ± 340 | $0.67^{*}$ | 6 ± 167 | 159 ± 44 | $0.71^{**}$ |
| 4. 'Infilling' | 198 ± 136 | -25 ± 64 | -0.12 | 35 ± 42 | 9 ± 11 | 0.23 |
| 5. 'Destroyed' | 762 ± 849 | 1172 ± 401 | $0.68^{*}$ | 70 ± 206 | 193 ± 55 | $0.70^{**}$ |
| 6. 'DestRatio' | $^{a}$0.70 ± 0.07 | $^{b}$0.04 ± 0.03 | 0.56 | $^{a}$0.72 ± 0.19 | $^{b}$-0.02 ± | -0.14 |

B○, open burrow, B⊗, partly closed burrow. Significance: $^{*}$ p=≤ 0.05, $^{**}$ p≤0.01. $^{a}$Dimensionless coefficient, $^{b}$Dimension of coefficient: $y^{-1}$

burrows were considered to be partly destroyed, giving lower destruction rates compared with the method used for this study. The best estimation of the true burrow destruction rate will be the sum of the rate found by thin section analysis and the time-dependent rate found by Ligthart et al. (submitt.):

$$D_{d,\,t} = \beta_{D\,d} + (Q_{d,\,t-1} * f_d) \tag{6.1}$$

In which $D_{d,\,t}$ is the destruction rate ($m^{-2}.y^{-1}$) at depth $d$ and time $t$ ($t \geq 1$), $\beta_{D\,d}$ is burrow destruction rate estimated with thin section analysis at depth $d$ (Table 6.5), $Q_{d,\,t-1}$ is the numerical density ($m^{-2}$) of open burrows at depth $d$ and time $t-1$ and $f_d$ is the fraction of burrows destroyed each year ($y^{-1}$) at depth $d$ (0.89 at 2.5 cm, 0.11 at 22.5 cm). At $t = 0$ the numerical density of open and destroyed burrows is given by $\alpha_{B\,d}$ and $\alpha_{D\,d}$ (Table 6.5). Describing the numerical density of open burrows ($Q_d$) as a regression with time Eq. 6.1 can then be expressed as:

$$D_{d,\,t} = \beta_{D\,d} + f_d(\alpha_{B\,d} + \beta_{B\,d}*(t-1)) \tag{6.2}$$

where $\alpha_{B\,d}$ and $\beta_{B\,d}$ are the regression coefficients for the numerical density of open burrows. When $\beta_{B\,d} \neq 0$ (the number of open burrows changes with time), as is the case here (Table 6.5), the destruction rate of burrows is time-dependent. The contribution of the second term, mainly determined by the destructive action of trampling, becomes progressively more important with time ($\beta_{B\,d} \neq 0$) especially at shallow depth (Fig. 6.2).

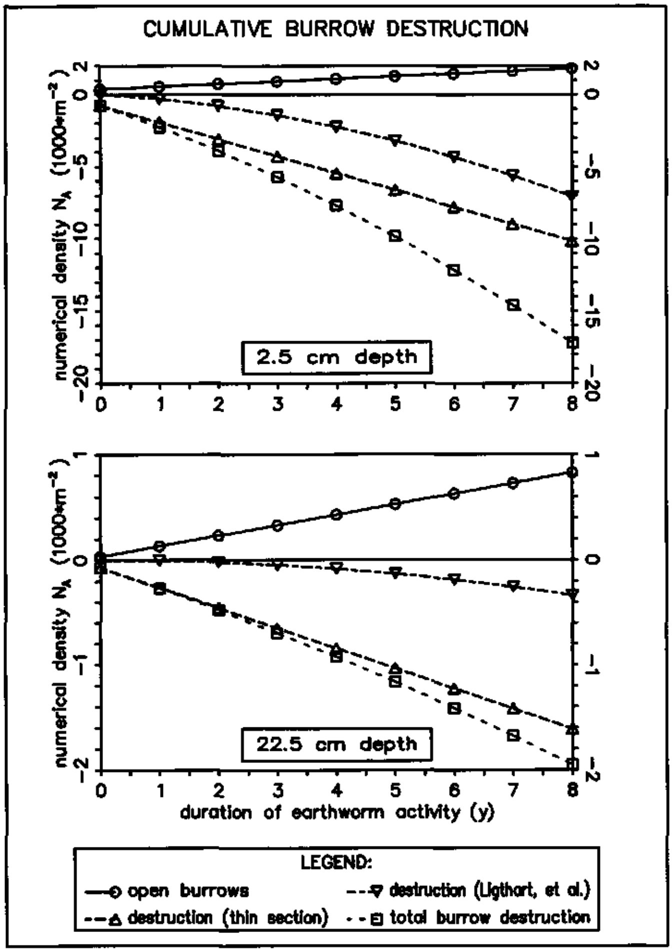


*Figure 6.2 Development of open burrows with time observed on thin sections (regression results), the cumulation of destroyed burrows based on thin section analysis (regression), the cumulation of destroyed burrows expected with stepwise destruction rates (Eq. 6.2) and the cumulation of total destroyed burrows at 2.5 (top) and 22.5 cm (bottom) depth. All dependent variables are given in thousands per m².*

At greater depth (22.5 cm) 83% of the total destruction after 8 y of earthworm activity is induced by the processes found with thin section analysis (>70% casting by earthworms). Casting by earthworms is thus the main cause (>60%) of burrow destruction at 22.5 cm depth.

According to Kretzschmar (1982) the main destruction of burrows by casting takes place before the onset of the dry period. It is clear that between February and

August 1976 more than 80% of the burrows are destroyed (Kretzschmar, 1982, Fig. 2); the estimated destruction rates are 50,000 $m^{-2}.y^{-1}$ or expressed in burrow volume (Kretzschmar, 1982, Fig. 4) 7.7 $l.m^{-2}$ in 6 months. The earthworms thus have to produce a considerable volume of casts (7.7 $l.m^{-2}$) or expressed in mass (bulk density range 1.1 to 1.5) roughly 8 to 12 $kg.m^{-2}$ in 6 months, albeit still within the reported range of cast production (approx. 1 to 26 $kg.m^{-2}.y^{-1}$, Lee, 1985). According to A. Kretzschmar (personal commun., 1995) no other destructive process could explain the vast decrease in burrow density. The question arises how such an amount of casts, needed to destroy the burrows, can be produced without making new burrows. Even if we assume that a) the complete earthworm community retreats into aestivation chambers, b) that the volume of excavated soil needed to form these chambers is equal to the volume of the animals and c) that the volume of the earthworms is equal to their mass (0.2 $kg.m^{-2}$, Kretzschmar, 1982) only a fraction (2 $l.m^{-2}$) of the volume of the destroyed burrows can be accounted for.

## Conclusions 6.4

Destruction of earthworm burrows, as assessed with thin section analysis, appears to be caused mainly (>70%) by earthworms casting excrements into burrows. Failing to recognize compressed burrows is the most probable cause of their apparent absence in the interpretation of the thin sections.

The destruction rates, expressed in number of burrows per $m^2$ per year, are near the soil surface (2.5 cm: 1172 ± 401 $y^{-1}$) 6 times higher than at 22.5 cm (193 ± 55 $y^{-1}$). Actual destruction rates will even exceed these values as compression of burrows, which certainly will have occurred, could not be detected in the thin sections. The best estimation of the true destruction rates will be the combination of the rates found here and the rate found by Ligthart et al. (submitt.) which depends mainly on trampling.

Near the surface - at 2.5 cm depth - trampling by cattle becomes more important with time as a process destroying earthworm burrows in the sequence of developing burrow systems. At greater depth (22.5 cm) casting by earthworms (>60%) remains the most important source of destruction.

Clearly, casting by earthworms is one of the main processes destroying earthworm burrows, however it remains questionable wether this process can account completely for the seasonal destruction of burrows observed before the onset of the dry season by Kretzschmar (1982).

**Acknowledgements**

This study was part of a project funded by the Netherlands Integrated Soil Research Programme. The author would like to thank N. van Breemen and R. Miedema, Department of Soil Science and Geology, Wageningen Agricultural University, for comments on an earlier version of the manuscript.

## References

Babel, U. and Kretzschmar, A.. (1994) Micromorphological observations of casts and burrow walls of the Gippsland giant earthworm (*Megascolides australis*, McCoy, 1878). In: Ringrose-Voase, A.J. and Humphreys, G.S. (Editors), Soil Micromorphology: Studies in Management and Genesis. Proc. IX Int. Working Meeting on Soil Micromorphology, Townsville, Australia, July, 1992. *Developments in Soil Science* **22**, 451-457.

Bullock, P., Fedoroff, N., Jongerius, A., Stoops, G., and Tursina, T. (1985) *Handbook for soil thin section description.* Waine Research Publications, Wolverhampton, UK, 152 pp.

FAO (1990) *Soil map of the world, revised legend (reprinted).* Food and Agricultural Organization of the United Nations, UNESCO, International Soil Reference and Information Service, FAO World Soils Resources Report 60, Rome.

FitzPatrick, E.A. (1984) *Micromorphology of Soils.* Chapman and Hall Ltd. London, UK, 433 pp.

Hoogerkamp, H., Rogaar, H. and Eijsackers, H.J.P. (1983) Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. In: Satchel, J.E. (Editor), *Earthworm ecology*, Chapman and Hall, London, 495 pp.

Kretzschmar, A. (1982) Description des galeries de vers de terre et variation saisonnière des réseaux (observations en conditions naturelles). *Rev. Écol. Biol. Sol,* **19** (4), 579-591. (In French)

Kretzschmar, A. (1987) Caracterisation microscopique de l'activite de lombriciens endoges. In: Fedoroff, N., Bresson, L.M. and Courty, M.A. (Editors), *Micromorphologie des Sol - Soil Micromorphology*, Proc. VIIth Int. Working Meeting Soil Micromorph., Paris, July 1985, Association Française pour l'Étude du Sol, Plaisir, France. pp. 325-330.579-591. (In French)

Lee, K.E. (1985) *Earthworms their ecology and relationships with soils and land use.* Academic Press Australia, Sydney, 411 pp.

Ligthart, T.N., Miedema, R. and Van Breemen, N. (submitted) Modes and rates of destruction of artificial earthworm burrows in an intensively used pasture. *Soil Biol. Biochem.*

Ligthart, T.N. and Peek, G.J.C.W. (in press) Evolution of earthworm burrow systems after inoculation of lumbricid earthworms in a pasture in the Netherlands. *Soil Biol. Biochem.*

Miedema, R., Pape, T. and van der Waal, G.J. (1974) A method to impregnate wet soil samples, producing high quality thin sections. *Neth. J. Agric. Sci.*, **22**, 37-39.

Nordström, S. (1975) Seasonal activity of lumbricids in southern Sweden. *Oikos*, **26**, 307-315.

Schrader, S. (1993) Semi-automatic image analysis of earthworm activity in 2D soil sections. *Geoderma*, **56**, 257-264.

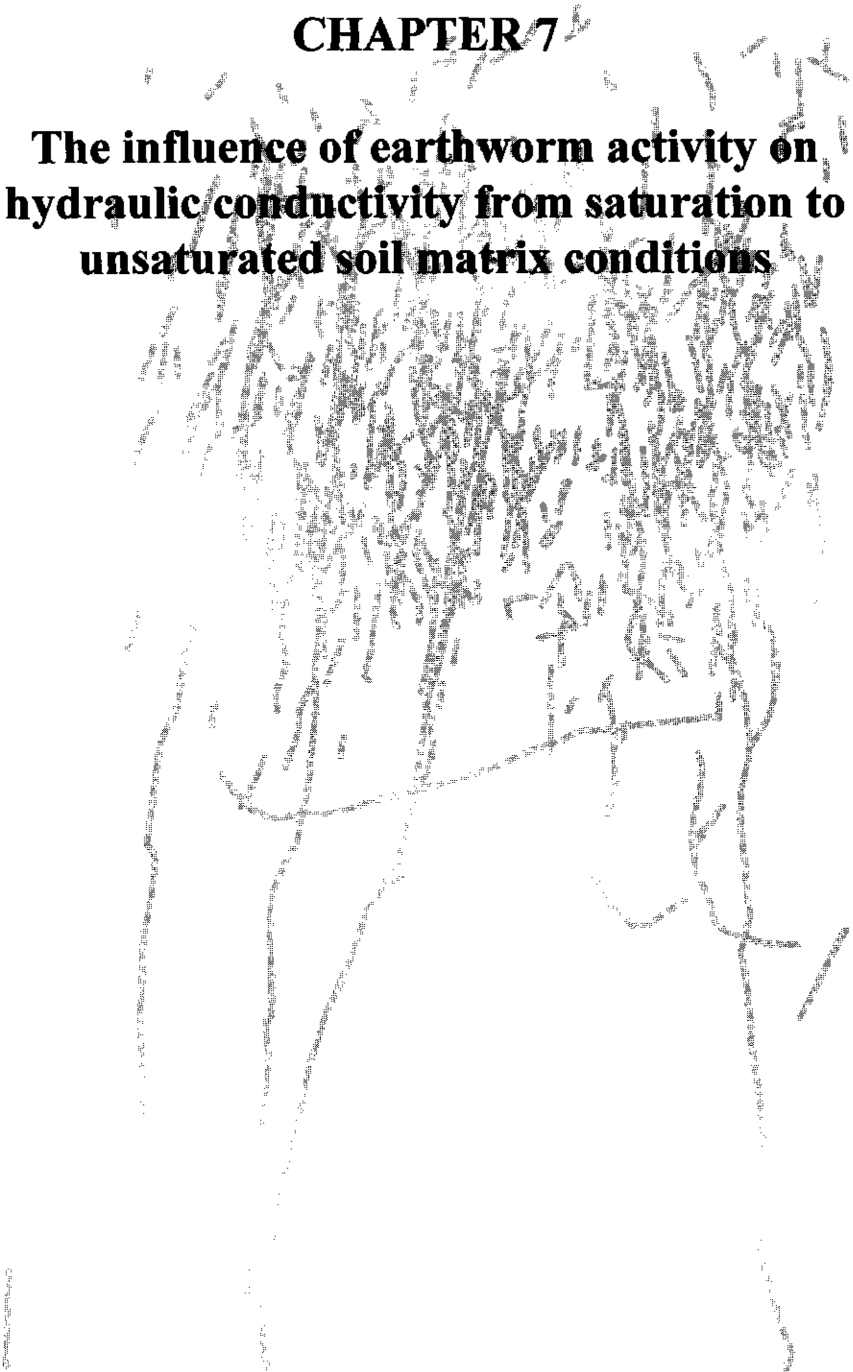
Stockdill, S.M.J. (1982) Effects of introduced earthworms on the productivity of New Zealand pastures. Pedobiologia, **24**, 29-35.

Tomlin, A.D., McCabe, D. and Protz, R. (1992) Species composition and seasonal variation of earthworms and their effect on soil properties in Southern Ontario, Canada. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.*, **24** (12), 1451-1457.

Weibel, E.R. (1979) *Stereological Methods.*, Vol. 1, Practical Methods for Biological Morphometry. Academic Press Inc. (London) Ltd., London, Great Britain.

# CHAPTER 7

# The influence of earthworm activity on hydraulic conductivity from saturation to unsaturated soil matrix conditions



Ligthart, T.N. The influence of earthworm activity on hydraulic conductivity from saturation to unsaturated soil matrix conditions. *Geoderma* (submitted)

## Abstract

The influence of earthworms on the saturated hydraulic conductivity ($K_{sat}$) has been studied by many authors. The effect of earthworms on conductivities close to saturation and at more negative pressure heads unjustly remains underexposed and is therefor studied in this paper. Earthworms did not only increase $K_{sat}$, they also increased $K$ down to -200 kPa. The increase in $K$ was caused by the change in soil structure due to earthworm presence. The structure of the subsoil proved to be crucial for the drainage capacity of individual earthworm burrows.

## 7.1 Introduction

The importance of earthworm activity for the infiltration of precipitation into the soil was recognized more than two centuries ago by White (1789) (cited in Graff and Makeschin (1979)). In many following studies (e.g. Ehlers, 1975, Stockdill, 1982, Hoogerkamp et al., 1983, Edwards et al., 1988, Joschko et al., 1992) lumbricid earthworms were said to considerably affect soil hydraulic properties. The majority of these studies focuses on the increase of the saturated hydraulic conductivity ($K_{sat}$) or ponded infiltration rates by earthworm burrows. Smettem (1992) postulated that if one knows the architecture of a burrow system one can predict the resulting change in hydraulic properties of a soil.

Only when ponding at the soil surface occurs - which depends on the initial moisture content of the soil, the saturated hydraulic conductivity of the matrix and the rainfall rate - a burrow system will substantially affect the flux of water through the soil (Bouma, 1991, Edwards et al., 1992, Smettem, 1992, Booltink and Bouma, 1993). The efficiency of earthworm burrows in increasing $K_{sat}$ will depend on the connectivity of the burrows with 1) the soil surface, 2) each other, and 3) the non-burrow macropore system (Bouma et al., 1982, Urbánek and Doležal, 1992). Yet, many other authors take it for granted that earthworm burrows invariably increase $K_{sat}$.

The connectivity between a burrow and the soil depends on the properties of the burrow wall and of the immediate surroundings of the burrow (West et al., 1991). Earthworm burrows may have 1) a lining covering the burrow wall (Jeanson, 1964, Kretzschmar, 1987), 2) a compressed zone around them (Dexter, 1978) or 3) may not have influenced their surroundings (Dexter, 1978). A lining or a dense zone reduces the connectivity of the burrow with the non-burrow macropore system. Burrows created by exerting radial pressure to widen existing voids cause the soil around the burrow to become compacted, though radial cracks may be formed (Dexter, 1978, Lee, 1985). If an earthworm burrows by ingesting soil, e.g. because it cannot overcome the soil strength (Lee, 1985), the soil around the burrow remains undisturbed (Dexter, 1978) and burrow walls are smooth (Söchting and Larink, 1992).

Earthworm burrow systems are the sum of both the formation and the destruction of burrows (Ligthart et al., revised) and show a seasonal (Kretzschmar, 1982) and year to year variation (Ligthart and Van Breemen, subm.). Consequently hydraulic properties will also have a dynamic character. Furthermore land management events may affect hydraulic properties. E.g. burrows close to the surface may be destroyed by grazing cattle (Beven and Germann, 1982, Ligthart et al. revised) thereby reducing infiltration rates.

Earthworms also alter the structure of the soil matrix (e.g. Jeanson, 1964, Geyger, 1979, Stockdill, 1982, Shaw and Pawluk, 1986, Kretzschmar, 1987, Knight et al. 1992), changing its pore system. These changes in the soil matrix are expected to change the hydraulic properties which depend on pore size distribution, pore continuity and tortuosity. Hoogerkamp et al. (1983) found that earthworms in a pasture soil increased the air filled pore volume down to the micropore range (pressure head -50 kPa). However, a marked decrease in (macro)porosity does not have to result in a decrease in conductivity, a distinct increase in infiltration rate may even be the result (Stockdill, 1982). Probably the continuity or connectivity of the pore system was increased, resulting in a pore system more efficiently conducting water.

The majority of studies on the influence of earthworms on soil hydraulic properties focuses on the effect of burrows on $K_{sat}$. Little is known about the effect of earthworms on hydraulic conductivity near saturation and in unsaturated conditions. In this paper an attempt is made to clarify the impact of these animals on hydraulic conductivities at more negative pressure heads, in addition to their effect on $K_{sat}$. The often ignored 'chicken and egg' problem in the relation between earthworm activity and soil hydraulic properties, was circumvented by using a chronosequence of earthworm burrow systems. Surface-connected burrows in three-dimensionally mapped burrow systems (Ligthart and Van Breemen, subm.) were studied in combination with measurements of hydraulic conductivities of individual burrows to predict the resulting $K$ of the systems. The effect of earthworms on $K_{sat}$ was also measured directly in soils that were influenced by earthworms for different lengths of time. The burrow wall and the surrounding pore system were analyzed to estimate the connectivity between burrow and soil matrix. Measurements of $K$ near saturation were performed to reveal a possible effect of the earthworm affected macropore system. Finally, the effect of earthworms on $K$ of the unsaturated matrix was assessed.

## Method and materials 7.2

### Field sites 7.2.1

The main study site is a pasture at the experimental farm 'ir. A.P. Minderhoudhoeve' (APM) at Swifterbant, The Netherlands. The soil is a Calcaric Fluvisol (FAO, 1990a) with a silt loam texture in the upper 70 cm. After reclamation from the 'IJsselmeer' lake in 1957, the land was ploughed to 35 cm depth and used as tilled arable land till 1981. Drainage was provided by permeable pipes at a depth of approx. 1 m, spaced 12 m apart (Hoogerkamp and Donker, 1979). At the end of 1981 grass was sown and the parcel has since then been used for grazing cattle/sheep and fodder production. In October and November 1983 earthworms (*Aporrectodea caliginosa, A. longa, Lumbricus rubellus and L. terrestris*) were inoculated on one side of the parcel. After 0.5 year earthworms started to spread into the parcel (Ligthart and Peek, in press). The area not colonized by the inoculated earthworms is called the 'no-earthworm' site.

Due to earthworm activity the soil structure changed from a superficial medium platy structure (FAO, 1990b) overlying coarse prisms consisting of coarse angular blocky elements, into a 2.5 cm thick Ah horizon with a fine/medium subangular blocky structure over medium sized prisms of medium angular blocky elements (Ligthart and Van Breemen, subm.).

In the summer of 1992 the green phase of *Allolobophora chlorotica* had invaded the pasture, especially at the 'no-earthworm' site (unpublished data). This species was most likely introduced by spreading farmyard manure. Before 1992 *A. chlorotica* was only present in small numbers at a few isolated spots (Ligthart and Peek, in press). *A. chlorotica* lives near the roots of plants (Sims and Gerard, 1985) and probably has a superficial burrow system. This infestation with *A. chlorotica* will reduce any contrast between hydraulic conductivities in the area colonized by the inoculated species and the 'no-earthworm' site after 1991.

A second site, with comparable soil and land use, the DLO-Institute for Animal Science and Health (ID-DLO) at Lelystad, 7 km SW of APM, was also used in this study. ID-DLO also has a Calcaric Fluvisol (silt loam texture), but it lacks the sand layer at 35 cm depth present at the APM site, although its sedimentary make-up was otherwise similar (Ligthart and Van Breemen, subm.). Grass was sown in the spring of 1971 and in the end of 1971 earthworms (species as at APM) were inoculated (Hoogerkamp and Donker, 1979).

### K at saturation 7.2.2

$K_{sat}$ was measured twice, first at APM in early April 1992 when the field had been free of cattle for at least three months. A single ring infiltrometer of 30 cm

***Table 7.1** Saturated hydraulic conductivity (mean and SD) in relation with duration of earthworm presence, burrow density $N_A$ at 0.05 m, pressure head at soil surface and hydraulic gradient.*

| earthworm presence (y) | $K_{sat}$ ($10^{-5}$ m.s$^{-1}$) | $N_A$ (m$^{-2}$) | $h$ (kPa) | $\Delta H/\Delta z$ (.) | n |
|---|---|---|---|---|---|
| 0.0 | 0.74 ± 0.27 a* | 0.0 | 0.47 ± 0.24 | 2.2 ± 0.3 | 3 |
| 0.9 | 6.36 ± 4.02 ab | 407.4 | -0.10 ± 0.52 | 1.0 ± 1.0 | 3 |
| 3.3 | 7.34 ± 2.43 ab | 830.3 | -0.24 ± 0.31 | 1.8 ± 1.6 | 3 |
| 5.7 | 9.86 ± 5.84 b | 609.9 | -0.66 ± 0.33 | 0.4 ± 0.5 | 3 |
| 8.0 | 3.06 ± 2.20 ab | 555.3 | -0.39 ± 0.12 | -0.2 ± 1.8 | 2 |

*Group at the 0.05 level.

diameter and 10 cm height was used without making use of a confined column. The ring was inserted through the sward into the soil. Using a Mariotte device water was infiltrated at a head of 0.2 kPa into the initially moist to wet ($h$ = -4.5 kPa) soil. Two tensiometers (at 2.5 and 6.0 cm depth) were used to calculate the hydraulic gradient. Triplicate measurements were made at plots with 0.9 to 8.0 y of earthworm presence and at a 'no-earthworm' plot (Table 7.1). Actual measurements started when steady state was reached. In case of air leakage into the head space of the infiltrometer or when the surface soil outside the infiltrometer became noticeably wetter during measurement, measurements were discarded.

Numerical density of earthworm burrows ($N_A$, m$^{-2}$) was measured at APM in the chronosequence of earthworm activity at depths of 5, 10, 15 and 35 cm in July 1992 (Ligthart and Van Breemen, subm.). The numerical density strongly increased during the first three to four years after colonization by earthworms, and later stabilized at a lower level. Values of $K_{sat}$ will be related to $N_A$ at 5 cm depth (Tables 7.1 and 7.2). To interpolate between measured $N_A$ values the data were fitted with a fourth-order polynomial (Fig. 7.1).

The second measurement of $K_{sat}$ took place in April 1993 after removing the crust from the confined soil columns prepared for the suction crust infiltrometer (see section 7.2.6). Before measuring $K_{sat}$ a methylene blue solution was poured onto the surface to stain surface-connected burrows. These burrows (≥ 2 mm diameter) were counted directly below the ring at 10 cm depth and at 20 cm depth.

***Table 7.2** Correlations (R) and 2-tailed significance (p) between $K_{sat}$, duration of earthworm presence (Time), burrow density ($N_A$), pressure head at surface (h0), pressure head at 6 cm depth ($h_{-6}$) and hydraulic gradient ($\Delta H/\Delta z$). n=14.*

| | $K_{sat}$ | | Time | | $N_A$ | | $h_0$ | | $h_{-6}$ | | $\Delta H/\Delta z$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | R | p | R | p | R | p | R | p | R | p | R | p |
| $K_{sat}$ | 1 | . | 0.284 | 0.324 | 0.571 | 0.033 | -0.805 | 0.001 | -0.442 | 0.113 | -0.357 | 0.210 |
| Time | 0.284 | 0.324 | 1 | . | 0.614 | 0.020 | -0.661 | 0.010 | 0.066 | 0.822 | -0.570 | 0.033 |
| $N_A$ | 0.571 | 0.033 | 0.614 | 0.020 | 1 | . | -0.652 | 0.012 | -0.270 | 0.351 | -0.256 | 0.378 |
| $h_0$ | -0.805 | 0.001 | -0.661 | 0.010 | -0.652 | 0.012 | 1 | . | 0.147 | 0.616 | 0.705 | 0.005 |
| $h_{-6}$ | -0.442 | 0.113 | 0.066 | 0.822 | -0.270 | 0.351 | 0.147 | 0.616 | 1 | . | -0.564 | 0.036 |
| $\Delta H/\Delta z$ | -0.357 | 0.210 | -0.570 | 0.033 | -0.256 | 0.378 | 0.705 | 0.005 | -0.564 | 0.036 | 1 | . |

### K of individual burrows 7.2.3

In October 1993 the saturated hydraulic conductivity of individual surface open burrows ($K_b$, $m^3.s^{-1}$) was measured (Fig. 7.2) at three areas (*c.* 0.1 $m^2$) in the oldest part of the chronosequence (APM). The first two cm of soil were removed after staining surface-connected burrows by a methylene blue solution. Saturated hydraulic conductivity was then measured by infiltrating water through a needle inserted into the burrow, at a rate which kept a water level just below the entrance of the burrow (Bouma et al., 1982). After the rate had been constant for some minutes its value was assessed. At the time of measurement the soil was moist, so sorptivity effects were assumed to be negligible. Afterwards water-diluted latex paint was injected into the burrow to visualize macropores connected with the burrow. The diameter of the burrow at 2 cm depth and its maximum depth ($z_b$) were recorded.

### Surface-connected burrows

7.2.4 In 1992 two earthworm burrow systems were mapped three-dimensionally (Ligthart and Van Breemen, subm.) at APM and at ID-DLO. The systems differed in burrow density $N_A$ (APM: 2056 $m^{-2}$, ID-DLO: 6163 $m^2$) and duration of earthworm presence (APM: 8.3 y, ID-DLO: 20.3 y). The earthworm populations at APM were largely (80 %) in aestivation, while at ID-DLO the earthworms were fully active. Surface-connected burrows had been stained before mapping by ponding the surface with 0.05 $m^3.m^{-2}$ methylene blue solution.

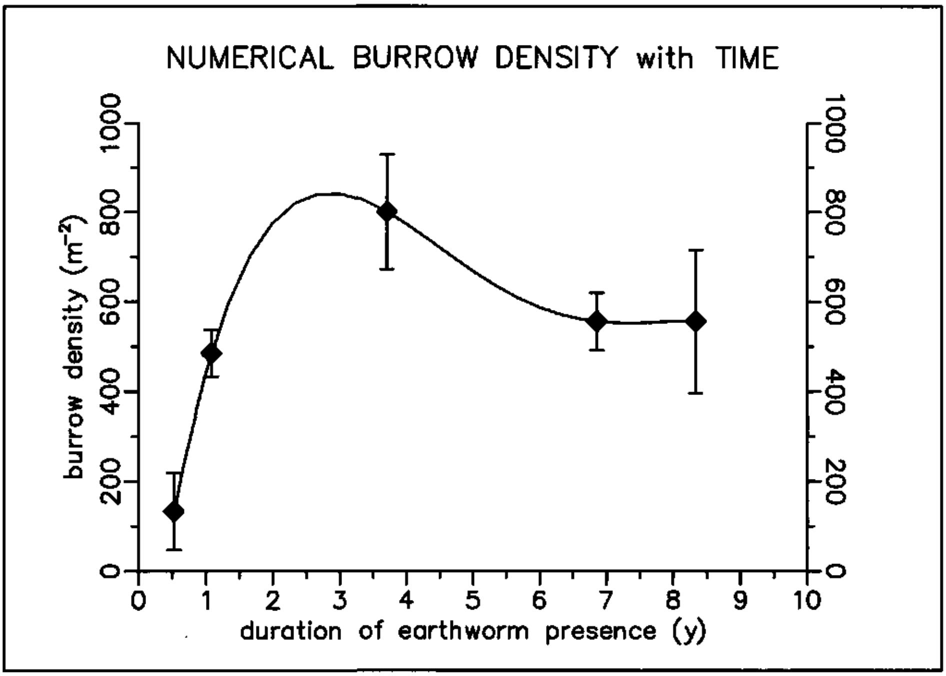


*Fig. 7.1 Observations (mean ± SD) and 4th order polynomial fit of burrow density $N_A$ (m$^{-2}$) at 0.05 m depth with duration of earthworm presence (y) for APM site.*

### 7.2.5 Pore system around burrows

Lining of the burrow wall or compaction of the soil matrix around a burrow appeared to be absent in horizontally orientated thin sections (7.5 by 7.5 cm) taken in triplo at 2.5 and 22.5 cm depth at 0.6 to 7.3 y of earthworm presence (Ligthart and Peek, in press). Lining or compaction were expected to result in an increase in the percentage of large pores and, consequently, a decrease in the percentage of small pores with distance from the burrow. To verify the visual observations six representative burrows were analyzed with the image analyzer Quantimet 570 (Leica Cambridge Ltd.). Reliable detection of pores requires a clear contrast with other soil components (organic and mineral materials). Photograms with voids black and other components grey or white were made following a procedure described Kooistra by (1991) based on Jongerius et al. (1972) and Ismail (1975).

Photograms (2.5 by 3 cm) were made with the burrow in center or, in case of burrows ≥ 5 mm, with the burrow wall at one side of the photogram (Fig. 7.3a). Of one large burrow (no. 1) two photograms were made, photogram 1a covered an adjacent void filled with earthworm casts, while 1b was situated in the soil matrix not affected by earthworms (Table 7.3). The area used in the analysis (1.25 by 1.25

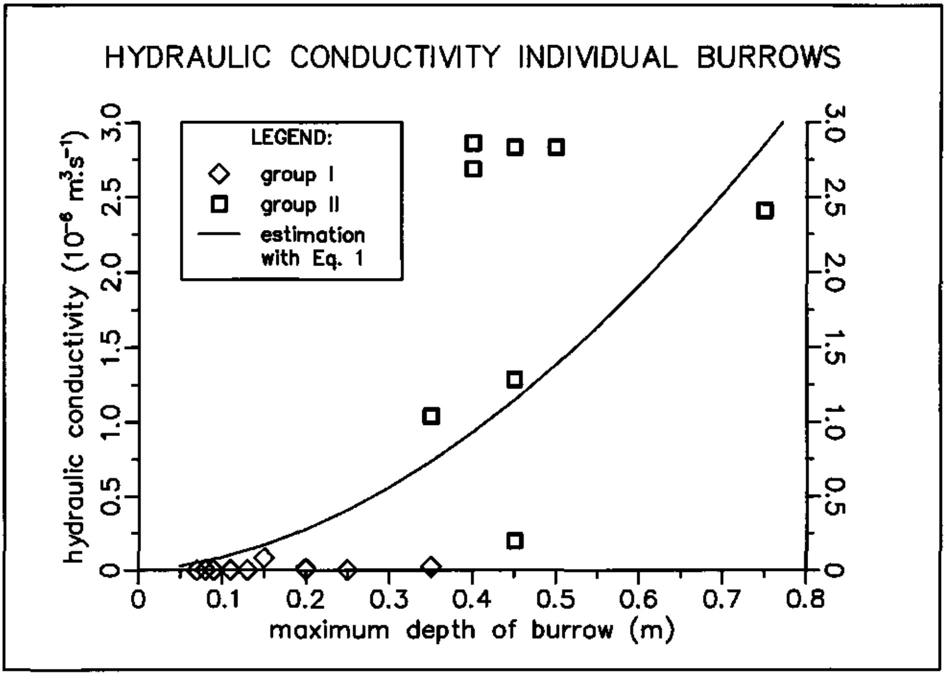


*Fig. 7.2 Measured and estimated (Eq. 7.1) saturated hydraulic conductivity of individual surface open burrows, $K_b$ ($m^3.s^{-1}$), in relation with their maximum obtained depth, $z_b$ (m). Group I, low conductivity ($\leq 10^{-7}$ $m^3.s^{-1}$), group II high conductivity ($> 10^{-7}$ $m^3.s^{-1}$).*

cm) allowed a pixel size of 25 × 25 μm (625 $\mu m^2$) (Fig. 7.3). The grey level at which pores (black) were detected, was estimated for each image with a line profile crossing the burrow and other pores. Pore sizes were measured in 15 concentric zones of 7 pixels wide (175 μm) around the burrow. The first zone was created in three steps: 1) separate burrow from pores connected to it, 2) circular dilation of burrow with 7 pixels, and 3) subtraction of burrow from the dilated burrow. The 14 successive zones were created by: 1) dilation of the preceding zone with 7 pixels followed by 2) subtraction of the preceding zone from the dilated zone. Pores protruding outside a zone were truncated and their sizes were thus underestimated. Pore size was divided into six classes and expressed as area density ($m^2.m^{-2}$).

### $K_{(sat)}$ and $K$ near saturation 7.2.6

Bouma (1982) proposed to use the symbol $K_{(sat)}$ for the hydraulic conductivity of a soil with a saturated matrix, but with air-filled macropores. The value of $K_{(sat)}$ may be much smaller than that of true $K_{sat}$ measured with water-filled macropores

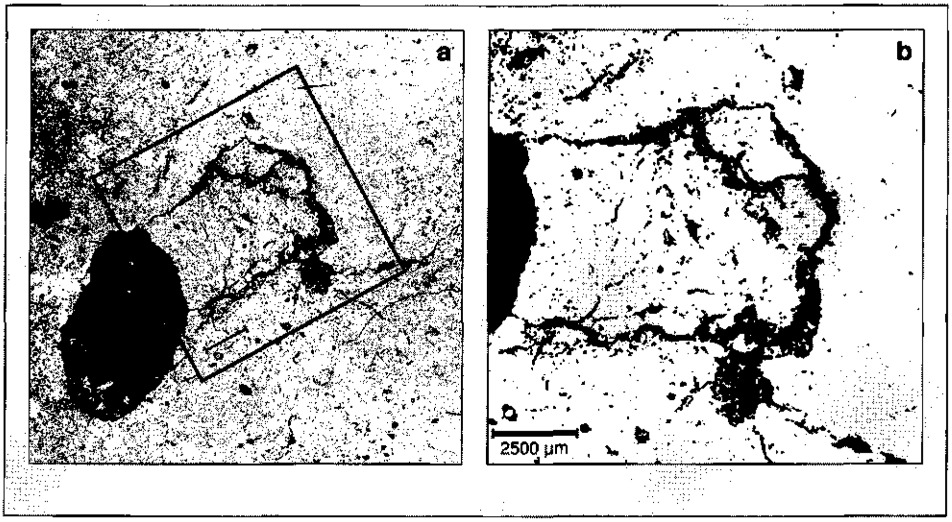


*Fig. 7.3 a. Photogram of burrow 1 (Table 7.3) in which pores are black and other materials are grey or white. Inserted frame shows burrow 1a. b. Digitized pore space of burrow 1a. Bars indicate 2500 µm.*

(Bouma, 1982, Booltink et al., 1991). Triplicate in situ measurements of $K_{(sat)}$ and of $K$ near saturation were made with a suction crust infiltrometer (30 cm diameter) at a plot with 9.1 y earthworm presence and at a 'no-earthworm' plot in April 1993 following the procedure described by (Booltink et al., 1991). *A. chlorotica* was, however, present at the 'no-earthworm' plot. Taking care not to smear the soil surface the first two cm of soil were removed and the infiltrometer was installed. Infiltration at five pressure heads (Fig. 7.5 and 7.6) in the range of -0.1 to -1.0 kPa was obtained with a connected Mariotte device. Pressure heads directly below the crust were calculated from tensiometer readings at 2.0 and 5.5 cm depth.

To compare the $K$ - $h$ relations between the two treatments the data were standardized in the range from -0.75 to 0.0 kPa at intervals of 0.05 kPa by fitting an exponential relation between $K$ and $h$: $K = a + b(h) + c(exp(h))$.

### 7.2.7 K at unsaturated conditions

The hydraulic conductivity of the unsaturated matrix was estimated from water content measurements in 300 cc rings taken at 2 and 20 cm depth close to the four burrow systems mapped in August-September 1991 (Ligthart and Peek, in press) and at a 'no-earthworm' plot. The water content $\Theta$ was measured at saturation, at -2.0 to -126 kPa using the one step outflow method (Parker et al., 1985) and at

-1600 kPa using a pressure pan (data not shown). The Van Genuchten parameters ($\Theta_r$, $\alpha$, $n$, and $K_s$) describing the $\Theta$-$h$ relation were then estimated from 5 to 6 measured $\Theta$-$h$ points, among which $\Theta_s$, with the program SFIT (Kool and Parker, 1987). Three optimization runs, using random perturbed starting parameter values, yielded three possible sets of (non-unique) solutions for the Van Genuchten parameters for each sample. The set with the best fit was selected. The $K$-$h$ relation was estimated with the parameter $l$, also generated by SFIT. For each sample $K$ was predicted in the range of -2.0 to -200 kPa (Fig. 7.7). $K$ was not extrapolated to less negative $h$ values, as results may become questionable (Leummens et al., 1995).

## Results and discussion 7.3

### *K* at saturation 7.3.1

The use of a ring infiltrometer without taking precautions to force one-dimensional flow could lead to divergence of the flow below the ring. The burrows are highly vertical (Ligthart et al., 1993, Ligthart and Peek, in press) and presumably enforce one-dimensional saturated flow. Divergence of flow is expected to cause steep gradients and unsaturated conditions below the ring at the deepest (6 cm) tensiometer, especially at low burrow density. Both the gradient and the pressure head at 6 cm depth did not show a significant relation (respectively $p=0.38$ and $p=0.35$) with burrow density ($N_A$) (Table 7.2), so one-dimensional flow may be assumed.

As the pasture had not been grazed for three months, destruction of macropores by trampling was absent and differences within the chronosequence would have been maximal. The saturated hydraulic conductivity was significantly correlated ($p= 0.03$) with $N_A$ though not ($p= 0.33$) with duration of earthworm presence (Table 7.2). It appeared that mean $K_{sat}$ only differed significantly ($p \leq 0.05$) between its lowest and highest value which was found after 5.7 y of earthworm presence (Table 7.1). $K_{sat}$ showed to be inversely proportional to the pressure head at the surface (Table 7.2); high $K_{sat}$ values ($>5.95 \times 10^{-5}$ m.s$^{-1}$) led to negative pressure heads. Probably the matrix could not reach saturation due to bypass effects.

Saturated conductivities measured in April 1993 after removal of the crust (suction crust infiltrometer) were not correlated ($p>0.5$) with the number of surface open burrows at 0.1 and 0.2 m depth, nor ($p \geq 0.5$) with the total burrow density at those depths (Fig. 7.5). An effect of duration of earthworm presence ('no-earthworm' and 9.1 y) on $K_{sat}$ was also absent ($p=0.85$). The $K_{sat}$ values were all below the measured or estimated values of $K_{(sat)}$ at zero pressure head (Fig. 7.5). A possible explanation is that infiltration induced slaking at and near the surface of

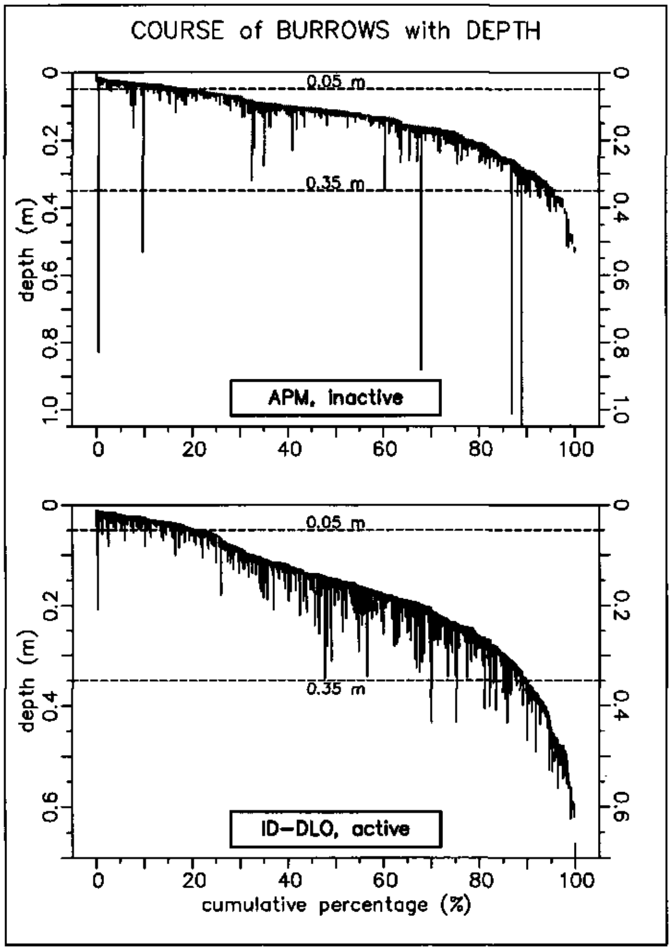


*Fig. 7.4 The course of surface-connected burrows, indicated by a line from top to bottom, with depth (m) in a burrow system mapped during earthworm aestivation at APM and in a burrow system related to active earthworms at ID-DLO.*

the very silty (70% silt) soil and so reduced $K_{sat}$. A superficial layer with reduced conductivity also explains the occurrence negative pressure heads at the soil surface (estimated from the observed gradient) during infiltration (Fig. 7.5).

## 7.3.2 *K* of individual burrows

Smettem (1986, 1992) demonstrated that the flux $q$ ($cm^3.h^{-1}$) through a burrow, discharging into the matrix, strongly depends on the water-filled burrow length $h$

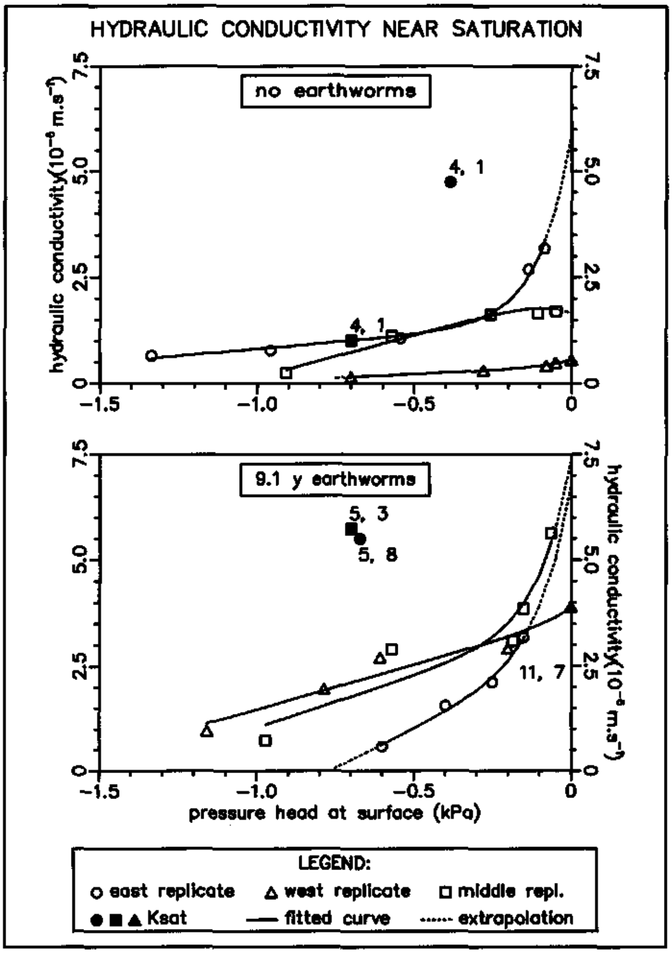


*Fig. 7.5 $K_{sat}$, $K_{(sat)}$ and K near saturation ($m.s^{-1}$) in the 'no-earthworm' site and at 9.1 y of earthworm presence. Solid symbols give $K_{sat}$ measured after removal of crust (crust infiltrometer), numbers near solid symbol indicate the number of surface-connected burrows at respectively 0.1 and 0.2 m depth.*

(cm) and the burrow diameter $a$ (cm). If capillary absorption can be neglected, as in our case, the relation is:

$$q = K_{(sat)} * a^2 * \frac{h}{a}(4.117\frac{h}{a} * (\ln(2\frac{h}{a}) - 1)^{-1}) \qquad (7.1)$$

For our experiment $h$ will be the maximum depth obtained by a burrow ($z_b$). The relation of $q$ with $z_b$, taking $K_{(sat)}$ 5.98 × $10^{-6}$ $m.s^{-1}$ (see Fig. 7.5) and taking for $a$ the mean burrow diameter (4.3 mm), is given in Fig. 7.2. Clearly, measured values of

$K_b$ differ from the values predicted from Eq. 7.1.

Multiple regression analysis that $z_b$ governed $K_b$ (standardized regression coefficient Beta=0.79, p=0.001), while burrow diameter did not (Beta=-0.03, p=0.88). Based on $K_b$ (Fig. 7.2) two groups of burrows could be distinguished: burrows ending above 0.35 m depth with very low conductivities (group I, $K_b \leq 10^{-7}$ $m^3.s^{-1}$, mean $1.2 \times 10^{-8} \pm 2.4 \times 10^{8}$ ) and burrows ending below 0.35 m with generally much higher conductivities (group II, $2.1 \times 10^{-6} \pm 1.0 \times 10^{6}$ $m^3.s^{1}$). The difference between the two groups was highly significant ($p<0.00005$). Within a group $K_b$ was not related to $z_b$.

The sudden increase in $K_b$ for burrows ending below 0.35 m is explained by the soil structural profile. Below 0.35 m depth, clay-rich sedimentary layers are present. Due to physical ripening a network of cracks, up to several millimeters wide, developed there which separates elements of *c.* 10 cm width. Infiltration with latex paint showed that these cracks were connected to the burrows and acted as an effective sink for the infiltrating solution. Assuming an equal $K_{(sat)}$ for all burrows (Smettem, 1992) is not realistic under these circumstances and probably contributed to the discrepancy between the $K_b$ values estimated with Eq. 7.1 and the measured values.

### 7.3.3 Surface-connected burrows

The 8.3 y old APM burrow system (Fig. 7.4) was dominated by relatively short, vertical burrows in the upper 0.4 m. Below 0.4 m a few long vertical burrows continued. The 20.3 y system at ID-DLO (Fig. 7.4) had many shallow (up to 0.07 m depth) and horizontal burrows underlain by a thin (± 0.05 m) zone with fewer burrows and abundant vertical burrows between 0.1 and 0.4 m depth of which few continued deeper. The difference in architecture between the APM and ID-DLO systems is probably related to a difference in state of activity caused by better capillary water supply at ID-DLO (Ligthart and Van Breemen, subm.).

Surface-connected (methylene blue stained) burrows did not necessarily begin close to the surface, but could start at nearly any depth, both at APM and ID-DLO. Clearly, surface-connected burrows starting well below the soil surface must have received the methylene blue solution through other macropores. Apparently, and contrary to the assumption by Kretzschmar (1988), the contribution of an earthworm burrow system to water infiltration need not be influenced greatly by the prevailing earthworm activity, and may still be high when many animals are aestivating as at APM.

As mentioned before, $K_b$ of surface open burrows ending in the sedimentary layering was relatively high. The mapping of earthworm burrows was difficult in the first few centimeters (Ligthart and Peek, in press). We therefor assumed that surface-connected burrows starting within 5 cm depth function as if they are surface open burrows. Surface open burrows ending in the sedimentary layering (depth $\geq$ 0.35 m) will control $K_{sat}$ of the burrow system to a large extent. However, the number of these highly conductive burrows appeared to be very low (2 per 0.25 $m^2$) at APM and nil (per 0.09 $m^2$) at ID-DLO (Fig. 7.4).

Even under these circumstances the effect of earthworm burrows on $K_{sat}$ should be noticeable. Assuming 8 highly conductive burrows per $m^2$ at APM, each with a $K_b$ $2.1 \times 10^{-6}$ $m^3.s^{-1}$, results in a contribution to $K_{sat}$ of $1.68 \times 10^{-5}$ $m.s^{-1}$. Adding $K_{sat}$ of the matrix without earthworms ($0.74 \times 10^{-5}$ $m.s^{-1}$) yields a $K_{sat}$ of $2.42 \times 10^{-5} m.s^{-1}$. This value has the same order as $K_{sat}$ at 8.0 y of earthworm activity ($3.06 \times 10^{-5}$ $m.s^{-1}$).

### The pore system around burrows 7.3.4

Absence of compaction of the soil matrix around a burrow was confirmed by quantitative analysis, which did not reveal a decrease of the smallest pore class with distance from the burrow wall (Table 7.3). In three (burrows 1a, 2, and 6) of the seven cases, however, the abundance of large pores (>40000 $\mu m^2$) increased with distance. Only for burrow 1a this could be related to compaction of cast material nearby the burrow (Fig. 7.3, Table 7.3). It appears that the soil matrix immediately adjacent to burrows has in general a pore system very similar to that of the normal matrix, and so does not hamper the transport of water into the matrix.

### $K_{(sat)}$ and $K$ near saturation 7.3.5

Conductivities showed an exponential increase with negative pressure head (Fig. 7.5). For some cases standardized data were obtained by extrapolation of the fitted curves to 0.0 or -0.75 kPa. Earthworms significantly ($p \geq 0.05$) increased $K$ in the $h$ range of -0.15 to -0.30 kPa. This range expanded to -0.05 to -0.45 kPa when taking the confidence limit at 0.1 (Fig. 7.6). Translating the pressure ranges into ranges of equivalent pore diameters (Bouma, 1991) it appears that an increase in burrows (up to 5.6 mm diameter, $p=0.10$) and smaller earthworm-affected macropores ($\geq$ 0.6 mm, $p=0.10$) are the cause of the increase in $K$ (Fig. 7.6).

Soils with macropores have been described as two-domain systems; one domain is the matrix, the other consists of the macropores (Beven and Germann, 1982, Smettem, 1992). A bisection in the pore system should be reflected by a bias or twist in the $K$ - $h$ relation. Indeed three samples (Fig. 7.5) indicate such a bias at a $h$ of approximately 0.25 kPa, or an equivalent pore diameter of 1.1 mm. These in-

**TABLE 7.3** *Duration of earthworm presence, depth of sample, nature of soil material and correlation (R) of pore areal density ($m^2.m^{-2}$) per pore size class for the seven analyzed burrows. Nature of material: C, earthworm cast, UM, matrix unaffected by earthworms, CM, matrix consisting of reworked casts and I, infilling of non-earthworm origin.*

| | burrow number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1a | 1b | 2 | 3 | 4 | 5 | 6 | all burrows |
| earthworm presence (y) | 0.9 | 0.9 | 4.1 | 7.3 | 7.3 | 4.1 | 7.3 | . |
| depth (m) | 0.025 | 0.025 | 0.025 | 0.025 | 0.025 | 0.225 | 0.225 | . |
| nature soil material | C | UM | C | CM | CM | UM,I | UM | . |
| ≤ 625 μm$^2$ | 0.10 | 0.46 | -0.49 | 0.21 | -0.75$^{**}$ | -0.44 | -0.01 | -0.16 |
| > 625 - ≤ 1250 μm$^2$ | 0.17 | 0.30 | -0.36 | 0.34 | 0.10 | -0.51 | -0.24 | -0.01 |
| > 1250 - ≤ 2500 μm$^2$ | -0.05 | 0.48 | -0.17 | 0.13 | -0.50 | 0.01 | -0.1 | -0.03 |
| > 2500 - 10000 μm$^2$ | 0.37 | 0.34 | -0.63$^*$ | -0.06 | -0.49 | -0.44 | -0.54$^*$ | -0.14 |
| > 10000 - ≤ 40000 μm$^2$ | 0.59$^*$ | -0.19 | 0.14 | -0.25 | -0.26 | -0.56$^*$ | -0.41 | -0.05 |
| > 40000 μm$^2$ | 0.58$^*$ | -0.19 | 0.86$^{**}$ | 0.42 | 0.46 | 0.42 | 0.77$^{**}$ | 0.24$^*$ |
| total pore population | 0.85$^{**}$ | 0.05 | 0.89$^{**}$ | 0.27 | -0.32 | -0.01 | 0.69$^{**}$ | 0.18 |

Significance of correlation: $^*$ $p \leq 0.05$, $^{**}$ $p \leq 0.01$.

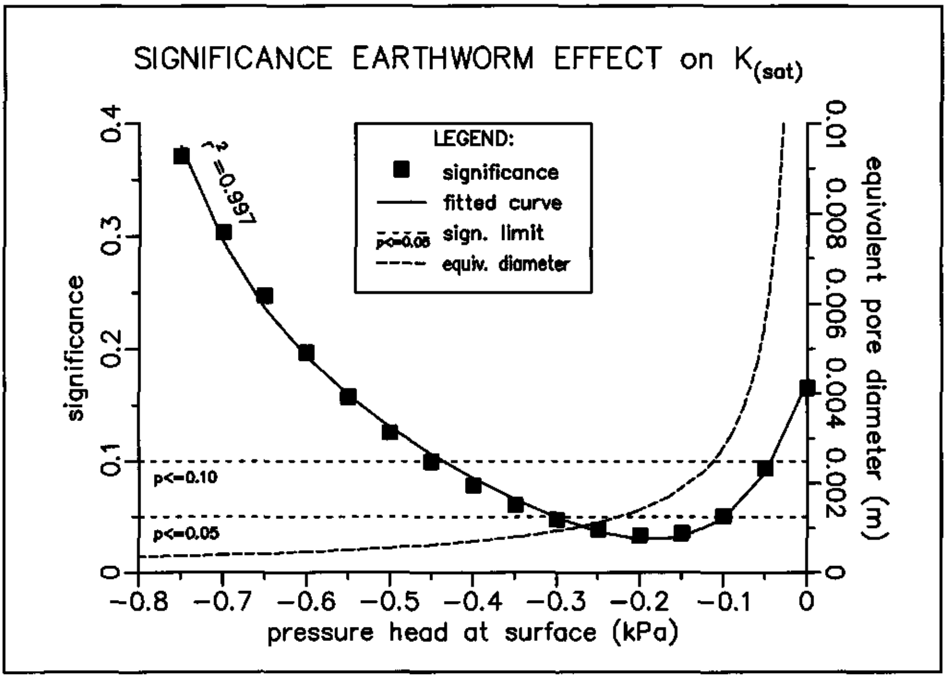


*Fig. 7.6 Significance of effect of earthworm presence on K ($m.s^{-1}$) with pressure head (kPa) and associated equivalent pore diameter (m).*

clude, however, one 'no-earthworm' sample, where the bias probably can be ascribed to the presence of inter-aggregate macropores (cracks).

### *K* at unsaturated conditions 7.3.6

Unsaturated hydraulic conductivity, $K_{unsat}$, showed a highly significant increase with duration of earthworm presence (Table 7.4, Fig. 7.7). This illustrates the development of an earthworm-induced Ah horizon with a changed soil meso- and micropore system. Remarkably the variation in *K* increased with earthworm presence (Fig. 7.7). The decrease of *K* with depth (R=-0.09, p=0.000) shows the impact of earthworms on the soil structure (the non-burrow pores) diminishing with depth (Lee, 1992, Tomlin et al., 1992). At 0.2 m depth, where the influence of earthworms will be strongly limited, the effect of duration of earthworm presence appeared to be significant, but $K_{unsat}$ did not steadily increase. The highest mean conductivity was found at 7.3 y, while the lowest were found at 4.1 and 1.0 y. At 0.2 m depth the variability in *K* is probably of a spatial origin and not due to variations in earthworm activity.

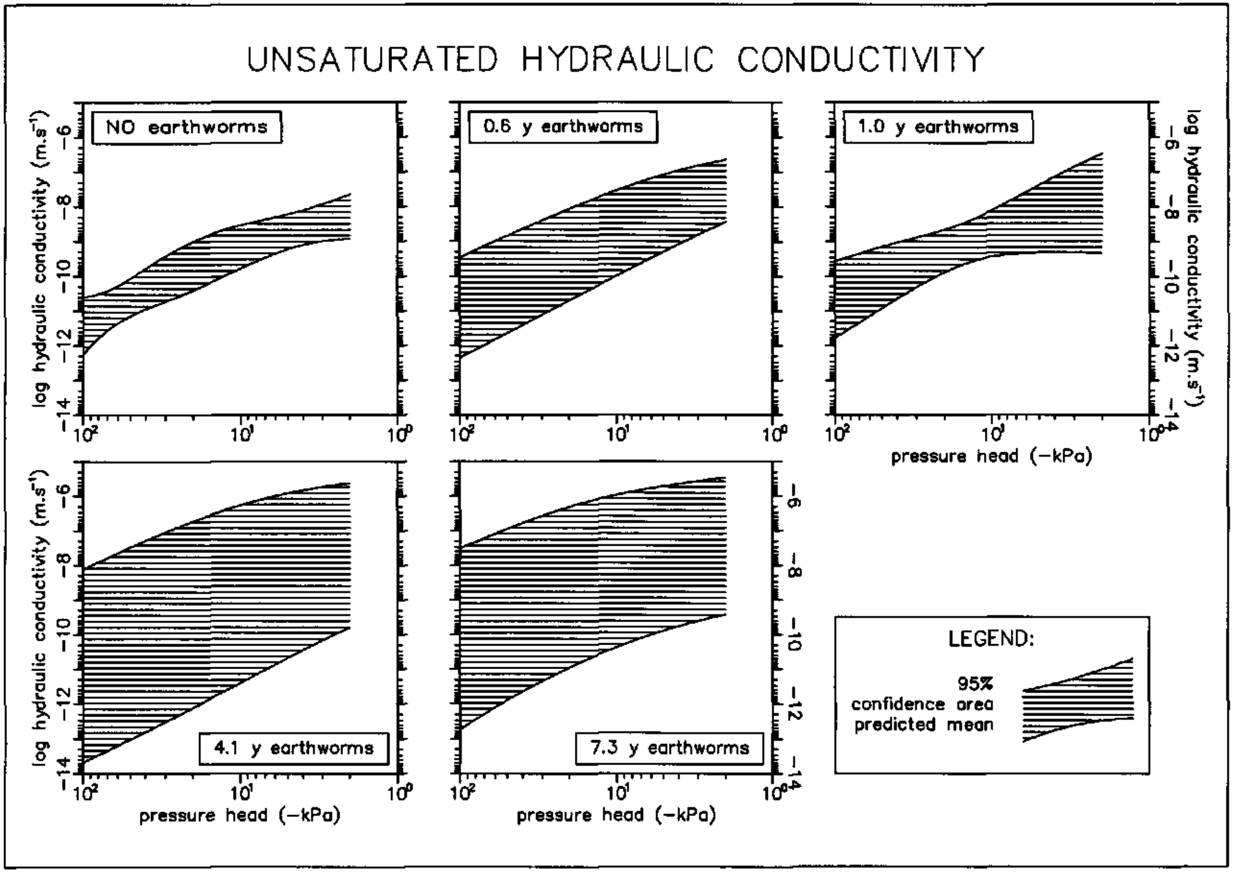


*Fig. 7.7 Confidence area (95%) of predicted mean unsaturated hydraulic conductivity ($m.s^{-1}$) with pressure head (kPa) from no earthworm presence up to 7.3 y of earthworm presence.*

***Table 7.4** Effect of duration of earthworm presence on $\log K_{unsat}$ (mean ± SE, $m.s^{-1}$), groups significantly different at the 2-sided 0.05 level within a column and significance of the earthworm effect at 0 and 0.2 m depth.*

| | **0.0 m** | | | **0.2 m** | | |
|---|---|---|---|---|---|---|
| earthworm presence (y) | log*K* | group* | n | log*K* | group* | n |
| 0.0 | -9.21 ± 0.04 | a | 480 | -9.16 ± 0.07 | b | 320 |
| 0.6 | -8.70 ± 0.05 | b | 480 | -8.40 ± 0.10 | c | 160 |
| 1.0 | -8.78 ± 0.04 | b | 480 | -9.51 ± 0.06 | a | 640 |
| 4.1 | -8.79 ± 0.06 | b | 480 | -9.66 ± 0.06 | a | 480 |
| 7.3 | -8.23 ± 0.05 | c | 480 | -7.69 ± 0.07 | d | 480 |

*Significance of earthworm effect < 0.0001

***TABLE 7.5** Rainfall rates ($m.s^{-1}$) at recurrence time $T_p$ of 0.2, 0.33, 0.5 and 1 year for rain events of 5 to 60 minutes duration. Rates have to be compared with K at -0.15 kPa, which is at 9.1 year of earthworm presence $3.48 \times 10^{-6}$ $m.s^{-1}$.*

| | $T_p$ (y) | | | |
|---|---|---|---|---|
| Duration (minutes) | 0.20 | 0.33 | 0.50 | 1.00 |
| 5 | $7.18 \times 10^{-6}$ | $1.06 \times 10^{-5}$ | $1.33 \times 10^{-5}$ | $1.80 \times 10^{-5}$ |
| 15 | $3.35 \times 10^{-6}$ | $5.48 \times 10^{-6}$ | $7.25 \times 10^{-6}$ | $1.02 \times 10^{-5}$ |
| 30 | $2.13 \times 10^{-6}$ | $3.51 \times 10^{-6}$ | $4.65 \times 10^{-6}$ | $6.56 \times 10^{-6}$ |
| 45 | $1.77 \times 10^{-6}$ | $2.76 \times 10^{-6}$ | $3.59 \times 10^{-6}$ | $4.97 \times 10^{-6}$ |
| 60 | $1.53 \times 10^{-6}$ | $2.32 \times 10^{-6}$ | $2.97 \times 10^{-6}$ | $4.06 \times 10^{-6}$ |

### When do earthworm burrow systems conduct rain water? 7.3.7

At a pressure head of -0.15 kPa burrows of ≥ 1.9 mm diameter become water-filled and contribute to the drainage of the soil. At 9.1 y of earthworm presence *K* at -0.15 kPa was $3.48 \times 10^{-6}$ $m.s^{-1}$. When this value of *K* is exceeded by the rain intensity, water will start to pond at the soil surface. At time T(c) (Booltink and Bouma, 1993) surface-stored water will flow into surface-connected macropores. The value of T(c) mainly depends on rain intensity and initial pressure head. At APM an initial pressure head of 25 kPa was considered realistic and T(c) was assumed to be between 30 and 45 minutes (estimated from Booltink and Bouma, 1993). The annual frequency of rainfall events with a duration equal to T(c), and the associated rainfall rate, can now be computed (Buishand and Velds, 1980). For T(c)= 30 minutes the rainfall rate ($3.51 \times 10^{-6}$ $m.s^{-1}$) exceeds $K$ at -0.15 kPa three times per year (Table 7.5). In case T(c) is 45 minutes, the rainfall rate ($3.59 \times 10^{-6}$ $m.s^{-1}$) exceeds $K$ only 2 times per year.

Ponding, however, will occur earlier at a given rainfall rate at the 'no-earthworms' site than in the situation with earthworms, as the unsaturated hydraulic conductivity of the topsoil increases with duration of earthworm presence. Flow through macropores will thus occur most frequently in a situation without earthworms.

## 7.4 Conclusions

Earthworms did increase hydraulic conductivities from full saturation of the soil down to unsaturated soil matrix conditions. This impact of earthworms on the soil hydraulic conductivity is due to changes in the soil structure induced by earthworm activity. The presence of burrows increased $K_{sat}$ and $K$ close to saturation. The change from a platy structure of the topsoil to a finer subangular blocky structure was reflected in the increase of $K$ from a nearly saturated to an unsaturated soil matrix.

Earthworm burrows mainly affect the soil moisture regime at extreme conditions. Water flow through burrows can be substantial, but this happens only two to three times per year on average. However, bypass flow may occur more frequently at the 'no-earthworm' site, because of the lower $K$ of the matrix in the absence of earthworms.

True bypass effects may explain why at high values of $K_{sat}$ the matrix did not reach full saturation during $K_{sat}$ measurements. In these conditions more than two tensiometers are needed to reliably calculate hydraulic gradients.

The structure of the subsoil, which developed after reclamation of the lake sediments, strongly influenced the effect of earthworm burrows on $K_{sat}$. Burrows starting well below the soil surface were connected with the surface by intra-aggregate macropores. The drainage ability of surface open burrows was strongly increased by a network of cracks, which developed as a result of physical ripening of the sediment, below the plough layer. The connectivity of burrows with the soil matrix was not reduced as burrow walls did not show signs of linings nor had, in most cases, the soil surrounding the burrow been compacted by burrowing earthworms.

Simulation of the soil water economy should be used to clarify the effect of the more variable $K_{unsat}$ due to earthworm activity, as the consequence may be a more varied soil water economy. In this light the probable seasonal variation of $K$ also needs further attention.

## Acknowledgements

Discussion of draft versions of the manuscript by Dr. Ole Wendroth (Zentrum für Agrarlandschafts- und Landnutzungsforschung e.V., Müncheberg, Germany) and Johan Bouma, Nico van Breemen and Rienk Miedema (Dept. Soil Science & Geology) is highly valued by the author. This study was part of a project funded by the Netherlands Integrated Soil Research Programme.

## References

Beven, K. and Germann, P. (1982) Macropores and water flow in soils. *Water Resour. Res.* **18**, 1311-1325.

Booltink, H.W.G. and Bouma, J. (1991) Physical and morphological characterization of bypass flow in a well-structured clay soil. *Soil Sci. Soc. Am. J.* **55**, 1249-1254.

Booltink, H.W.G. and Bouma, J. (1993) Sensitivity analysis on processes affecting bypass flow. *Hydrological Processes* 7, 33-43.

Booltink, H.W.G., Bouma, J. and Giménez, D. (1991) Suction crust infiltrometer for measuring hydraulic conductivity of unsaturated soil near saturation. *Soil Sci. Soc. Am. J.* **55**, 566-568.

Bouma, J. (1982) Measuring the hydraulic conductivity of soil horizons with continuous macropores. *Soil Sci. Soc. Am. J.* **46**, 438-441.

Bouma, J. (1991) Influence of soil macroporosity on environmental quality. *Advances in Agronomy* **46**, 1-37.

Bouma, J., Belmans, C.F.M. and Dekker, L.W. (1982) Water infiltration and redistribution in a silt loam subsoil with vertical worm channels. *Soil Sci. Soc. Am. J.* **46**, 917-921.

Buishand, T.A. and Velds, C.A. (1980) *Neerslag en verdamping.* Klimaat van Nederland 1, KNMI (Royal Dutch Meteorological Institute), De Bilt, The Netherlands. 206 p. (In Dutch).

Dexter, A.R. (1978) Tunneling in soil by earthworms. *Soil Biol. Biochem.* **10**, 447-449.

Edwards, W.M., Norton, L.D. and Redmond, C.E., 1988. Characterizing macropores that affect infiltration into nontilled soil. *Soil Sci. Soc. Am. J.* **52**, 483-487.

Edwards, W.M., Shipitalo, M.J., Traina, S.J., Edwards, C.A. and Owens, L.B. (1992) Role of *Lumbricus terrestris* (L.) burrows on quality of infiltrating water. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24 (12)**, 1555-1561.

Ehlers, W. (1975) Observations on earthworm channels and infiltration on tilled and untilled loess soil. *Soil Science* **119**, 242-249.

FAO (1990a) *Soil map of the world, revised legend (reprinted).* Food and Agricultural Organization of the United Nations, UNESCO, International Soil Reference and Information Service FAO World Soils Resources Report 60, Rome.

FAO (1990b) *Guidelines for Soil Description.* (3rd ed.) Food and Agricultural Organization of the United Nations, International Soil Reference and Information Service, Rome.

Geyger, E.; (1979); Bodenstruktur und Regenwurm-Aktivität in einem Wiesenboden im Sölling; *Z. Pflanzenernähr. Bodenk.* **142**, 318 - 329. (In German)

Graff, O. and Makeschin, F. (1979) Der Einfluß der Fauna auf die Stoffverlagerung sowie die Homogenität und die Durchlässigkeit von Böden. *Z. Pflanzenernaehr. Bodenk.* **142**, 476-491. (In German)

Hoogerkamp, M. and Donker, W. (1979) *Aanleg van blijvend grasland op de bedrijven van instellingen voor landbouwkundig onderzoek nabij Lelystad.* Internal Report CABO, Wageningen and IVVO, Lelystad. 48 pp (In Dutch)

Hoogerkamp, H., Rogaar, H. and Eijsackers, H.J.P. (1983) Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. In: Satchel, J.E. (ed.) *Earthworm ecology* Chapman and Hall, London, 495 pp.

Ismail, S.N.A. (1975) Micromorphometric soil porosity characterization by means of electro-optical image analysis (Quantimet 720). *Soil Survey Papers* **9**, Soil Survey Inst., Wageningen, The Netherlands.

Jeanson, C. (1964) Micromorphologie et pédozoologie expérimentale. Contribution à l'étude sur plaques minces de grandes dimensions d'un sol artificiel structuré par les Lombricides. In: Jongerius, A. (ed.) *Soil Micromorphology*. Proc. 2nd Int. Working-meeting on Soil Micromorphology, Arnhem, The Netherlands, Sept. 22-25 1964. pp. 47-55. (In French)

Jongerius, A., Schoonderbeek, D. and Jager, A. (1972) The application of the Quantimet 720 in soil micromorphometry. *Microscope* **20**, 243-254.

Joschko, M., Söchtig, W. and Larink, O. (1992) Functional relationship between earthworm burrows and soil water movement in column experiments. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24 (12)**, 1545-1547.

Knight, D., Elliott, P.W., Anderson, J.M. and Scholefield, D. (1992) The role of earthworms in managed, permanent pastures in Devon, England. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24 (12)**, 1511-1517.

Kooistra, M.J. (1991) A micromorphological approach to the interactions between soil structure and soil biota. *Agric. Ecosystems Environ.* **34**, 315-328.

Kool, J.B. and Parker, J.C. (1987) *Estimating soil hydraulic properties from transient flow experiments: SFIT user's guide.* Electric Power Research Institute Palo Alto, California, USA.

Kretzschmar, A. (1982) Description des galeries de vers de terre et variation saisonnière des réseaux (observations en conditions naturelles). *Rev. Écol. Biol. Sol* **19**, 579-591. (In French)

Kretzschmar, A. (1987) Caracterisation microscopique de l'activite de lombriciens endoges. In: Fedoroff, N., Bresson, L.M. and Courty, M.A. (Editors) *Micromorphologie des Sol - Soil Micromorphology*, Proc. VIIth Int. Working Meeting Soil Micromorph., Paris, July 1985, Association Française pour l'Étude du Sol, Plaisir, France. pp. 325-330. (In French)

Kretzschmar, A. (1988) Structural parameters and functional patterns of simulated earthworm burrow systems. *Biol. Fert. Soils* **6**, 252-261.

Lee, K.E. (1985) *Earthworms their ecology and relationships with soils and land use.* Academic Press Australia, Sydney.

Lee, K.E. (1992) Some trends and opportunities in earthworm research or: Darwin's children - the future of our discipline. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24 (12)**, 1765-1771.

Leummens, H., Bouma, J. and Booltink, H.W.G. (1995) Interpreting differences among hydraulic parameters for different soil series by functional characterization. *Soil Sci. Soc. Am. J.* **59**, 344-351

Ligthart, T.N. and Van Breemen, N. (submitted) Density of earthworm burrow systems in permanent pastures in relation to earthworm mass density and earthworm activity. *Soil Biol. Biochem.*

Ligthart, T.N. and Peek, G.J.C.W. (in press) Evolution of earthworm burrow systems after inoculation of lumbricid earthworms in a pasture in the Netherlands. *Soil Biol. Biochem.*

Ligthart, T.N., Miedema, R. and Van Breemen, N. (revised) Modes and rates of destruction of artificial earthworm burrows in an intensively used pasture. *Soil Biol. Biochem.*

Ligthart, T.N., Peek, G.J.W.C. and Taber, E.J. (1993) A method for the three-dimensional mapping of earthworm burrow systems. In: L. Brussaard and M.J. Kooistra (Eds.), Int. Workshop on Methods of Research on Soil Structure/Soil Biota Interrelationships. *Geoderma* **57**, 129-141.

Parker, J.C., Kool, J.B. and Van Genuchten, M.Th. (1985) Determining soil hydraulic properties from one-step outflow experiments by parameter estimation: II Experimental studies. *Soil Sci. Soc. Am. J.* **49**, 1354-1359.

Stockdill, S.M.J. (1982) Effects of introduced earthworms on the productivity of New Zealand pastures. *Pedobiologia* **24**: 29-35.

Smettem, K.R.J. (1986) Analysis of water flow from cylindrical macropores. *Soil Sci. Soc. Am. J.* **50**, 1139-1142.

Smettem, K.R.J. (1992) The relation of earthworms to soil hydraulic properties. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24 (12)**, 1539-1543.

Shaw, C. and Pawluk, S. (1986) The development of soil structure by *Octolasium tyrtaeum, Apporectodea turgida* and *Lumbricus terrestris* in parent materials belonging to different textural classes. *Pedobiologia* **29**, 327-339.

Sims, R.W. and Gerard, B.M. (1985) *Earthworms.* Synopses of the British Fauna (New Series) no. 31., London.

Söchtig, W. and Larink, O. (1992) Effect of soil compaction on activity and biomass of endogeic lumbricids in arable soils. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24 (12)**, 1595-1599.

Stockdill, S.M.J. (1982) Effects of introduced earthworms on the productivity of New Zealand pastures. *Pedobiologia* **24**, 29-35.

Tomlin, A.D., McCabe, D. and Protz, R. (1992) Species composition and seasonal variation of earthworms and their effect on soil properties in Southern Ontario, Canada. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24 (12)**, 1451-1457.

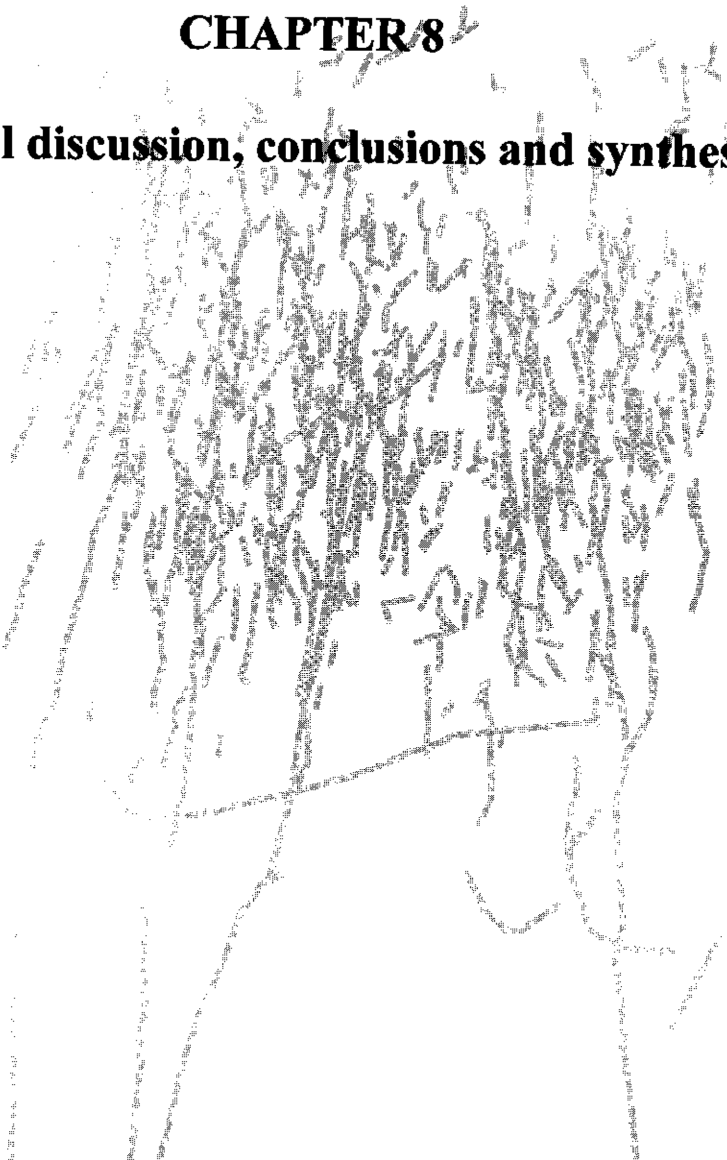
Urbánek, J. and Doležal, F. (1992) Review of some case studies on the abundance and on the hydraulic efficiency of earthworm channels in Czechoslovak soils with reference to the subsurface pipe drainage. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24 (12)**, 1563-1571.

West, L.T., Hendrix, P.F. and Bruce, R.R. (1991) Micromorphic observation of soil alteration by earthworms. *Agric. Ecosystems Environ.* **34**, 363-370.

White, G. (1789) The natural history and antiquity of Selborne. *Letter XXXV*, 216-217, London.

# CHAPTER 8

# General discussion, conclusions and synthesis



## Dispersal and development of earthworm community after inoculation 8.1

Dispersal of earthworms can both be active as passive (Schwert, 1980). Man can promote the spreading of earthworms, as is illustrated by the introduction of European species in North-America and Australia (Lee, 1985). Local dispersal rates depend on among others the type of land use and the species involved (Van Rhee, 1969, Hoogerkamp et al., 1983). Dispersal rates are generally higher in pasture than those in arable land (Marinissen, 1991), as pasture provides a more stable environment. Inoculation of earthworms may be followed by a lag phase, with no or only slow dispersal (Stockdill, 1982, Hoogerkamp et al., 1983). This lag phase may last up to 4 y (Stockdill, 1982). Dispersal rates in temperate pastures have been found to be in the range of 4 - 13 $m.y^{-1}$ (Van Rhee, 1969, Stockdill, 1982, Hoogerkamp et al., 1983, Stein et al., 1992). At the 'Ir. A.P. Minderhoudhoeve' (APM) the dispersal rate of the total community (*Aporrectodea caliginosa, A. longa, Lumbricus rubellus* and *L. terrestris*), based on a lag phase of 0.5 y, was in 1991 6.3 $m.y^{-1}$ (Ch. 3). Later the rate strongly increased up to 29.3 $m.y^{-1}$ between 1991 and 1994 (Fig. 8.1).

Earthworm biomass at APM peaked (0.364 $kg.m^{-2}$) at approximately 4 y after start of the dispersal, and seemed to stabilize afterwards at a lower level (Ch. 3, Ch. 4). The decrease in biomass after the peak is most likely related to reduced food supply. After approximately 4 y the O horizon, formed previously in the absence of earthworms, had almost completely been consumed.

*A. longa* was found to be the colonizing species at APM (Ch. 3, Ch. 4). Stein et al. (1992) studied an inoculation experiment at a site (ID-DLO) which was comparable to APM in soil, land use and inoculated species, they found *A. Longa* to be a slow colonizer. The soil profile at APM has a sand layer at 35 cm depth that hinders capillary rise, the sand layer is absent at ID-DLO (Ch. 3, Ch. 4). As a result the topsoil at APM dries out in dry summer periods, while below the sand layer the soil remains moist. The colonizing behaviour of *A. longa* at APM is most probably explained by the drying out of the top soil. Contrary to *A. caliginosa*, *A. longa* is a deep-burrowing species (Sims and Gerard, 1985) and may better overcome the drought in the topsoil as its burrow extends into the moist subsoil.

Before 1992 *Allolobophora chlorotica* was present in low numbers at some spots in the APM pasture. From 1992 onward it spread throughout the parcel, especially in the area not yet colonized by the inoculated species (Ch. 4). The impact of *A. chlorotica* on the soil structure will be restricted to the topsoil, as it usually burrows shallowly (6 cm depth) and lives near plant roots (Sims and Gerard, 1985). In 1992 the invading *A. chlorotica* had consumed almost all of the remaining O horizon (Ch. 4), and this may have caused the inoculated species, in search for more abundant food, to increase dispersal.

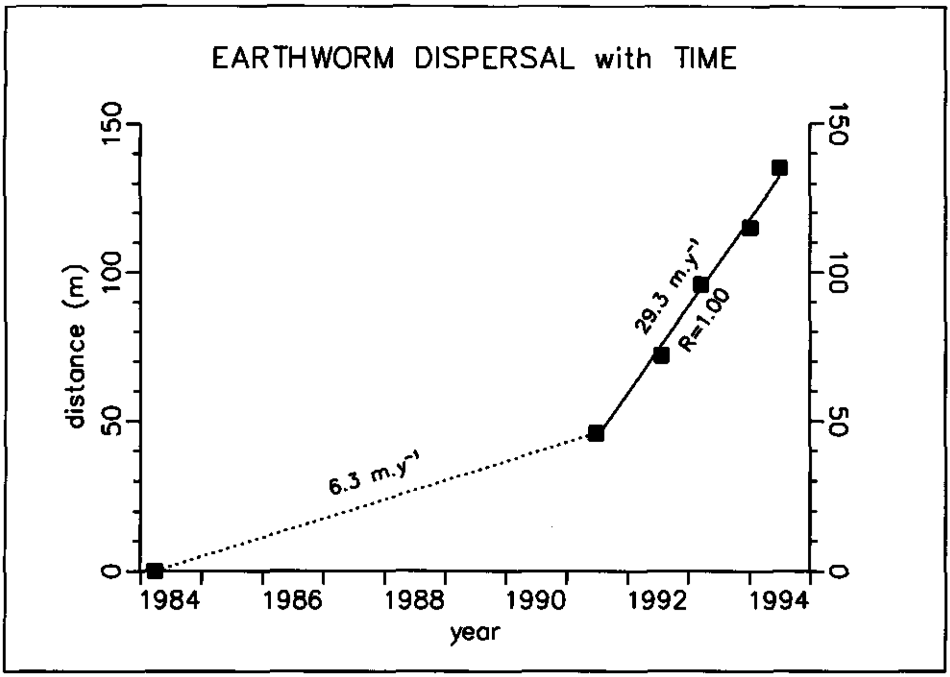


*Fig. 8.1 Dispersal (m) of inoculated earthworms with time. Dispersal of earthworms started in March 1984, solid squares give the maximum distance from the inoculation line at which individual earthworms or burrows ≥ 4 mm in diameter were found. Dispersal rates (m.y$^{-1}$) are given for the periods of March 1984 - June 1991 and June 1991 - July 1994. Solid line gives the regression of dispersed distance with time.*

## 8.2 3D mapping of earthworm burrow systems

The method and accompanying hand-operated mapping device (Ch. 2) proved to be reliable in mapping earthworm burrow systems over a wide range of densities ($N_A$, 120 m$^{-2}$ to 6163 m$^{-2}$) (Ch. 3,4). By measuring both position and orientation of a burrow a relatively large spacing (1-2 cm) between horizontal layers could be used to precisely characterize vertically oriented earthworm burrow systems by serial sectioning. This spacing was much wider than the one suggested by the rule of thumb on serial sectioning (DeHoff et al. 1972), which for the earthworm burrow system called for a spacing of 0.4 to 1.3 mm. The reconstruction procedure was later improved for the two burrow systems mapped in 1992 (Ch. 4) by calculating angles between burrows on consecutive layers, instead of using search windows based on average distance between layers (Ch. 3). Ponding the surface with a methylene blue solution, showed the hydraulic functionality of both burrows and other macropores.

Due to the crumb structure and the abundance of grass roots the preparation of the top layers was difficult, resulting in missed burrows. No reliable estimation can be made of the percentage of missed burrows in the top layers. The large labour requirements of mapping 3D architecture of earthworm burrow systems is a major disadvantage. Replicated 2D burrow density measurements (Ch. 3) showed that the 3D mapped burrow systems are representative at 10 - 35 cm depth, as between those depths the variability in burrow density was low (SD 20% of mean).

The connection of the burrow system with the non-burrow macropore system proved to play an important role in explaining the hydraulic properties of burrows (Ch. 7). Though the labour requirement will even increase, the combined mapping of burrows and other large macropores as cracks would reveal their interconnection in greater detail.

To test the reliability of the method and to check the absence of biases in the reconstructed systems, Computer Aided Tomography (CT or CAT scan) of soil columns (Fig. 8.2) was performed in 1994 in cooperation with M. Joschko and H. Rogasik of the Zentrum f. Agrarlandschafts- u. Landnutzungsforshung e.V., Müncheberg, Germany. CT scans confirmed the highly vertical orientation of the systems and practical absence of more horizontal burrows.

## Development of earthworm burrow systems

8.3

The numerical burrow density ($m^{-2}$) of the burrow systems at APM followed a pattern similar to the abundance of earthworms, and peaked at 4 years after which it dropped to a lower level. Burrow systems may very quickly develop, illustrated by the maximum net burrow creation rate of 110 $m.m^{-2}.y^{-1}$, which occurred 0.6 years after the dispersal of the earthworms started. Length and numerical density of earthworm burrow systems correlated closely (R = 0.97) with the development of the mass of the earthworm community (Ch. 3, 4). From this viewpoint the burrow systems can be said to be in equilibrium with earthworm mass density. A rapid response of burrow system densities to a decrease in earthworm density implied that the destruction rate of burrows was high. A steady deepening of earthworm burrow systems, illustrated by the slow increase of depth at which burrow density is at maximum (Ch. 3), and the steady increase of density below this depth, can be explained by lower destruction rates at greater depth (Ch. 5,6).

Other trends that were clear in the 1991 chronosequence are the increased verticality of the systems and the decrease in the proportion of branched burrows with time (Ch. 3). These can be understood as a reaction to the increased competition between individuals over time. The chance of overlapping territories is reduced when verticality increases and branching decreases.

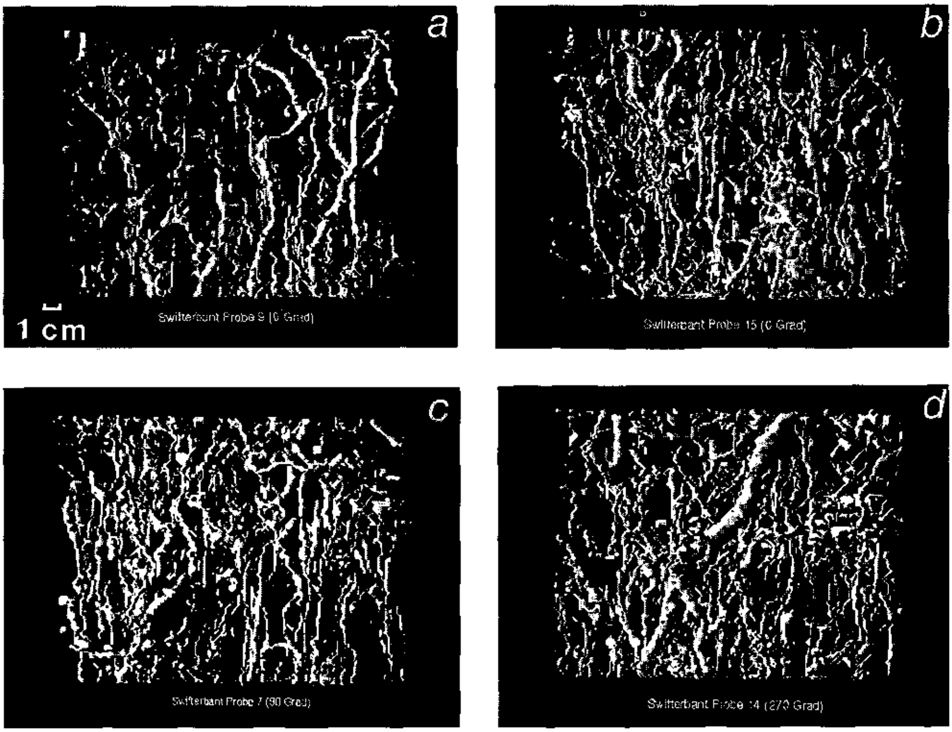


***Fig. 8.2** Examples of burrow systems of different ages, reconstructed from CT scans of soil cores taken in October 1994 at 5 to 23 cm depth at Ir. A.P. Minderhoudhoeve. **a)** 1.9 y old system, **b)** 3.9 y old system, **c)** 7.0 y old system, and **d)** 10.6 y old burrow system (note large burrow, probably of Lumbricus terrestris). Burrow systems are c. 19 cm in diameter and 17 cm in height.*

Long burrows (>0.3 m length), as made by *A. longa*, *A. caliginosa* (morphotype *nocturna*) and *L. terrestris*, scarcely occurred in the six burrow systems (Ch. 3, 4). Long burrow starting at or near the surface, were even virtually absent (only 4 occurrences). Truncation of long burrows in the topsoil is the most probable reason for this absence, the truncation may be related to the inactive state (aestivation) of the largest part of the earthworm community. Kretzschmar (1982) observed a decline of the number of burrows in the superficial layer (0-20 cm) in dry periods.

Despite lower earthworm biomass at the point of inoculation at the 'Ir. A.P. Minderhoudhoeve' in 1992 (i.e. after 8.3 y earthworm activity) than in 1991 burrow density increased. This cannot be explained by further development of the system with age, as is illustrated by the 2D data on burrow point density collected in 1992, which did not reveal an effect of duration of earthworm presence on burrow density between 6.8 and 8.2 y of earthworm activity. The increase in burrow density between 1991 and 1992 must thus be ascribed to an increase in burrowing activity.

The steeper slope of burrow density to earthworm density confirms this view. The increased burrowing efficiency in 1992 is most likely due to differences in weather, which caused a shorter and interrupted active period of the earthworms in 1991.

At ID-DLO earthworm mass density (0.465 kg.m$^{-2}$) was in 1992 almost three times higher than at APM the same year (Ch. 4). The lower earthworm mass density at APM can be explained by a less favourable soil-moisture regime, caused by a sand layer that hindered capillary rise. The absence of such an layer at ID-DLO allowed longer active periods of the soil dwellers.

The architecture of the burrow system at ID-DLO differed from the systems at APM by having a bimodal depth distribution of burrows (Ch. 4). One of the local maxima was located just below the soil surface. This high burrow density at ID-DLO at shallow depth is most probably related to the active state of the earthworm community at the time of mapping. It is not inconceivable that burrow systems belonging to active earthworm populations at APM will also show high burrow density just below the soil surface.

## Destruction of earthworm burrows 8.4

Earthworm burrow systems are dynamic systems, as they result from both the formation and the destruction of burrows. In a field experiment at APM (Ch. 5) the fate of artificial earthworm burrows was followed to determine the rate at which earthworm burrows are destroyed.

Trampling by cattle was the most important destroying earthworm burrows in intensively grazed pastures (Ch. 5). Burrow destruction is thus not a continuous process, but an event-driven process. The soil strength during a grazing event, depending among other things on the actual soil moisture content, will be an important factor determining the extent of the destruction. The timing and relative short duration of the field experiment might have led to the underestimation of the contribution of earthworms to the destruction of burrows (Ch. 5, 6).

Appreciable destruction did not occur below 15 cm depth, apparently because overlying soil offered burrows considerable protection against destruction by trampling (Ch. 5). The burrow presence at 25-30 cm depth after one year of normal pasture use was estimated to be 8.4 times larger than at the surface. Vertical burrows were the most stable, as trampling resulted mainly in vertically orientated forces.

Destruction of earthworm burrows was assessed over a longer time span (7 years) by studying soil thin sections (Ch. 6). Contrary to the field experiment, destruction of burrows appeared to be caused primarily (>70%) by earthworms casting excrements into burrows. Burrows closed by compression could, however, not be recognized in thin sections and have thus been underestimated.

To obtain the best possible estimation of burrow destruction rates, the rates found with thin section analysis were combined with the rates found in the field experiment (Ch. 5). It then appeared that near the surface, at 2.5 cm depth, trampling by cattle became progressively more important with time in destroying earthworm burrows. At greater depth (22.5 cm) casting by earthworms remained the most important source of destruction (>60% of total destruction).

The sensitivity of burrows being closed off at the surface has implications for their capacity to conduct oxygen and water into the soil. Earthworm burrows that are not maintained, can contribute only a relatively short period to the drainage and aeration of the soil, because destruction rates are high: *c.* 50 % of functional burrows are lost per average grazing event (Ch. 5).

According to Kretzschmar (1982) and Monestiez et al. (1993) main destruction of burrows takes place in the top soil when this becomes hot and dry. The authors assume that casting by earthworms is the dominant process destroying the burrows. The volume of casts needed to close those burrows in the situation of Kretzschmar (1982) is not insignificant (7.7 l.m$^{-2}$). It is not clear how such an amount of casts, needed to destroy the burrows, can be produced without making new burrows. Even if we assume that a) the complete earthworm community retreats into aestivation chambers, b) that the volume of excavated soil needed to form these chambers is equal to the volume of the animals, and c) that the volume of the earthworms is equal to their mass (0.2 kg.m$^{-2}$, Kretzschmar, 1982), only a fraction (2 l.m$^{2}$ ) of the volume of the destroyed burrows can be accounted for. Other destructive processes must play certainly a role in the seasonal destruction of burrows.

## Earthworms and soil hydraulic properties 8.

The majority of studies on the relation earthworms - soil hydraulic properties (e.g. Ehlers, 1975, Stockdill, 1982, Hoogerkamp et al., 1983, Edwards et al., 1988, Joschko et al., 1992) focused on the increase of the saturated hydraulic conductivity ($K_{sat}$) due to the presence of earthworm burrows. Besides the effect of earthworms on $K_{sat}$, their influence on hydraulic conductivities, from a nearly saturated soil matrix down to an unsaturated matrix, was studied in Chapter 7.

At APM earthworm activity did increase hydraulic conductivities from full saturation of the soil down to unsaturated soil matrix conditions. The presence of burrows increased $K_{sat}$ and $K$ close to saturation. Surface-connected (water-conducting) burrows did not necessarily begin close to the surface, but could start at nearly any depth, both at APM and ID-DLO. Surface-connected burrows starting well below the soil surface must have been connected with the surface through non-burrow macropores. Apparently, and contrary to the suggestion by

Kretzschmar (1988), the contribution of an earthworm burrow system to water infiltration need not be influenced greatly by the prevailing earthworm activity, and may still be high when many animals are aestivating as at APM.

A network of cracks, which developed in the subsoil below 0.35 m depth due to physical ripening after reclamation of the IJSSELMEER sediments, strongly increased the hydraulic conductivity of surface-open earthworm burrows (mean $2.1 \times 10^{-6}$ $m^3.s^{-1}$). Surface-open burrows ending above the subsoil had very low conductivities ($< 10^{-7}$ $m^3.s^{-1}$). Burrow walls did not show signs of linings nor had, in most cases, the soil surrounding the burrow been compacted, the connection of burrows with the soil matrix was thus not reduced.

The percentage of surface open burrows was expected to be lower in a system with a aestivating community, than in a system of an active community. Before the onset of the dry season earthworms will close burrows, especially in the top of the system (Kretzschmar, 1982, Monestiez et al., 1993). A comparison between an 'active' system at ID-DLO, with nil surface open burrows per 0.09 $m^{-2}$, and an 'inactive' system at APM, which had 2 of these burrows per 0.25 $m^2$ showed that our expectation was not valid.

Earthworm activity increased the hydraulic conductivity of the matrix near saturation in the 0.6 to 5.6 mm range of equivalent pore diameters. Formation of burrows and the presence of earthworm-affected macropores are the cause of the increase in $K$.

Surface open earthworm burrows mainly affect the soil moisture regime at extreme rain events. Before water can flow through burrows at APM, water must pond at the soil surface for more than *c.* 30 minutes. Ponding occurs when the rainfall intensity exceeds the saturated hydraulic conductivity of the soil matrix. Burrow systems at APM can therefor only two to three times per year substantially drain the soil. However, flow through macropores may occur more frequently at the 'no-earthworm' site, because the $K$ of the matrix is lower in the absence of earthworms. This could eventually lead to higher losses of nutrients from surface dressed fertilizers at the 'no-earthworm' site.

Unsaturated hydraulic conductivity, $K_{unsat}$, showed an increase with duration of earthworm presence. This illustrates the development of an earthworm-induced Ah horizon with a changed soil meso- and micropore system. Remarkably the variation in $K$ increased with earthworm presence, which may lead to a soil water economy with a higher variability in both space and time in the presence of earthworms.

## 8.6 Final remarks

Earthworms inoculated in a pasture have the ability to form within a few years extensive burrow systems, which improve the drainage of the soil. Burrow systems will show seasonal and year-to-year variations, due to variability in e.g. weather, burrowing behaviour, and population density. Also grazing practices may result in variations of the percentage of surface open burrows. Consequently the drainage capacity of burrow systems will vary.

Monitoring of burrow systems and of soil hydraulic properties, followed by simulation of the soil water economy, will give better insight into the role of earthworms in this aspect of the soil ecosystem. Perhaps, the increase of conductivity near saturation by earthworm activity may then be proved to be a more important effect than the increase in conductivity by the presence of burrows on which many focus.

## References

DeHoff, R.T., Aigeltinger, E.H. and Craig, K.R. (1972) Experimental determination of the topological properties of three-dimensional microstructures. *J. Microscopy* **95**, 69-91.

Edwards, W.M., Norton, L.D. and Redmond, C.E. (1988) Characterizing macropores that affect infiltration into nontilled soil. *Soil Sci. Soc. Am. J.* **52**, 483-487.

Ehlers, W. (1975) Observations on earthworm channels and infiltration on tilled and untilled loess soil. *Soil Science* **119**, 242-249.

Hoogerkamp, H., Rogaar, H. and Eijsackers, H.J.P. (1983) Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. In: Satchel, J.E. (Editor), *Earthworm ecology*. Chapman and Hall, London, pp 85-105.

Joschko, M., Söchtig, W. and Larink, O. (1992) Functional relationship between earthworm burrows and soil water movement in column experiments. In: A. Kretzschmar (Editor), ISEE 4, 4th Int. Symposium on Earthworm Ecology. *Soil Biol. Biochem.* **24 (12)**, 1545-1547.

Kretzschmar, A. (1982) Description des galeries de vers de terre et variation saisonnière des réseaux (observations en conditions naturelles). *Rev. Écol. Biol. Sol* **19**, 579-591. (In French)

Kretzschmar, A., (1988) Structural parameters and functional patterns of simulated earthworm burrow systems. *Biol. Fert. Soils* **6**, 252-261.

Lee, K.E. (1985) *Earthworms their ecology and relationships with soils and land use.* Academic Press Australia, Sydney.

Marinissen, J.C.Y. (1991) Colonization of arable fields by earthworms in a newly reclaimed polder in the Netherlands. In: G.K. Veeresh, D. Rajagopal, C.A. Viratamath (eds.) *Advances in management and conservation of soil fauna.* Oxford and IBH, New Delhi, pp 431-348.

Monestiez, P., Kretzschmar, A. and Chadœuf, J. (1993) Modelling natural burrow systems in soil by fibre process: Monte-Carlo test on independence of fibre characteristics. *Acta Stereologia* **12(2)**, 237-242.

Schwert, D.P. (1980) Active and passive dispersal of lumbricid earthworms. In: D.L. Dindal (ed.) *Soil Biology as Related to Land Use Practices*. Proc. 7th Int. Colloq. Soil Zool., Syracuse, 1979. Environmental Protection Agency, Washington D.C., USA. pp. 182-189

Sims, R.W. and Gerard, B.M. (1985) *Earthworms.* Synopses of the British Fauna, no. 31. E.J. Brill/Dr. W. Backhuys, London. 171 pp.

Stein, A., Bekker, R.M., Blom, J.H.C. and Rogaar H. (1992) Spatial variability of earthworm populations in a permanent polder grassland. *Biol. Fertil. Soils* **14**, 260-266.

Stockdill, S.M.J. (1982) Effects of introduced earthworms on the productivity of New Zealand pastures. *Pedobiologia* **24**, 29-35.

Van Rhee, J.A. (1969) Development of earthworm populations in polder soils. *Pedobiologia* **9**, 133-140.

# DE ONTWIKKELING VAN REGENWORMGANGENSTELSELS

## en de invloed van regenwormen op de waterhuishouding van de bodem

## SAMENVATTING

## Samenvatting

Regenwormen spelen een belangrijke rol in het herstellen van de kwaliteit van verplaatste bovengrond, zoals dat bijvoorbeeld bij de dagbouw van steenkool voorkomt. Door het stimuleren van de aanwezige regenwormgemeenschap of door het uitzetten van nieuwe dieren, kunnen bodemeigenschappen zodanig worden verbeterd of op peil gehouden, dat een duurzame landbouw mogelijk wordt. De door regenwormen gemaakte gangen en het onder invloed van regenwormactiviteit wijzigen van de bodemstructuur, beïnvloeden de waterhuishouding van de bodem en zijn daarmee van belang voor het herstel, het verbeteren of het onderhouden van bodemeigenschappen. De wijze waarop en de snelheid waarmee regenwormgangenstelsels zich ontwikkelen zijn echter nagenoeg onbekend. Het vaststellen en verklaren van de ontwikkeling van regenwormgangenstelsels vormt daarom het belangrijkste doel van dit proefschrift.

Het zogenaamde 'kip of het ei' dilemma is een belangrijk probleem bij het bestuderen van de relatie regenwormen - bodemeigenschappen. Bestaande correlaties tussen regenworm activiteit en bijvoorbeeld de waterdoorlatendheid van de bodem laten zich niet ontrafelen om zo oorzaak (regenworm of bodemeigenschap) en gevolg te bepalen. Wanneer echter regenwormen zijn uitgezet in een perceel of gebied dat daarvoor zonder regenwormen was, dan speelt het voornoemde probleem niet. Indien de wormen niet over het gehele perceel/gebied, maar gelokaliseerd worden uitgezet, ontwikkelen zich door het verspreiden van de regenwormen zogenaamde chronosequenties. In een chronosequentie hebben regenwormen hun invloed het langst doen gelden op het uitzetpunt, daar waar zij net zijn gearriveerd is hun invloed (zeer) gering. Voor dit proefschrift zijn twee van dergelijke chronosequenties onderzocht, die zich ontwikkelden in voor weiden en maaien gebruikt grasland. De in dit proefschrift meest gebruikte chronosequentie is gelegen op de proefboerderij Ir. A.P. Minderhoudhoeve te Swifterbant (Oostelijk Flevoland) waar eind 1983 regenwormen werden uitgezet.

In de eerste zeven jaren na de start van de verspreiding van de regenwormen trokken zij gemiddeld 6.3 m per jaar verder. In de daarop drie volgende jaren nam de verspreidingssnelheid van de dieren sterk toe tot bijna 30 m per jaar. Een veranderd voedselaanbod is de meest waarschijnlijke verklaring voor deze toename in snelheid.

Om de ontwikkeling van regenwormgangenstelsels goed te kunnen volgen werden een methode en bijbehorend apparaat ontwikkeld om deze stelsels driedimensionaal te karteren. In totaal werden op beide lokaties zes gangenstelsels ingemeten en gereconstrueerd. De dichtheid van de gangenstelsels (aantal gangen, lengte aan gangen per m$^2$) volgde vrij nauwkeurig de dichtheid van de regenwormgemeenschap en bereikte circa vier jaar na start van de verspreiding van de regenwormen een maximum. Regenwormgangenstelsels waren samengesteld uit enkele lange (> 0.3 m) en vele korte gangen. De stelsels bleken in hoge mate een verticale oriëntatie te hebben, wat van belang is voor de stroming van water door de grond. Verschillen in dichtheid en architectuur van de regenwormgangenstelsels tussen verschillende jaren konden worden teruggevoerd op verschillen in de actieve periode van de dieren, een gevolg van weersverschillen tussen de jaren. Verschillen in gangenstelsels tussen de beide chronosequenties werden eveneens veroorzaakt door een verschil in activiteit van de wormen.

Dat de dichtheid van de gangenstelsels ook afnam bij een afname van de dichtheid aan regenwormen, was een indicatie dat de afbraaksnelheid van gangen vrij hoog is. Om de afbraaksnelheid en haar bepalende factoren nader vast te stellen, werd een veldexperiment met kunstmatige regenwormgangen uitgevoerd. Tevens werd door analyse van slijpplaten, gemaakt van uit de chronosequentie genomen monsters, de afbraak van natuurlijke gangen op een aanvullende wijze bepaald. De hoogste afbraaksnelheid werd aan het bodemoppervlak gevonden. Het dichttrappen door weidend vee bleek de belangrijkste oorzaak van afbraak te zijn. Op grotere diepte (22.5 cm) was het door regenwormen opvullen van gangen de belangrijkste oorzaak van gangafbraak. Het sluiten van gangen aan het oppervlak beperkt de mogelijkheid van deze gangen om regenwater af te voeren zeer sterk. Per gemiddelde weidegang van het vee wordt circa de helft van de gangen aan het oppervlak gesloten. De heersende bodemvochtigheid zal het effect van weidend vee op regenwormgangen echter sterk beïnvloeden.

De meeste studies naar de relatie regenwormen - waterdoorlatendheid richten zich geheel op de eventuele toename van de verzadigde waterdoorlatendheid van de bodem. De bodemstructuur wordt, naast de vorming van gangen, nog op andere wijze door regenwormen gewijzigd, daardoor kan ook de doorlatendheid van de niet-verzadigde bodem matrix worden beïnvloed. In de chronosequentie op de Minderhoudhoeve werd het effect van regenwormen op de waterdoorlatendheid van zowel de geheel verzadigde bodem tot en met die van de onverzadigde matrix gemeten. De aanwezigheid van gangen verhoogde de doorlatendheid van de geheel water verzadigde bodem en die van de bijna verzadigde matrix. Niet alleen aan het maaiveld open gangen hadden de mogelijkheid van het voeren van water, ook gangen die aanzienlijk dieper begonnen, konden water voeren. Dit werd veroorzaakt door de verbinding van deze gangen met andere aanwezige macroporiën. De structuur van de ondergrond, gevormd door fysische rijping van het sediment, bestond uit een netwerk van scheuren. Gangen die dit netwerk aansneden, hadden een zeer hoge waterdoorlatendheid. Ook de onverzadigde doorlatendheid van de bovengrond nam toe onder invloed van regenwormactiviteit. Dit illustreert de verandering in het stelsel van meso- en microporiën door het zich ontwikkelen van een Ah horizont.

Uit het onderzoek is gebleken dat regenwormgangenstelsels en de hieraan gerelateerde drainage van de bodem zich na het uitzetten van regenwormen snel kunnen ontwikkelen. Mogelijk is de verspreidingssnelheid door het voedselaanbod te sturen. Vooral wanneer verbetering van de water infiltratie en de drainage de belangrijkste aspecten van de bodemverbetering zijn, moet worden voorkomen dat de gangen aan het maaiveld worden gesloten.

## Dankwoord

Nu we aan het einde van dit proefschrift zijn gekomen, wordt het tijd om allen te danken die mij direct of indirect hebben geholpen om zover te komen. Allereerst denk ik hierbij aan mijn lieve Hennie die mij door moeizame perioden heen heeft geholpen en ik daarom veel dank verschuldigd ben.

Mijn Pa en Ma hebben mij de liefde voor natuur en landschap bijgebracht en zonder deze bijdrage zou dit proefschrift er niet zijn geweest.

Nico en Rienk wil ik bedanken voor het vertrouwen dat zij in mij hebben gesteld en voor het zeer nuttige commentaar dat zij op eerdere versies van artikelen en onderdelen van dit boek hebben gehad. Vooral Nico was sterk in het helpen mijn gedachtenstroom begrijpbaar op papier te krijgen. Het werkoverleg met Rienk wordt door mij ook zeer gewaardeerd. Joke Marinissen heeft mij ingewijd in de wondere wereld van de worm en heeft mij laten delen in haar kennis en kunde op dit gebied. Mijn waardering gaat ook uit naar Johan Bouma vanwege zijn bijdrage die hij leverde in de discussies over het bodemfysische deel van mijn onderzoek.

Gert Peek verdient het ook om op deze plaats in het zonnetje te worden gezet, als het maar niet te warm wordt, nietwaar Gert? Ik waardeer zijn inspanningen die hij gedurende de vele maanden veldwerk leverde, in hoge mate. Door zijn persoonlijkheid was het zeker geen straf om met zijn tweeën in weer en wind en dag in dag uit in een kuil door te brengen. Hij hielp mij ook bij het opfrissen van mijn veldbodemkundige kennis.

Het personeel van de Ir. A.P. Minderhoudhoeve, in het bijzonder Joop Overvest, Spriensma en Klaas van Dijk, heeft mij, de wormenman, altijd graag geholpen bij het veldwerk op hun boerderij.

Ook vele andere collega's hielpen mij bij het karteren, monsteren en meten, Anneke van Liere, Piet Peters en Tom Pape noem ik met name. De ondersteuning en hulp die ik van Joke, Ineke, Mimi, Andrea en Thea mocht ontvangen, waardeer ik bijzonder. Te vaak wordt vergeten dat zij ons een flink deel van het werk uit handen nemen en mede zorgen voor een goede sfeer op de vakgroep.

La coopération avec André Kretzschmar de l'Institut National de la Recherche Agronomique à Avignon, France j'apprécie spéciallement.

Monika Joschko, Toni Rogasik und Ingrid vom Zentrum für Agrarlandschafts- und Landnutzungsforschung e.V., Müncheberg, Deutschland ermöglichten, etwas das in den Niederlanden nicht möglich war, nämlich die Darstellung einer großen Anzahl von Gängesystemen mit Computer Aided Tomography. Auch den Einsatz Ole Wendroths, ebenfalls von diesem Institut, habe ich außerordentlich geschätzt. Ich hoffe, daß ich mit diesen angenehmen Kollegen noch öfter zusammenarbeiten darf.

De dicussies die over mijn werk binnen groep 4 'Nutrient Dynamics and Soil

Structure' van de 'C.T. de Wit Graduate School Production Ecology' plaatsvonden, hebben ervoor gezorgd dat mijn resultaten op een meer begrijpelijke wijze konden worden neergeschreven.

De mooie vorm waarin ik uiteindelijk mijn resultaten heb kunnen neerleggen, is te danken aan de inspanningen van Hans van Reemst als art director en die van Hans Ruëdisuëli als lithograaf. De bijzondere kwaliteiten van Steven Zandgrond als scan operator en de inzet van Hans Ruëdisuëli maakten van de uitnodiging een lust voor het oog.

Als laatsten wil ik Arie van Dijk en Paul Verburg danken, Arie die zorgde voor een prettig verblijf in kelder van de Lawickse Allee 13 en Paul voor zijn inzet om het feest na afloop van de promotie tot een echt feest te maken.

# Notes / Aantekeningen

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Development of earthworm burrow systems