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Some soil morphological effects of earthworm activity; field data and X-ray radiography

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Summary

The effects of the burrowing activity of earthworms on recently reclaimed polder soils were studied in the field and by binocular microscopy and X-ray stereo-radiography. Most observations are from a worm experimental plot in a grass-mulched orchard (van Rhee, 1977); some from a permanent pasture.

Under grass cover, an A_1 horizon is formed, increasing in thickness with time since introduction of the worm population. Under clean cultivated conditions and in strongly compressed wheel tracks, however, development of an A_1 horizon is inhibited.

The A_1 horizon mainly consists of earthworm excreta, which fill most of the burrows. The pre-existing channel structure produced by roots is disrupted by the earthworms. The earthworm activity leads to a marked increase in air permeability of the surface horizon. This may not be sufficient explanation for the yield increase of the orchard or the divergence in compositions of the grass cover, however.

Species involved comprise *Lumbricus terrestris, Allolobophora caliginosa, A. rosea, A. chlorotica* and *L. rubellus.*

Several kinds of burrows are distinguished by their shapes and contents, and ascribed to different species or genera.

Introduction

The influence of earthworms on soil properties has long attracted the attention (e.g. Darwin, 1881). In 1966 van Rhee seized an opportunity to lay out a field experiment to study the effect of earthworms on the growth and production of apple trees on the virgin, not yet fully ripened soils of the Flevoland polder, reclaimed from the IJssel Lake (Netherlands) in 1957 (van Rhee, 1969, 1977).

This paper reports on the burrowing activity of the inoculated earthworms and its impact on the soil morphology, pososity and air permeability at one of van Rhee's experimental plots. These changes brought about in the recently drained sediment form part of the process of biological ripening[1] of alluvial soils.

Observations were made in the bare strips within the rows of apple trees; the grass-covered strips between the rows; and the strongly marked wheel tracks, which run through the grass strips. Additionally some reference will be made to a soil in an older polder, reclaimed in 1942 where the worm population is due to natural immigration.

The morphological data were obtained from field observation and by X-ray radiography. The medical application of the X-ray technique has been long known. Its application to earth science studies is more recent (Hamblin, 1962). X-ray radiography allows the study of the internal structure of undisturbed soil samples, making use of the differential absorption of the radiation by the various soil components present in thick sections of soil material. The different intensities of transmitted radiation are registered on X-ray film placed behind the sample. On the radiograph images of voids are black, and strong absorbers of X-rays, such as carbonates and iron concentrations, are white. The soil mass itself is shown in different shades of grey, depending on its texture, composition and density. Pieces of organic matter are depicted black, like voids, because of their low X-ray absorbance. Further details have been given by Bouma (1969), Krinitzsky (1970), Rogaar & Thiadens (1975). As yet this technique seems not to have applied to the study of the burrowing activity of earthworms (viz. Edwards & Lofty 1972, pp. 24-26).

The site

The worm experimental field is located in the Eastern Flevoland polder near the village of Dronten (Netherlands).

The soil is a stratified, calcareous silt loam, deposited under water under fresh and brackish conditions. It was reclaimed in 1957. Now the groundwater fluctuates between 1.1 and 1.6 m depth.

At the time of the field survey the apple orchard was 9 years old. Grass and tree roots extended down to 95 cm depth below the grass strips, and tree roots down to 135 cm below the bare strips under the trees.

The grass vegetation of the worm plot and control clearly differed in composition. curred in the wheel tracks. In the control plot, *P. trivialis* with a dense undergrowth *Poa trivialis*, some *Poa annua* and few other species; widely spaced *L. perenne* occurred in the wheel tracks. In the control plot, *P. trivialis* with a dense undergrowth of moss were the only occupants; *L. perenne* only dominated along and in the wheel tracks.

The earthworm populations recovered from the sites at the time of observation are listed in Table 1. *Allolobophora caliginosa* and *Lumbricus terrestris* were de-

[1] The term 'biological ripening' comprises all initial changes, which start on drainage of a sediment and in which organisms, both flora fauna, are involved. It forms part of the process of 'soil ripening', which turns an initially undrained, watersaturated sediment into a 'soil' (Pons & Zonneveld, 1965). The ripening forms the first stage in the soil formation of this type of soils.

Table 1. Earthworm species recovered by hand picking from studied sites in August 1974.

Species	Orchard[1]		Grassland[1]
	worm plot	control	
A. chlorotica	+	+	+
A. caliginosa	+	—	+
A. cupulifera	+	—	—
A. rosea	+	—	+
L. terrestris	+	—	+
L. rubellus	—	+	—

[1] The orchard soil had been recovered 9 years ago, the grassland soil 30 years ago.

liberately introduced by van Rhee 1 year after planting of the trees, the other species probably unintentionally, with the plant material, and possibly along with the deliberately introduced species. This is why the control plot has a limited worm population as well.

The observations in the older polder (the North-East Polder, reclaimed in 1942) were made in a permanent pasture near Marknesse. Its worm population is due to natural immigration (Table 1).

The investigated soils differ in the development of the A_0 and A_1 horizons (see formation of the A_1 horizon, below). Below the A_1 horizon, they are similar, having a strong, medium, angular blocky structure, grading into strong coarse prismatic with depth. There are vertical cracks up to 2 cm wide between the prisms. They are due to shrinkage of the soil mass by the irreversible loss of water on drainage. Below 80 cm depth the prismatic structure grades into massive, only dissected by widely spaced, narrow vertical cracks down to 100 - 130 cm depth.

The soils can be classified as aeric Fluvaquets (Soil Survey Staff, 1975).

Methods

Undisturbed samples from the soil profiles studied were impregnated by polyester resin without preliminary oven drying (Miedema et al., 1972). A greenish dye was added to the resin in order to obtain a clearer picture of the voids in the soil. Thick (2 and 5 mm) plane-parallel sections were cut from the hardened samples. After polishing, these allowed study of the surfaces by binocular microscope under incident light, for example for estimation of the number and size distribution of root and worm channels in the soil (Boswinkel, 1975), and for the study of the type and composition of infillings. The morphological terms, particularly the classification of tubules, is according to Brewer (1964).

The sections have also been X-rayed under a Philips-Rotalix X-ray tube with 0.3 mm point focus, operated at 43 kV and 20-25 mA, on Kodak Industrex-C film at 97 cm focus-film distance and variable exposure times.

The radiographs reproduced in this paper were electronically improved by a Milligan dodging printer. The radiographs were produced as pairs in order to allow

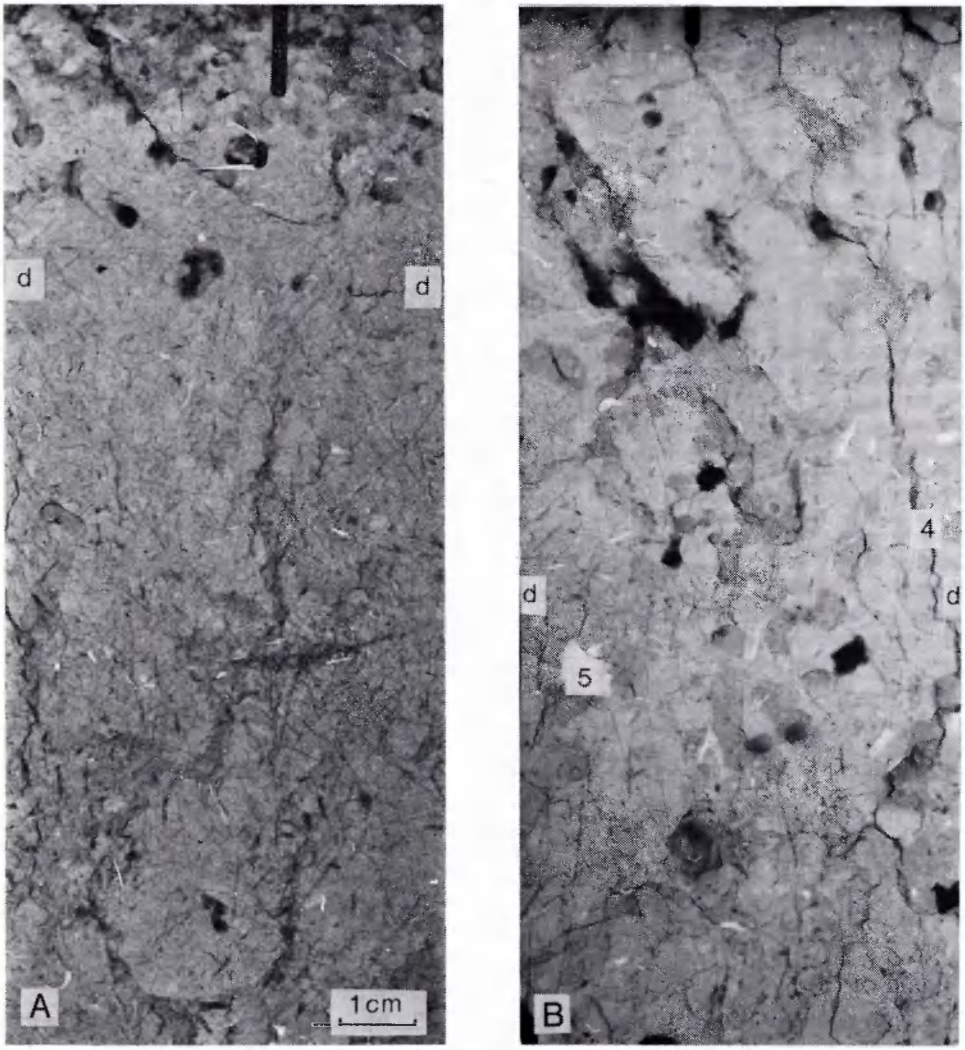
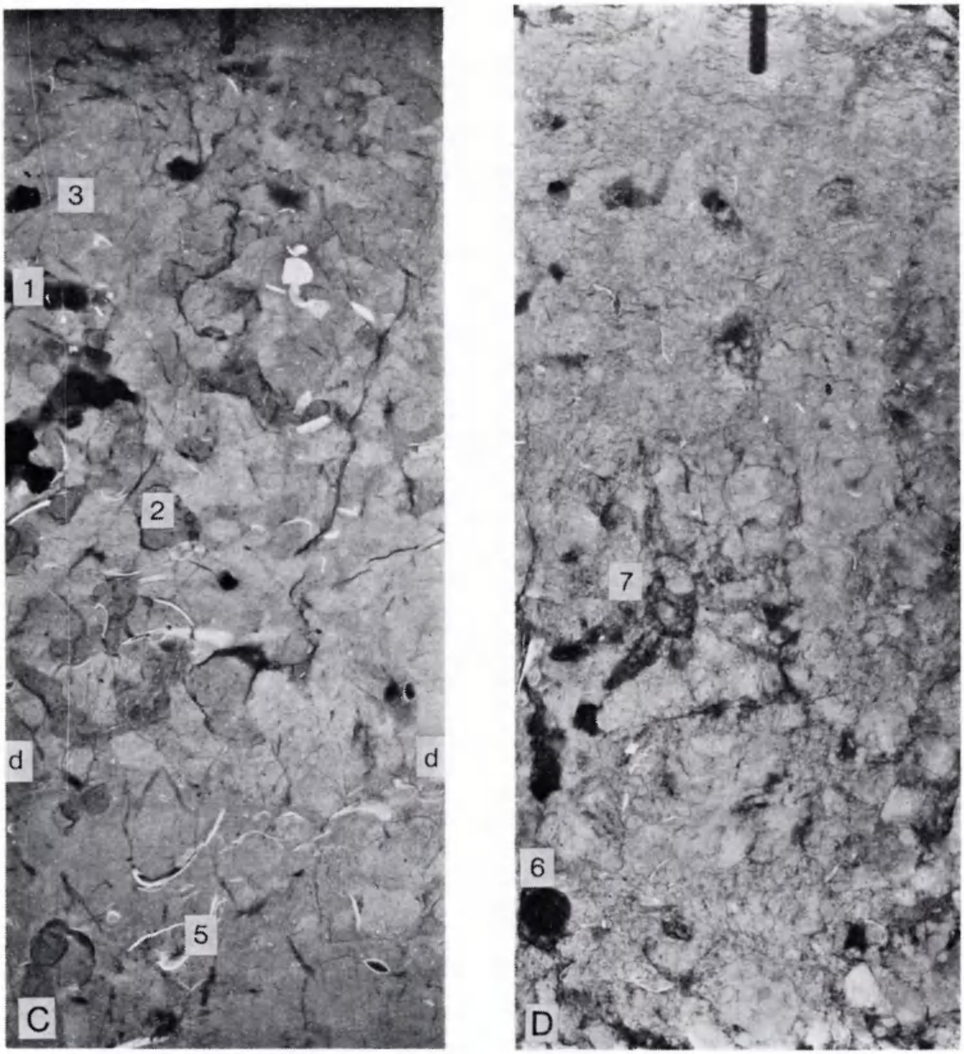


Fig. 1. Depth (d-d) of intensive soil mixing bij earthworms and simultaneous A1 development under grass cover. Depth increasing with the age of the worm populations. Explanation: A = orchard, control; B = orchard, worm plot; C = 30 year-old, permanent pasture; D = orchard, bare strip; 1 = open; 2 = filled-in channel; 3 = root channel (gray, very thin, smooth lines); 4 = crack (gray, irregular shaped lines); 5 = shell fragments (white dots); 6 = tree roots (black); 7 = worm hole with many connected channels. Radiographs of 2 mm (A, B, C) and 5 mm (D) thick, vertically oriented soil sections; A = 0-14 cm; B = 1-15 cm; C and D = 2-16 cm.

study of a three-dimensional image of the pore systems (Bouma, 1969). Some soil physical characteristics were determined on ring samples of 100 cm^3. The data presented in the tables are means of 10 samples per layer.



Formation of the a_1 horizon

Earthworms change the soil morphology in different ways: by disturbance, mixing and aggregation of the soil, formation of a channel structure, and incorporation of organic matter from the surface.

The grass strips
Radiographic and microscopic comparisons of samples from the grass-covered profiles show that with increase in time since introduction of the worm population, the depth of complete reworking of the soil increased from about 3.5 cm in the

control plot of the experimental field, which only has a limited population of earthworms, through about 8 cm in the plot with the population introduced 8 years ago, to about 12.5 cm depth at the permanent pasture in the North-East Polder that is 30 years old (Fig. 1 and 3).

These depths coincide approximately with the depths of the dark-coloured A_1 horizons observed in the field. The control plot has a very thin, very dark-grey (10YR3/1), friable, granular A_1 horizon with abundant grass roots and with an abrupt transition to the horizon below. The A_1 horizons in the worm plot and in the pasture extend to greater depths, the grass roots are not so concentrated at shallow depth and the colours are less dark. Moreover, the soil in the pasture has a more gradual transition from the A_1 to the lower horizon.

The radiographs (Fig. 1) and the polished sections show that the A_1 horizons mainly consist of fecal material (see 'Morphology of burrows', below), but contain occasional subrounded peds of undisturbed, stratified material. The latter become more abundant with depth.

The soil mixing activity of the earthworms has reduced the number of channels with a diameter of less than 0.5 mm, mainly resulting from roots and rootstocks (Fig. 1, Table 2). Stereoscopic study of the radiographs has also shown, that in the completely reworked topsoils, the remaining or newly formed extremely fine root channels become discontinuous and rather irregular in shape. On the other hand, the number of channels wider than about 0.8 mm, mainly burrows, has increased. This corresponds with a threefold increase in air permeability of the topsoil, which

Table 2. Number of open channels in horizontal (hor.) and vertical (vert.) direction in grass-covered profiles, estimated by stereo-microscope on surfaces of polished sections.

Plot[1]	Depth 0–6 cm		Depth 6–16 cm		Depth 18–33 cm		Depth 60–70 cm	
	hor.	vert.	hor.	vert.	hor.	vert.	hor.	vert.
Channels 0.1–0.5 mm Ø (1 cm²)								
orchard, control	14	14	17	n.d.[2]	9	7	6[3]	4[3]
orchard, worm plot	7	5	19	n.d.	10	10	4	5
grassland, about 30 years old	15	10	19	n.d.	29[4]	23[4]	6	5
Channels 0.5–1 mm Ø (1 cm²)								
orchard, control	n.d.	n.d.	3	n.d.	1	3	<1[3]	6[3]
orchard, worm plot	3	<1	1	n.d.	2	2	2	4
grassland, about 30 years old	4	3	2	n.d.	3[4]	3[4]	1	1
Channels 1–2 mm Ø (10 cm²)								
orchard, control	0	n.d.	0	n.d.	0	1	0[3]	0[3]
orchard, worm plot	3	<1	2	<1	<1	<1	0	<1
grassland, about 30 years old	<1	<1	0	<1	0[4]	<1[4]	<1	<1

[1] In brackets the unit area.
[2] n.d. = not determined.
[3] 71–75 cm.
[4] 33–38 cm.

Table 3. Some physical characteristics of the grass strips of the earthworm experimental field. Bulk density of all samples: 1.21 (S* = 0.04) g/cm^3; total pore space: 54.2 (S* = 1.4) % (v/v). S* = standard deviation of individual determinations.

	Depth (cm)	Pore space at pF2 (% v/v)				Permeability at pF2 (darcy)	
		water-filled	S*	air-filled	S*		S*
Worm plot	0–10	43.6	0.8	10.8	1.9	111.9	38.7
	10–20	40.4	0.8	13.4	1.5	99.1	46.6
Control	0–10	43.1	0.7	11.2	1.0	30.5	9.1
	10–20	40.0	0.6	14.3	1.0	38.9	13.6

appears to be the only clear physical difference between the worm plot and the control (Table 3).

The differences in air and water contents at pF 2 between the 0-10 and 10-20 cm layer at the worm plot (Table 3), which indicate narrower pore sizes in the upper layer, cannot be attributed to the earthworm activity, because the control shows the same trend. This contradicts the statement by Russell (1973, p. 202) about an increased water content at pF 2 following the redistribution of pore sizes by earthworm activity. The differences in C and N contents of the upper 20 cm between the worm plot and control are slight and erratic (Table 7).

The wheel tracks

The soil of the wheel tracks in the grass strips has been compressed into a thin platy structure with firm consistence down to 15 cm depth, but the soil of the tracks in the worm plot was less firm and somewhat more blocky than that of the control.

The wheel track in the control plot lacks a mineral A_1 horizon. An organic (A_0) horizon, 2 cm thick, occurs on the surface, clearly separated from the mineral soil below (Fig. 2). This organic horizon consists of interwoven grass roots, pruned branches in different stages of decomposition, dark-coloured, organic worm excreta and some mineral material. The worm activity is mainly restricted to this horizon. Only few vertical tunnels extend into the mineral soil below, down to about 5 cm.

In contrast, the soil of the wheel tracks in the worm plot lacks a superficial organic horizon, and the upper centimetres of the mineral soil comprise a friable and dark coloured A_1 horizon. This appears to be due to superficial worm activity, and additionally to some fecal material brought to the surface from greater depth. The worm activity is mainly restricted to this upper layer, but few vertical tunnels up to 8 mm wide penetrate the compressed platy layer and continue downward.

The shallow depth of earthworm activity in the wheel tracks is also clear from the differences in physical characteristics between the wheel tracks (Table 4), and from the differences between the tracks and the bordering grass-covered surfaces (Table 5). From the latter it appears that the earthworms counteract the increase in bulk density and decrease in total pore space down to 10 cm depth. Even so,

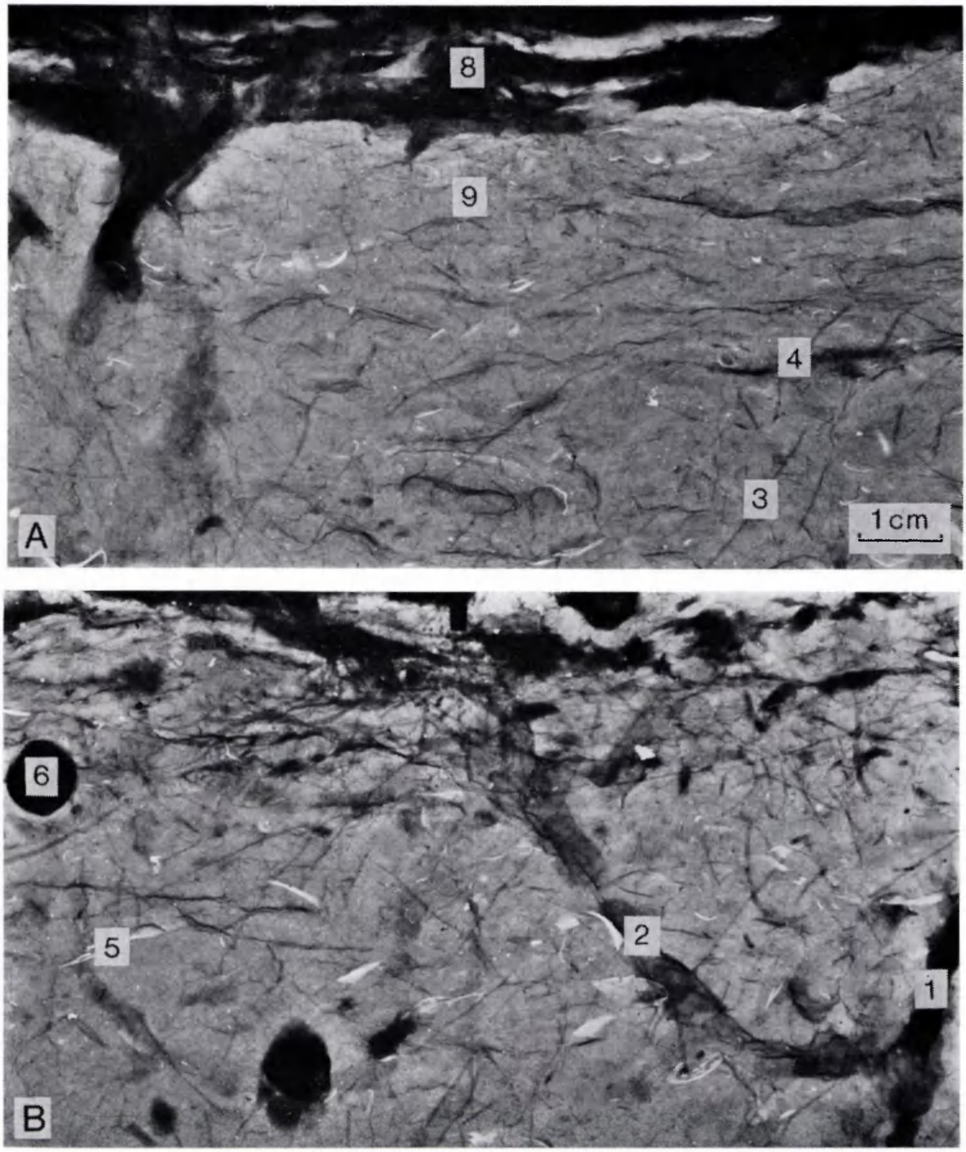


Fig. 2. Radiographs of 5-mm thick vertically oriented soil sections, 0-7 cm deep, of wheel tracks at control (A) and worm plot (B). Differently from B, A clearly shows a thin platy structure, deliniated by predominantly horizontal cracks (4), hardly any open (1) or filled-in (2) burrows and an abrupt change from the mainly organic toplayer (8) to the mineral soil (9); plant root channels (3), shell fragments (5) and tree roots (6) are observable in both.

Table 4. Some physical characteristics of the wheel tracks of the earthworm experimental field. S* = standard deviation of individual determinations.

	Depth (cm)	Bulk density (g/cm³)		Pore space at pF2 (% v/v)				Permeability at pF2 (darcy)	
				water-filled		air-filled			
			S*		S*		S*		S*
Worm plot	0–10	1.22	0.05	45.0	1.3	8.9	1.2	66.5	28.1
	10–20	1.28	0.02	41.9	0.4	10.0	0.9	73.3	27.0
Control	0–10	1.36	0.04	40.8	1.2	8.2	1.7	24.4	16.7
	10–20	1.31	0.03	41.4	1.0	9.6	1.9	48.2	23.0

samples from the tracks still have a smaller mean pore size as shown by the lower air-filled and higher water-filled pore spaces at pF 2.

In spite of the compaction, the mineral soil mass in both wheel tracks is accessible to roots, as shown by the presence of well defined, randomly distributed root channels mainly narrower than 0.5 mm in both tracks. The worm plot and the control hardly differ in this respect (Fig. 2).

The bare strips

In the bare strips the worm activity has not produced a clearly defined A_1 horizon. Burrows and fecal material occur scattered throughout the upper 18 cm (Fig. 1 and 3). No clear differences in physical characteristics were found between worm plot and control (Table 6), except for the theoretical improvement of the air permeability. The occasional very wide tunnels of *Lumbricus terrestris* in the worm plot were excluded from sampling, however.

In the surface samples the bulk densities are somewhat higher and air permeabilities lower than in the lower samples. Water and air contents show trends comparable to the soils of the grass strips. The trends are clearly related to the morphological differences between the fine granular and somewhat platy upper decimetre and the coarser, subangular blocky second decimetre with open tunnels.

Table 5. Differences in physical characteristics of the wheel tracks compared with the adjacent grass-strips in relative per cents.

	Depth (cm)	Change in pore space			Change in permeability
		total	water-filled	air-filled	
Worm plot	0–10	—1	+3*	—17.5*	—40.5*
	10–20	—3.5*	+3.5*	—25.5*	—26
Control	0–10	—10*	—5*	—27*	—20
	10–20	—6*	+3*	—33*	+12.5

* $P < 0.05$.

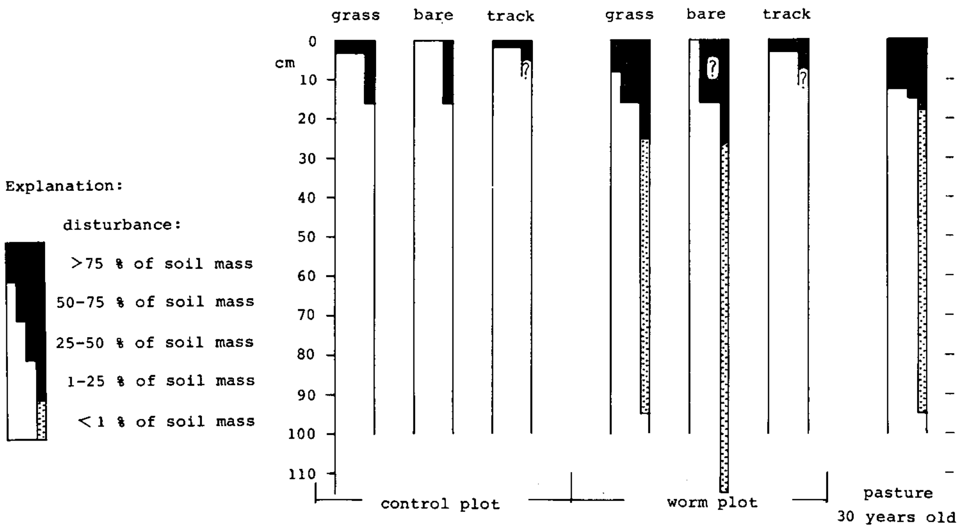


Fig. 3. Depth and degree of disturbance of the soil by earthworm activity in the form of open and filled-up channels, accumulations of fecal material and absence of a clear plant root channel structure, from field and laboratory observations. In wheel tracks no laboratory data below 7 cm depth are available, in bare strip at worm plot uncertainty exists because of the presence of clusters of granular aggregates which may or may not result from worm activity.

Table 6. Some physical characteristics of the bare strips at the earthworm experimental field. S* = standard deviation of individual determinations.

	Depth (cm)	Bulk density (g/cm³)		Pore space at pF2 (% v/v)				Permeability to air (darcy)	
				water-filled		air-filled			
			S*		S*		S*		S*
Worm plot	0–10	1.21	0.02	40.2	1.0	14.3	1.6	15.1	16.6
	10–20	1.16	0.02	39.0	1.5	17.3	2.4	55.2	33.7
Control	0–10	1.20	0.04	39.9	1.3	15.2	2.2	20.4	14.9
	10–20	1.16	0.05	38.9	1.2	17.6	2.6	49.6	31.8

Morphology of burrows

Morphological characteristics of at least 2 types of burrows could be established on the basis of field observations, binocular study of polished sections and stereoscopic study of X-ray radiographs.

Twisting burrows of 0.8-5 mm diameter, filled with mineral material. Under grass cover these are abundant in the A_1 horizons and unoriented. At greater depth they are only occasionally present (2 or less per dm²), mainly vertical. In the bare strips

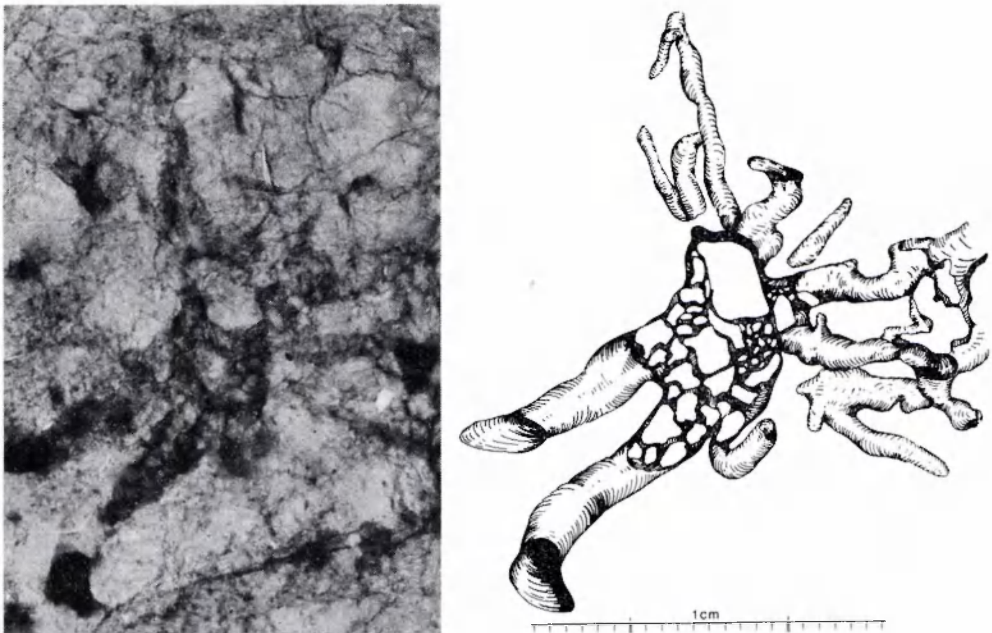


Fig. 4. Worm chamber from which many channels of 1.5 to 3.5 mm branch out; both are for the larger part stuffed with excrements; observed at about 10 cm depth in bare strip of control plot. Excision and drafted interpretation from the radiograph of Fig. 1D (indication 7).

of the worm experimental field these burrows are dispersed throughout the whole upper 18 cm. Below 18 cm depth they are virtually absent, both in the grass and in the bare strips. This depth corresponds with the depth of original mechanical mixing of the soil before the planting of the orchard (Fig. 3). In the older pasture they were found down to about 27 cm (Fig. 1 and 3). The channels may run into larger chamber-like voids, up to 12 mm in diameter. From such voids many channels may branch out (Fig. 4 and 5). Fig. 4, for example, shows a chamber of 9 mm diameter from which 8 channels, branch out within a soil section only 5 mm thick. It is remarkable that the channels from the single chamber are of different diameter, ranging from 1.5-3.5 mm. Other burrows were observed which show a chamber-like widening along their course. In the densely compacted wheel tracks hardly any chambers were observed. Branching of channels also occurs (Fig. 6).

At all locations the partly or completely filled-in burrows far outnumber the open ones, and in the bare strips open channels are predominantly found below 10 cm depth. The in-fillings consist of dark-grey (e.g. 10YR4/1) mineral material, which is sometimes darker but normally of the same colour as the surrounding soil mass. It includes occasional dark coloured pieces of organic matter, mainly less than 0.1 mm in size. Most in-filling do not show any internal structure (isotubules) or at most a weak, transverse striation due to the presence of prolate pieces of organic matter. Some of the burrow fillings are in the form of single or welded aggregates (single or welded aggrotubules). This indicates that the fillings represent fecal material.

The burrows are attributed to the activity of *Allolobophora, A. rosea* and *A. chlorotica.* All three are endogene living species, feeding on organic matter containing, mineral soil material, which were found at the site (Table 1). The observations do not enable a further distinction.

At the control plot and predominantly in the 2.5 cm thick organic surface mat of the wheel tracks, a number of channels within the mentioned size range of 0.8-5 mm diameter are associated with predominantly black (5YR2.5/1) fecal material, which commonly completely fills the burrows. The tubules vary in composition, but commonly contain considerable dark-coloured, prolate and rounded plant remains up to 1 mm in size. The remainder is mineral material with an admixture of finely divided organic matter, and consequently has a darker colour than the surrounding soil mass. Few tubules comprise only loosely compiled organic remains, few others consist predominantly of closely packed mineral material. The diameter of the tubules vary in size with the burrows, but occasional tubules may be up to 8 mm thick, probably where they were deposited in a void of different origin. The tubules com-

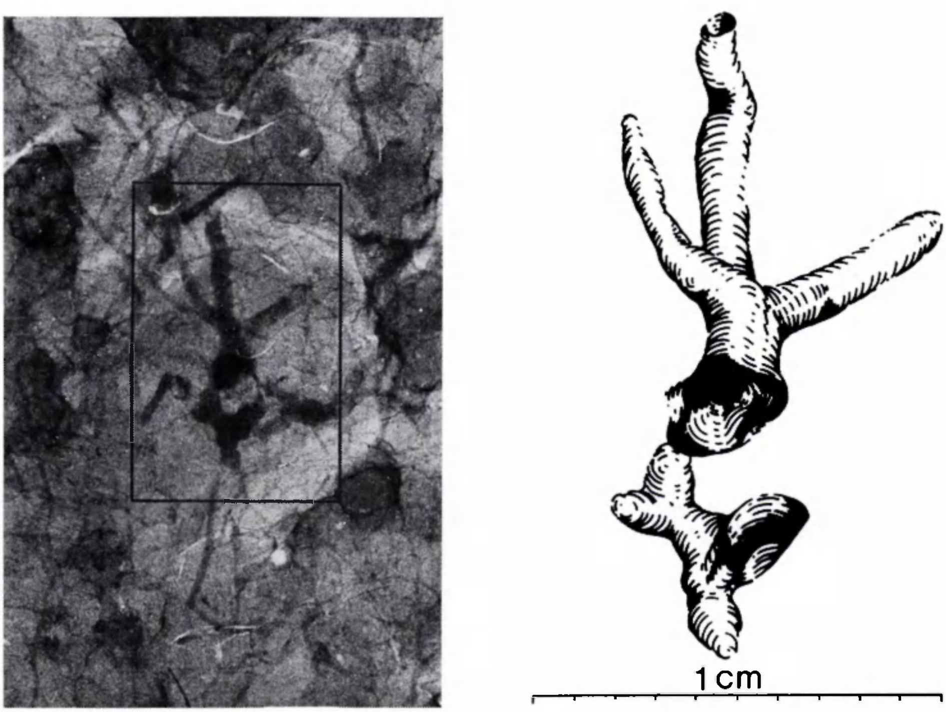


Fig. 5. Interconnected system of worm burrows and chambers, but, differently from Fig. 4, hardly stuffed with excrements; observed at about 11 cm depth in 30-year-old, permanent pasture. Excision and drafted interpretation from a radiograph of a 5 mm thick, vertical soil section.

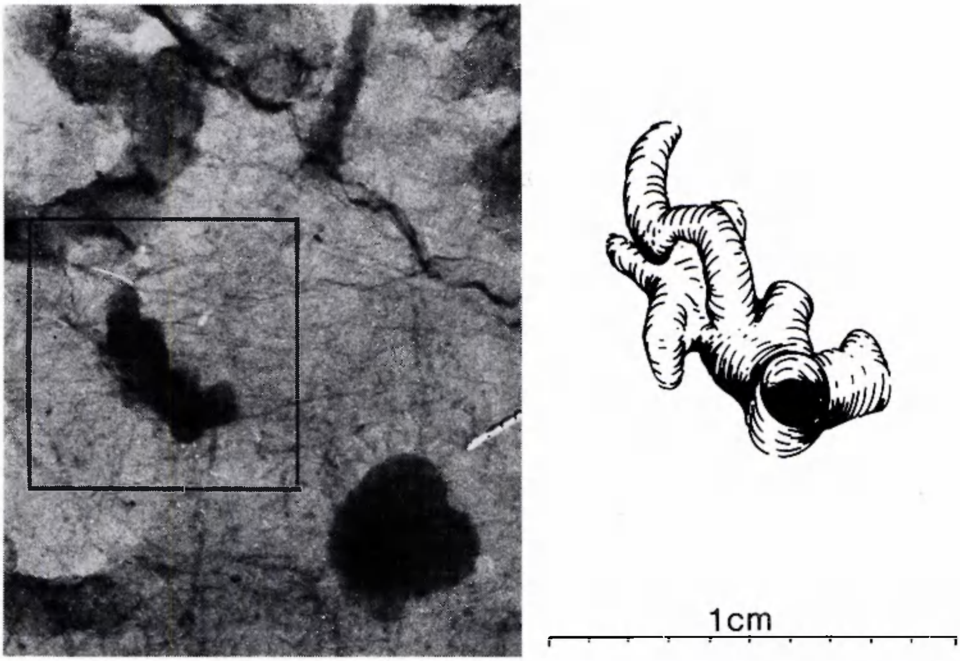


Fig. 6. Multiple branching worm channel made by an *Allolobophora* species; from about 4 cm depth in grass strip at control plot. Excision and drafted interpretation from a radiograph of 5 mm thick, vertically oriented soil section.

monly do not show any internal structure (isotubules), or at the most a weakly curving, transverse striation, partly due to the orientation of the prolate pieces of organic matter. Few of the tubules show a clear striation (striotubules), due to alternating layers of different composition. Single fecal pellets were not observed.

In the wheel tracks of the control plot the traces are abundant in the, mainly organic, upper 2.5 cm thick turf. In the dense mineral subsoil below, to at least 5 cm depth, there are about 1 - 2 horizontal burrows per dm^2. Vertical burrows are clustered and somewhat more abundant.

In the control plot outside the wheel tracks, occasional channels filled with this type of organic matter occur scattered throughout the upper 5 cm of the soil. The channels show occasional branching and connections to chamber-like voids.

The burrows with dark-coloured fillings probably may be attributed to *Lumbricus rubellus* which is common in the control plot (Table 1). This species lives mainly in organic surface and mull-like A_1 horizons and feeds on organic matter (Satchell, 1967; Bouché, 1972).

The observations in fact suggest a preference for the organic upper layer in the wheel tracks. However, in spite of its density, the mineral soil below also contains burrows with dark-coloured in-fillings. In view of the occasionally observed alternation of organic and predominantly mineral fecal material, these burrows were made by the same species.

Predominantly vertical burrows up to 8 mm wide: continue down to depths of 96 cm under grass cover and 115 cm in the bare strips of the worm plot. Interconnections or branching below the A_1 horizons were not observed. Their number is less than 1 per dm^2. Below the A_1 all channels are open and may be plastered with cutans up to 2 mm thick. In the A_1 horizon, these tunnels are difficult to follow, since most of them are completely filled-in with mineral fecal material very similar to the contents of the twisting burrows. Some of these tubules do not show internal structure, other are welded aggrotubules, the aggregates varying in size from less than 1 up to several millimetres.

The vertical burrows are attributed to adult *Lumbricus terrestris.*

Conclusions and discussion

1. In young, recently drained orchard soils the earthworm activity, and the resulting major changes in soil conditions, are restricted mainly to the previously cultivated surface horizon. At greater depths, the worm activity is still insignificant. The occasional vertical tunnels of *L. terrestris* down to 115 cm depth are unlikely to have caused any marked changes in soil conditions, in particular in air permeability, because the many wide, vertical, open cracks far outnumber the burrows at this depth.

2. The burrowing activity of the earthworms and its influence on the soil morphology is closely related to local differences in soil management. In the clean cultivated strips, burrows occur throughout the upper 18 cm, but under grass they are concentrated near the surface (Fig. 3).

3. At least two types of burrows with associated excreta could be recognised. These have to be attributed to a greater number of species however.

4. Most of the burrows of the smaller species are filled-in with fecal material. This is in accordance with the statement by Edwards & Lofty (1972, p. 118) that the species working at shallow depths do not have a well-defined system of burrows.

5. Under grass cover the worm activity leads to the formation of a mixed, dark-coloured A_1 horizon, extending down to 8 cm after 8 years and to 12.5 cm after 30 years. In the bare soil, no clear A_1 horizon was formed (Fig. 1 and 3).

6. The earthworms inhibit the formation of an A_0 horizon or surface mat (Fig. 2) (see also Russell, 1975, pp. 201, 205; Edwards & Lofty 1972, p. 141; Hoogerkerk, in prep.).

7. The burrowing earthworms disrupt the existing channel structure caused by the roots and rootstocks of the vegetation (Fig. 1).

8. The main change in physical characteristics of the soils, brought about by the earthworms is a significant increase in air permeability of the surface horizon in the grass strips.

9. In the wheel tracks the compaction of the soil is counteracted by the earthworms, but only in the upper centimetres.

The resulting loose topsoil and the absence of an organic surface mat may be in favour of plant growth, but it has an adverse influence on trafficability because the surface of the track becomes slippery.

Table 7. C and N contents of the earthworm experimental field, 0–20 cm depth; means of 5 determinations.

	Grass strips					Bare strips				
	%C	S*	%N	S*	C/N	%C	S*	%N	S*	C/N
Worm plot	2.10	0.14	0.135	0.007	15.5	1.80	0.58	0.135	0.010	13.3
Contiol	1.93	0.13	0.158	0.016	12.2	1.84	0.34	0.138	0.016	13.3

C = wet oxidation; N = Kjeldahl; S* = standard deviation of individual determinations.

10. Stereo-radiography proved to be of value for the study of burrow shapes, branching and connections (Fig. 4, 5, 6) and for the study of the influence of earthworm burrowing on the pre-existing channel structure produced by roots and root stocks.

It is doubtful whether the observed increase in air permeability would by itself account for the small but significant increase in fruit yield, observed by van Rhee (1977), because the total and air-filled pore space at pF 2 may be considered sufficient both in the worm plot and the control. Moreover, the increase in air permeability only refers to 2/5 of the total area. Since total N contents of worm plot and control (Table 7) are comparable, the overall nitrogen supplies may not be clearly different either (Schuffelen, 1974). Hence the observed increase in fruit yield probably results from a number of small differences in soil conditions, as affected by the earthworms. These may be present during part of the year, for example an increased level of plant-available N due to a somewhat better aeration in spring (Hoogerkerk, personal comm.), and an increased supply of readily available N (Russell, 1973, p. 204) and other nutrients (Edwards & Lofty, 1972, pp. 152-154) in freshly produced worm casts. There must indeed be differences in soil conditions, because also the compositions of the grass covers in the worm plot and the control have changed drastically, and in different directions, since the seeding (see 'The site', above).

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