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Investigations of the ecology of earthworms (Lumbricidae) in arable soil

Undersøgelser af regnormenes (Lumbricidae) økologi i dansk landbrugsjord

Niels Caspar Andersen
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by NIELS CASPAR ANDERSEN

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PREFACE

In the present thesis are treated a number of aspects of lumbricid ecology in relation to agricultural systems, emerging from ten years work at the Zoological Department of the Royal Veterinary and Agricultural University, Copenhagen. The thesis falls in two parts. In part I, are treated some of the more general aspects of lumbricid ecology, with reference mainly to arable land. These results have not been published previously, and have been gathered from a large body of material and experiments, which have accumulated and been performed during the years. These are data on temperature effects on field populations, respiration and growth, including field surveys of seasonal dynamics with respect to reproduction and general biology.

In part II, are summarized and updated the results from investigations carried out in different agricultural systems, some of which have been presented in the publications 1) - 4), listed at the end of the preface. As part of the thesis are enclosed two papers, 5) and 6), dealing with the effects of sewage sludge and uptake of heavy metals.

List of accompanying papers

1. Andersen, C. (1980): The influence of farmyard manure and slurry on the earthworm population (Lumbricidae) in arable soil. In: "Soil Biology as related to Land Use Practices". (ed. D.L. Dindal). pp. 148-156. Proceedings of the VIIth International Colloquium on Soil Zoology, Syracuse USA, 1979. US EPA 560/13-60-038.
2. Andersen, C. (1981): Regnorme. (in Danish). In: Report No.1. Reduceret jordbehandling, Ørritslevgård, 1972-1980. Statens Jordbrugstekniske Forsøg. pp. 75-80.
3. Andersen, C. (1983): Nitrogen turnover by earthworms in arable plots treated with farmyard manure and slurry. Chapter 11 in : "Earthworm Ecology" (ed. J.E. Satchell), pp. 139-150. Chapman and Hall.
4. Andersen, C., Eiland, F. and Vinther F.P. (1983): Ecological investigations of the soil microflora and fauna in agricultural systems with reduced cultivation, spring barley and catch crop (In Danish with English summary). Danish Journal of Plant and Soil Science 87 (3): 257-296.
5. Andersen, C. (1979): Cadmium, lead and calcium content, number and biomass in earthworms from sewage sludge treated soil. Pedobiologia 19. 309-319.
6. Andersen, C. and Laursen, J. (1982): Distribution of heavy metals in _Lumbricus terrestris_, _Aporrectodea longa_ and _A. rosea_ measured by atomic absorption and X- ray fluorescence spectrometry. Pedobiologia 24, 247-256

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The author wants to express his gratitude to the Zoological Department for providing excellent working conditions during the study period. Special thanks are given to Dr. A. Dam Kofoed, Askov Research Station, for support during the initiation of studies on earthworm ecology in agricultural soils in Denmark and to prof. Niels Haarløv for encouraging and inspiring comments throughout the study period. Further I want to thank the staff of the different research stations for technical assistance, K. Dalbro, Biometric Section, Danish Research Service for Plant and Soil Science, Lyngby, for advice and performance of some of the statistical analyses, and A. Olsen, M.B. Sørensen and H. Rawat for assistance during the extensive field work. Further is thanked the Royal Veterinary- and Agricultural University and the Danish Research Council, SJVF, for financial support.

PART I GENERAL ECOLOGY

CHAPTER I

EARTHWORMS AND TEMPERATURE REGIME

INTRODUCTION

It is well known that earthworm populations (density and species composition) may vary considerably from one year to another (Andersen 1980; Barnes and Ellis 1979) as well as throughout the year (Hopp 1948; Krüger 1952; Van Rhee 1967), with marked seasonality in mortality rates and emergence of new individuals (Nordström 1975). There is general agreement on the significance of climatic conditions for the development of earthworm populations, especially of moisture conditions (Satchell 198ob). However, it is less well documented to which extend the temperature regime of different years may influence population density, as well as how temperature and soil moisture conditions may interact. This stems mostly from the lack of continuous field data, covering several years in sufficient detail to undertake an analysis of this type. It may also be asked if there is a short term response to variations in temperature regime, or if a response is more easy to recognize if a general trend in temperature regime is observable, e.g., in relation to season or whole years.

Recently the influence of different climatic regimes on the evolutionary strategies (r- and K- selection) has been evaluated by Satchell (1980b), inspired by Bouchés (1977) ecological classification of earthworms into the three main groups of life forms, the epigeic, endogeic and anecique. The epigeic, e.g., *Eisenia fetida*, *Lumbricus castaneus* and *Dendrodrilus rubidus* are typically red- pigmented surface and litter dwellers. The endogeic, e.g., *Aporrectodea*, *Allolobophora* and *Octolasion* spp. are in contrast to these strongly associated with the mineral soil. They are generally non- pigmented and survive adverse seasons by retreating deeper in the soil profile, where they may enter a resting or aestivating state. Some species not found in Denmark possess an obligate diapause. The anecique, e.g., *Lumbricus terrestris* and *L.rubellus* are intermediate between the epigeic and endogeic and feed in the surface layers, but may also retreat to deeper horizons during adverse climatic conditions. Both endogeic and anecique species may survive for more than one season.

Adverse seasons may be represented by cold winters as well as hot and dry summers, and in fact (Satchell 1980b), selection pressures exerted by the two extremes, seem to have favoured the evolution of both life forms, epigeic and endogeic. Epigeic species are said to be r- selected (high reproductive rate and metabolism), which ensures production of enough cocoons to maintain the population. Epigeic life is very risky in terms of predation, and most of the population may die out during dry spells and during winter. The endogeic, which are said to be

K- selected are more protected from predation in the subsurface layers than the epigeic and tend to conserve energy (lower metabolism and reproduction, larger body size, utilisation of more low grade food and greater longevity). The aneciques are intermediate between these two extremes along the r- K- gradient. The terms r- and K- are derived from the Verhulst - Pearl equation: $dN/dt = r\ (1 - N/K)\ N$, where r is the intrinsic rate of natural increase, K, the carrying capacity of the environment and N, population density.

As to the endogeic, K- selected species, which are most common in agricultural soils, it might be suspected that a general positive increase in temperature regime may yield a positive response in population density (and vice versa, negative trends a negative one), so long as soil moisture levels do not become limiting. Lumbricids require a relative humidity of close to 100 % in their environment for optimal performance, and the population size is therefore believed to be greatly dependent on the amount of precipitation. Species which are closely associated with the mineral soil and possess good burrowing capabilities retreat to deeper horizons during periods with low precipitation, where they may aestivate until environmental conditions again become favourable. At extreme drought both epigeic and endogeic species may be seriously affected. During periods with excess amounts of precipitation, waterlogging and anaerobic conditions may develop, also increasing mortality. Under such conditions also increased migration may be induced, resulting in mortality from predation and exposure to sunlight.

Extremes of this kind occur from time to time also under the Danish climatic regime. In woodland extremes tend to be dampened by the insulating effect of canopy (summer) and litter layer (winter), but in agricultural soils, which will be under consideration in the following account, earthworms are generally more exposed to the impact of climatic extremes. Other important factors influencing earthworm density in agricultural soils are availability of food, mechanical treatment, pesticide treatment and soil type.

From a study of the influence of different levels of farmyard-manure and slurry at Askov Experimental Station, Jutland (Andersen 1980) a continuous 6 years record (1976-1981) of autumn densities of earthworms is available for an attempt to evaluate the response of 5 different species to changes in yearly temperature regime. Because the project was run as two separate ones, are the records of spring populations (for financial reasons), unfortunately not complete. The reason for looking at temperature regime at all, was that the variation between years of the different species (autumn populations), apparently did not follow the same pattern. Some species following a similar pattern, *A.longa*, *A. rosea* and *L.terrestris* might be suspected of being somewhat dependent of temperature regime, with *A.caliginosa* and *A.chlorotica* perhaps being more dependent of soil moisture (p.18). In the following account, it has been tried to derive a temperature index for the individual years, in a manner which attempts to perform a weighting of periods (seasonal), with positive, respectively negative deviations from normal temperatures.

MATERIAL AND METHODS

Sampling programme for the Askov study can be seen in Andersen (1980). Temperature and precipitation data for the station were obtained from the Danish Meteorological Institute.
In the attempt to look for an effect of temperature regime, it was chosen to keep so many environmental variables constant as possible. Organic matter input may be considered constant from year to year, at an input of 100 tons manure / ha / year. Only data from farmyard manure treatment (FYM) were used, because slurry depresses the deep burrowing species A.longa and L.terrestris (Andersen 1980). This amount of manure (100 tons) is most likely in excess, and therefore the effect of crop rotation (barley, ryegrass, sugar beets), which otherwise may be significant (Lofs-Holmin 1983a), has been ignored. Soil tillage was traditional (ploughing), however, with minor differences in relation to establishment of the different crops. The effect of these, however, cannot be analysed, because there was only one crop per year. The introduction of additional organic matter, e.g., catch crops (Andersen et al. 1983) seems able to compensate for negative effects of soil tillage. The positive effect of FYM on earthworms is, however, much more dramatic (p. 159), which probably renders these minor differences insignificant.

After calculation of a general temperature index, this can be set in relation to different species, precipitation and different amounts of organic matter input. However, it must be noted that a temperature index of the type derived in the following has a number of limitations, as well as different approaches to an evaluation of various climatic effects may be discussed.

Table 1.
Askov, L - field. Total no. of earthworms/m^2, 1976 - 1981.

	Year	A. longa	A. calig.	A. rosea	A. chlor.	L. terrestr.
Fert.	1976	20.0	38.2	19.0	18.3	4.5
90 N	1977	27.4	76.4	15.8	29.9	7.1
	1978	16.0	74.8	16.3	24.5	3.3
	1979	6.5	27.0	3.8	4.2	2.8
	1980	26.8	103.2	7.2	18.8	3.0
	1981	16.0	83.3	3.2	11.2	4.2
50 t FYM	1976	43.8	51.5	18.3	15.3	16.0
	1977	47.0	142.0	14.8	22.5	16.5
	1978	29.8	133.8	29.0	28.0	12.3
	1979	-	-	-	-	-
	1980	39.2	149.2	6.4	21.5	7.5
	1981	29.2	188.5	5.2	17.5	9.8
100 t FYM	1976	98.8	46.0	37.5	16.8	17.8
	1977	51.8	157.5	14.3	40.5	19.5
	1978	22.0	142.0	15.9	24.0	10.0
	1979	19.0	61.0	1.5	9.0	7.0
	1980	58.2	199.8	10.2	29.2	12.0
	1981	39.5	251.5	6.8	27.2	7.2
50 t SLU	1976	14.0	76.5	21.0	11.0	3.3
	1977	9.5	233.0	17.8	25.5	5.8
	1978	13.0	188.0	24.5	20.2	3.0
	1979	-	-	-	-	-
	1980	15.8	208.2	7.5	10.8	6.8
	1981	10.5	202.2	6.2	11.5	1.2
100 t SLU	1976	18.5	98.8	23.0	11.0	3.3
	1977	15.3	275.3	19.0	43.3	7.8
	1978	9.8	227.8	17.5	16.3	1.5
	1979	12.8	121.8	7.5	7.5	2.8
	1980	12.5	257.2	9.5	16.8	2.0
	1981	14.5	307.0	5.9	16.2	2.0

Fertilizer: kg N / ha / year. Manures: tons / ha / year.

ANALYSIS OF TEMPERATURE REGIME

Fig. 1A, shows the air temperatures at Askov Experimental Station from 1975-1981, i.e., mean weekly air temperature, absolute weekly maximum and absolute minimum. To make it more easy to recognize relatively hot and colder periods, different colours have been assigned to the following intervals of mean air temperature. Above 17 °C - red. 15-17 °C - orange. 14-15 °C - yellow. 10-14 °C - blue. 7-10 °C - green (April - May only). In Fig. 1A, is also given the mean weekly precipitation, likewise with a colour code. 0-30 mm- blank. 30-50 mm - green. Above 50 mm - blue.

When the temperature trends during the study period are summarized, it becomes evident that from 1975/76 to 1979, there was a general cooling trend, from relative mild winters and hot summers, towards colder winters and summers. Temperatures during the summer 1980 were much higher, and again somewhat lower in 1981. With respect to precipitation there was no clear trend, and a number of different combinations of temperature and precipitation occurred during the study period. Details of temperature and precipitation for individual years are given at the end of chapter I (Appendix, p. 55).

In Fig. 1B, population density of the different species in October has been plotted against the different years (1976-1981). Also the summer precipitation for the period, June - August, is shown. The precipitation during spring, March - May, was much

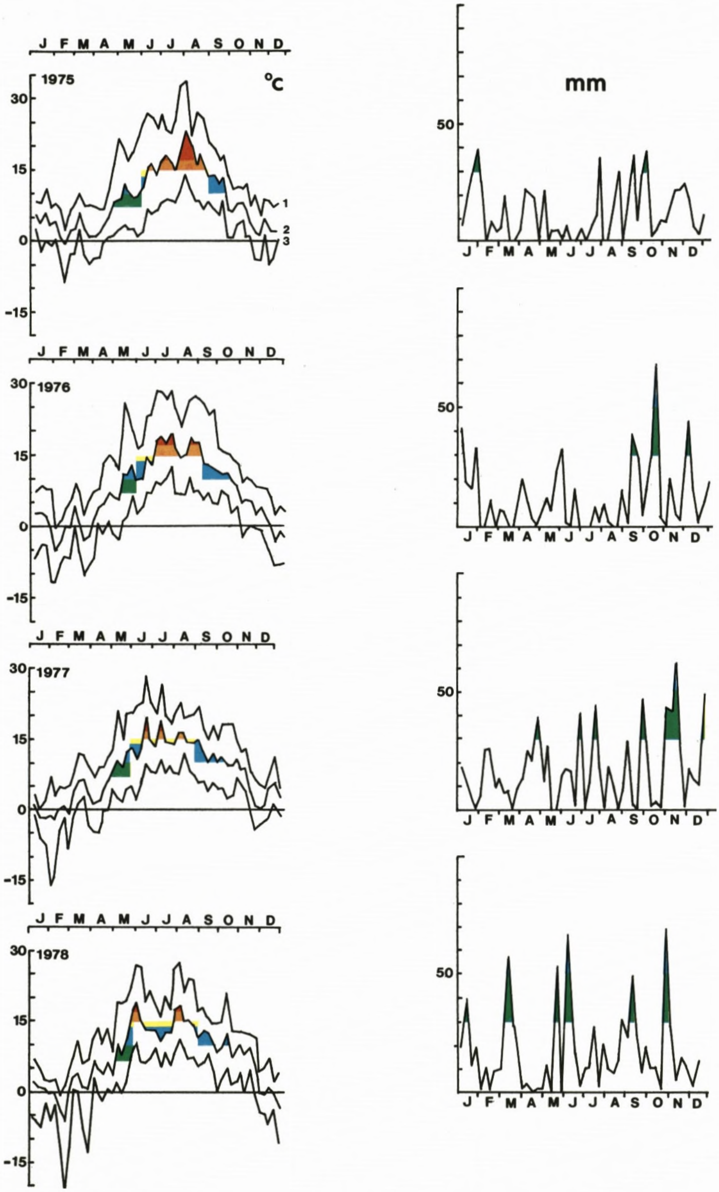


Fig. 1A. Weekly mean, absolute maximum and minimum temperatures and weekly precipitation at Askov Research Station.

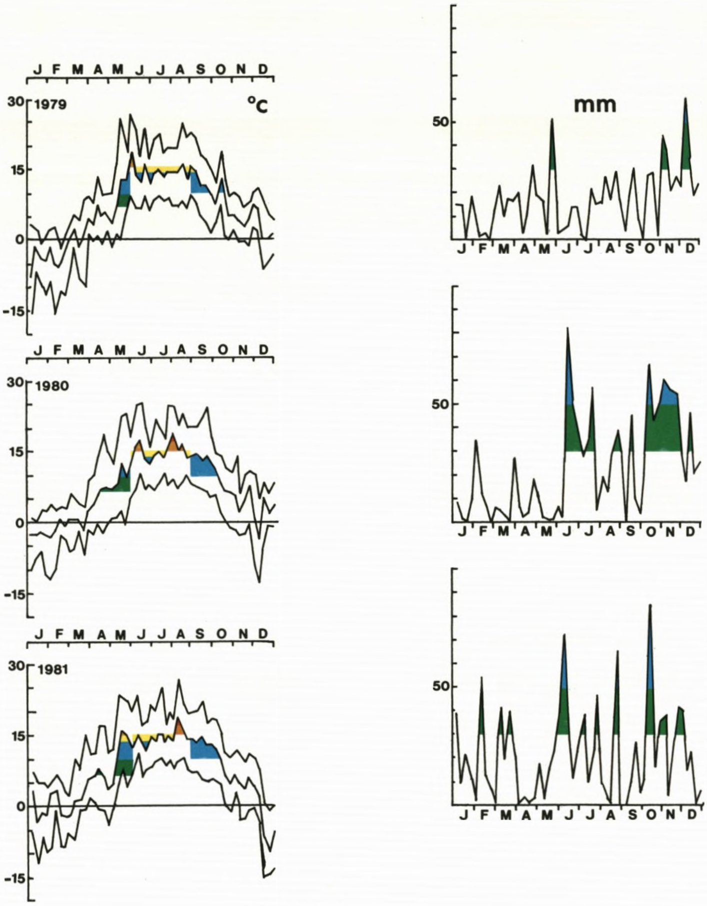


Fig. 1A. Continued.

less variable (Table 4B). Variations in precipitation during winter, November - February, were not considered.

The most abundant species was A.caliginosa (Fig. 1B). The variations in density between years of A.caliginosa, seem somehow to follow the summer precipitation. Also A.chlorotica seem to follow this pattern. The other species, A.longa, A,rosea and L.ter-

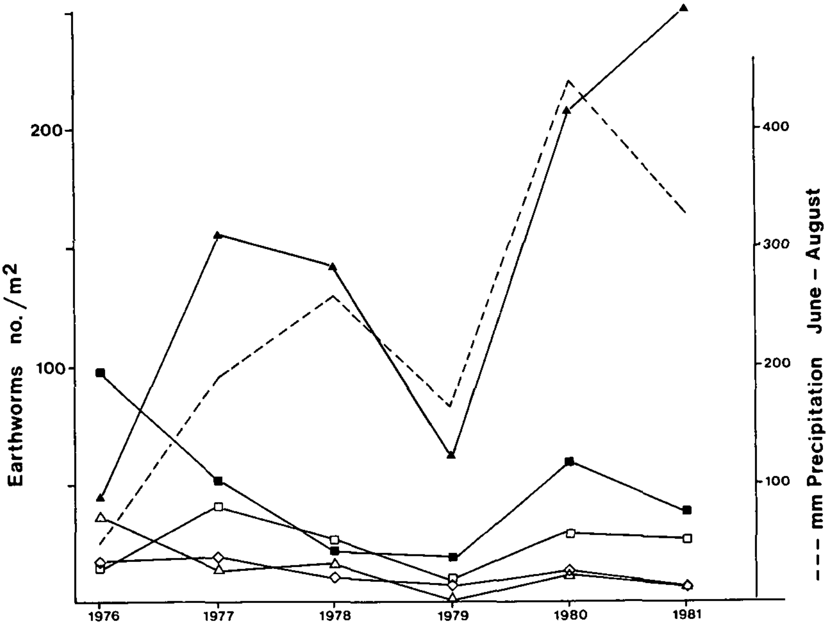


Fig. 1B. Autumn densities of different species of earthworms at Askov. 100 tons FYM / ha / year, 1976 - 1981. ■*A.longa*. ▲*A.caliginosa*. △*A.rosea*. □*A.chlorotica*. ◇*L.terrestris*. ---- mm precipitation, June - August, 1976-1981.

restris, of which *A.longa* was the most abundant, follow a different pattern. The response of these species, by comparison between Figs. 1A and 1B, seems to follow the general temperature regime of the different years, especially summer condtions.

The response of earthworms to the amount of precipitation is well documented, whereas, as mentioned before, a temperature response in field populations has been paid less attention. In the following, however, it is shown that a temperature index may be derived, summarizing positive and negative effects of the temperature regime experienced.

It must here be noted that the present experiment (p. 14) was not originally designed towards analysis of climatic factors, yet a significant effect of "year" has been established (Table 20) for part of the data (1976 - 1978), through a general analysis of variance (p. 159).

Population density in October may be considered a cumulative response to the preceding year. Therefore it may be possible to analyse, how positive and negative deviations from the normal air temperature during different periods (Table 2), winter, spring and summer), may be correlated with the October population data. This has been done on a weekly (cumulative) basis for winter (November - March), spring (April - May) and summer (June - August). The analysis was based on the most abundant of the three species apparently following the temperature regime: A. longa (Table 3A).

Winter

During most of the winter, the worms are generally quiescent deep in the soil, i.e., 30-60 cm below the surface (p. 87), and

Table 2.
Askov Research Station. Temperature data, 1975 - 1981.

Number of weeks: November - March, with mean air temperatures or absolute minimum					April-May		June - August		
	$t < 0^{o}C$	$t_a < -5^{o}C$	$t_a < -10^{o}C$	$t_a < -12^{o}C$		$t > 7^{o}C$	$t < 14^{o}C$	$t > 15^{o}C$	$t > 17^{o}C$
1974/75	1	2	0	0	1975	6	1	11	5
1975/76	7	11	3	1	1976	5	2	8	7
1976/77	9	9	2	1	1977	5	4	4	2
1977/78	5	8	4	2	1978	4	7	4	3
1978/79	13	13	7	3	1979	4	7	3	1
1979/80	10	10	2	1	1980	7	6	6	2
1980/81	7	11	2	1	1981	5	7	4	2

t_a, absolute minimum temperature, weekly
t, weekly mean air temperature

therefore perhaps only exposure to very low temperatures may be significant. The following temperatures were analysed. Number of weeks (November - March), with mean air temperatures below 0 ^{o}C and -5 ^{o}C, and number of weeks with absolute minimum air temperatures $\leq$ -10 and -12 ^{o}C. Analyses were done by linear regression, and the most significant relationship was found for -12 ^{o}C abs. min. after a log/log transformation ($p < 0.01$, Table 3A). Below -12 ^{o}C there were too few data for analysis. There were no significant relationships for 0 and -5 ^{o}C.

Spring

The normal mean air temperature for April - May is close to 7 ^{o}C. Positive deviations from this temperature were analysed in the same manner as above, showing a significance of $p < 0.05$ (Table 3A), when 1976 was excluded. This points towards some positive effect of higher spring temperatures.

Summer

Mean normal air temperature for the period June - August is close to 15 °C, and in the same manner as above for winter and spring, the number of weeks with positive deviations from 15 °C (Table 2) were analysed, i.e., mean air temperatures > 15 °C and 17 °C. Similarly negative deviations, i.e., mean air temperatures < 14 °C were analysed. Significant relationships were found for deviations > 15 °C and < 14 °C, $p < 0.01$ and $p < 0.05$,

Table 3.

A. Correlation between number of weeks with different temperature characteristics, during different seasons, and October densities of *A.longa*, 1976-1981 at Askov.

	t °C	Corr. r=	Sign. p <
Winter	$t < 0$	-	-
	$t < -5$	-	-
	$t_a < -10$	-	-
	$t_a < -10$ 1)	-0.9310	0.01
	$t_a < -12$	-0.7789	0.05
	$t_a < -12$ 2)	-0.9036	0.01
Spring	$t > 7$	0.4700	-
	$t > 7$ 3)	0.8879	0.05
Summer	$t > 17$	-	-
	$t > 15$	0.9380	0.01
	$t < 14$	-0.7950	0.05

B. Temperature index, C_i, of the different years

1975	1.82
1976	1.30
1977	0.70
1978	0.06
1979	-0.24
1980	0.84
1981	0.15

Winter: November-March. Spring: April-May. Summer: June-August. t, Mean weekly air temperature. t_a, Weekly absolute minimum air temperature. 1) log/log transformed, excl. 1975/76. 2) log/log transformed all years. 3) Excl.1976.

respectively (Table 3A). Deviations $\geq 17\ ^{\circ}C$ were not significant.

Temperature index

A temperature index was calculated for each of the different years (1975-1981) based on the number of weeks exhibiting the positive and negative deviations (spring, summer, winter), for which a significant relationship with A.longa (October densities) could be established. The temperature index, C_i (analogy with calories), was calculated as log a coefficient, performing a weighting of positive and negative deviations respectively:

$$C_i = \log \left[\frac{\Sigma i_1 \ \times \ \Sigma i_2}{\Sigma i_3 \ \times \ \Sigma i_4} \right]$$

With i = number of weeks for the periods 1 - 4 showing the significant temperature deviations:

1. Spring: Mean air temp. $\geq 7^{\circ}C$, $r= 0.8879$; $p < 0.05$
2. Summer: - - - ≥ 15 - $r= 0.9380$; $p < 0.01$
3. Summer: - - - ≤ 14 - $r=-0.7950$; $p < 0.05$
4. Winter: Abs. min. air ≤ -12 - $r=-0.9036$; $p < 0.01$

Thus the number of weeks with positive correlation coefficients are put into the numerator, and those with a negative into the denominator, where they are multiplicated. The calculated C_i values for the different years are given in Table 3B. After this, it was possible to plot the index values (C_i) of the respective years against the autumn population densities of the different species (log- transformed) and to perform a linear regression (Table 4A). It is here noted that there was an extremely good fit of C_1 with the A.longa data (Table 4A), both total density and newly hatched worms. The five different species are treated separately below.

The temperature effect may also be analysed by other approaches, i.e., by means of the slope of the regression lines for the discriminating temperature characteristics of the respective periods, or it could be attempted to perform a weighting of the individual contributions $\Sigma i_1 \ldots \Sigma i_4$ of the temperature index. This procedure, however, would probably not increase the accuracy of the index, taking the limited number of years into account.

Another method of analysing the data, could have been a detailed statistical analysis of all species and environmental data. This however, would have required that the response of the worms had been recorded with shorter intervals, e.g., monthly or biweekly determinations of density, biomass, vertical distribution, soil temperatures and soil moisture content. If this had been possible, also for a greater number of years, 10-15, a more generalized model could have been developed, perhaps also taking into account, the type and amount of organic matter introduced into the system. However, as already mentioned, there were not resources for a survey of this order of magnitude at the initiation of the study.

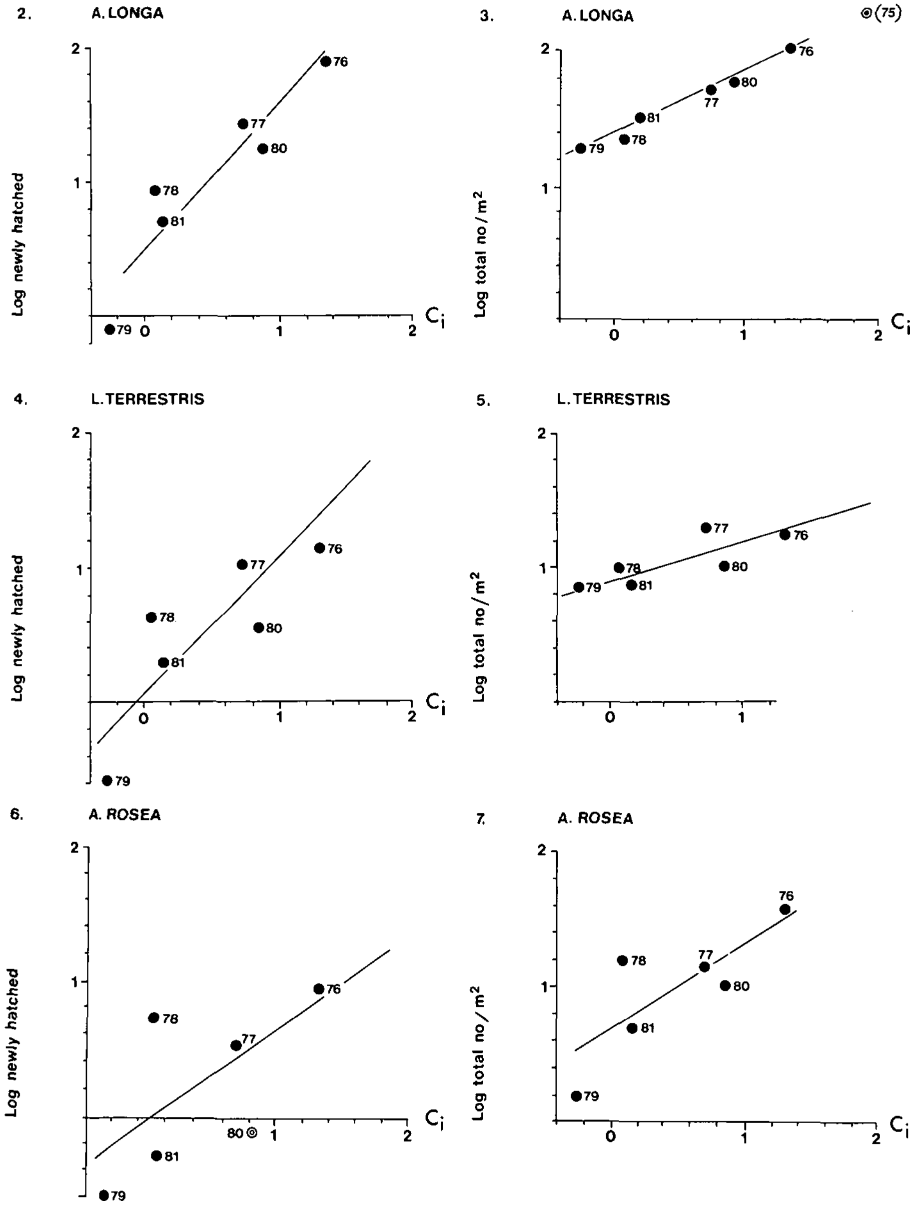
Thus the temperature index, as derived here, has a number of limitations. It applies specifically to the Askov site (sandy loam soil), and a situation with more or less unlimited food availability, a specific species composition, traditional soil tillage and a specific crop rotation (barley, ryegrass, sugar beets), all of which factors may influence the response of the worms. When these limitations are taken into consideration, however, it may still be reasonable, also from a statistical point of view (I. Skovgård pers. comm.), to consider an index of the present type as a good approximation to an idea of a generalized temperature response of field populations.

In the following the response of the different species is treated separately. When the amount of organic matter is reduced, the relationship with temperature may be somewhat modified. This has also been treated separately (p. 30). As to the combined effect of temperature, as visualized by the temperature index, and precipitation, this has been discussed (p. 45), by means of three dimensional plots of C_i, precipitation (June - August, and March - May, respectively) and density in October. This has been done for A.longa and A.caliginosa, representing a deep burrowing and a shallow working species, respectively, both belonging to the endogeic type (p. 11). In this context the same set of limitations must be taken into consideration as applied to the derivation of the temperature index.

TEMPERATURE INDEX AND AUTUMN DENSITY OF DIFFERENT SPECIES

A. longa

It is seen from Figs. 2 and 3, that apparently there is a very good fit between log A.longa density and the temperature index, C_i. The correlation coefficients for the total popualation and newly hatched worms were 0.9645 and 0.9281, respectively, $p <$ 0.001 and 0.01 (Table 4A). The slope of the regression line for the newly hatched was more steep than for that of the whole population, 1.123 vs. 0.455 (Table 4A), which may seem to indicate that reproduction is most sensitive to increasing C_i values. In Fig. 3, C_{1975} has been fitted onto the regression line. $C_i =$ 1.82 is very high and results from a mild winter 1974/75, being followed by a very warm summer. The estimated population size at this value is around 160 individuals m^{-2}. From Fig.1A-B, it is seen that precipitation during July and August 1975 was moderate in spite of the hot weather. Therefore probably no depression of the population size is likely to have occurred. However, it must be noted that the manure experiment was initiated in 1973, and that therefore , owing to the relatively long development time of A.longa (p. 73), some time may have elapsed before the full beneficial effect of the farmyard manure was achieved. This again means that the estimated 160 individuals m^{-2} may be somewhat too high. The summer of 1976 was also very hot, but here severe drought occurred during August and September. Nevertheless the highest population of A.longa was recorded, during October the same year. This is further discussed p. 23, when the combined effects of temperature and precipitation are discussed.



Figs. 2 - 7. Relationship between earthworm density and the temperature index, C_i.

Table 4.

A. Correlation between C_i and autumn density of different species (October), at Askov, 1976-1981. 100 tons FYM / ha / year.

		Corr. r=	Sign. p<	Slope
A.longa	Total	0.9645	0.001	0.4554
	Newly hatched	0.9281	0.01	1.1230
L.terrestris	Total	0.8456	0.02	0.2799
	Newly hatched	0.8277	0.05	0.8971
A.rosea	Total	0.7946	0.05	0.6447
	Newly hatched	0.6622	0.10	0.7250
A.caliginosa	Total	-0.0195	-	-
	Newly hatched	0.2735	-	-
A.chlorotica	Total	0.3655	-	-
	Newly hatched	0.2538	-	-

B. Seasonal precipitation mm at Askov, 1976-1981

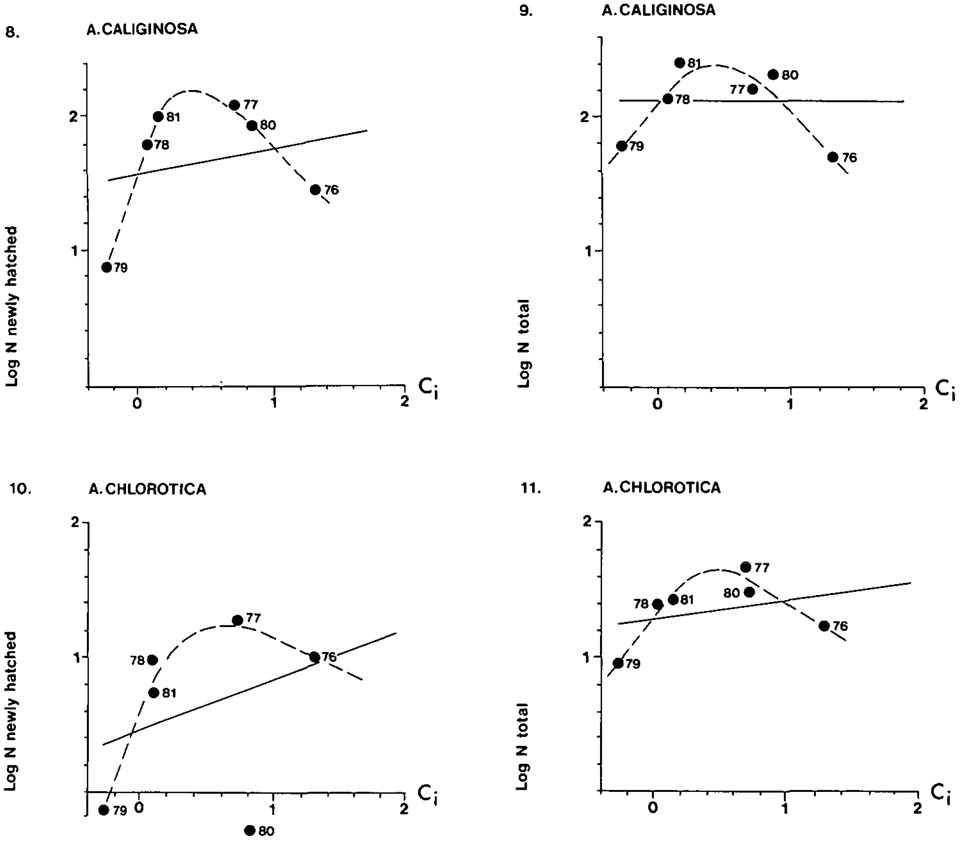
	March-May	June-August	September-Oct.
1976	130	52	196
1977	174	194	123
1978	169	256	196
1979	231	165	132
1980	83	443	271
1981	226	334	227

C. October densities of A.longa and A.caliginosa at Askov, 1976-81. 100 tons FYM / ha / year.

	Newly h. no/m^2		Newly h. % of tot.		Total no/m^2	
	A.longa	A.cal.	A.longa	A.cal.	A.longa	A.cal.
1976	80.8	28.0	82	37	98.8	46.0
1977	27.0	125.0	52	79	51.0	157.5
1978	8.8	76.8	41	54	22.0	142.0
1979	0.8	8.0	4	13	19.0	61.0
1980	17.2	87.2	30	44	58.2	199.8
1981	4.8	107.2	12	43	39.5	251.5

L. terrestris

This species is the other large sized species in Danish agricultural soils. However, because L.terrestris exhibits the anecique mode of life, in contrast to the endogeic A.longa, it never becomes very abundant (Table 1). Also L.terrestris population development showed a good correlation with C_i. For the whole population (Fig. 5), the correlation coefficient was 0.8456 ($p < 0.02$) and 0.8277 ($p < 0.05$) for newly hatched individuals (Fig. 4). Also here the slope of the regression line for the newly hatched individuals was steeper than for the whole population (Table 4A).



Figs. 8 - 11. Relationship between earthworm density and the temperature index, C_i.

A. rosea

A.rosea exhibits the endogeic mode of life, but never becomes very numerous (Table 1). This species also shows a reasonably good correlation with C_i. For the whole population (Fig. 7), the correlation coefficient was 0.7946 ($p < 0.05$). The correlation for the newly hatched individuals (Fig. 6) was less good, $r = 0.662$ ($p < 0.10$). There was only little difference between the slope of the regression lines for the whole population and newly hatched individuals (Table 4A).

A.caliginosa and A. chlorotica

There was no correlation between the number of A.caliginosa and C_i; neither for the whole population nor newly hatched individuals (Figs. 9 and 8). The same is true for Allolobophora chlorotica (Figs 10 and 11). On the contrary it appears that there is an optimum value of C_i around 0.40 - 0.60, which is further discussed p. 34.

DENSITY AT DIFFERENT LEVELS OF MANURE AND TEMPERATURE INDEX

Available food resources and the quality of food are some of the most important factors governing population density of earthworms. In the following it has been attempted to see how the temperature regime of the different years, exemplified by C_i may interact with different levels of manure. This has been done for 50 and 100 tons ha^{-1}year^{-1} of FYM and slurry, including fertilizer, 80 kg N ha^{-1}year^{-1}. In Figs. 12 - 19, population density in October of the different species has been plotted against C_i.

When temperatures increase from solar heating, standard metabolism of poikilotherms, together with activity level, will increase and typically result in increased constraints on available food resources. This generalized type of response has of course been modified in different groups of poikilotherms to fit specific ecological niches and climatic stresses by means of different behavioural patterns and physiological adaptations, as mentioned in the introduction p. 11. for earthworms.

A. longa

Being a deep burrowing species (although not making burrows as deep as those of L.terrestris), A.longa seems well protected against the effects of high temperatures and desiccation It must here be noted that although C_i is calculated from temperature data, it has an inherent soil moisture component at high temperatures, because low soil moisture tend to follow high temperatures during summer. This is a general rule, which of course is not without exceptions as is clearly demonstrated p. 51 , where precipitation is set in relation to temperature. Evans and Guild (1947) considered A.longa to possess a period of obligate diapause during summer, which, however has not been confirmed by other authors. During an investigation of vertical distribution at the study site, *A.longa* was found to be fully active in the middle of July 1978 (Andersen 1981b). Most likely *A.longa* is only aestivating under severe drought. During the present study (1976 - 1981), severe drought was only encountered in 1976, which however did not reduce the number of *A.longa* found in October. On the contrary, the highest density of *A.longa* for the whole study period was found in October 1976. However, at that time 80 % of the population of *A.longa* consisted of newly hatched individuals. This indicates that the drought period resulted in a significant mortality among adult and juvenile worms, whereas cocoons apparently were less affected. Contributing to the high number of newly hatched *A.longa* was probably a relatively high initial population size as a result of favourable climatic conditions during 1975 until the onset of drought in July 1976. Higher soil temperatures probably also reduced the incubation time of cocoons.

From Fig. 12 it can be seen that unlimited access to food, i.e. 100 tons FYM ha^{-1}year^{-1} and high temperatures in general favoured *A.longa*. At the lower dose, 50 tons, it is seen that density, as C_i increases, is levelling off, whereas density in 100 tons FYM was still increasing. In fertilizer, 80 N, maximum density of *A.longa* was reached at a C_i value of 0.75, after which density decreased at higher C_i values. From this it follows that food resources in the fertilizer plots were relatively more quickly exhausted than in the manured plots. Phillipson et al. (1976) showed a significant correlation between the distribution of A.longa and Mercurialis perennis, and a less significant correlation to drying out patterns of the soil during July - August. Nordström and Rundgren (1974) found a significant correlation to soil organic matter content beween 2o and 6o cm depth, and Lindquist (1941), that A.longa is able to distinguish between different kinds of litter.

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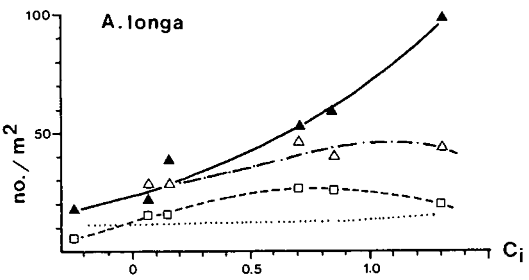

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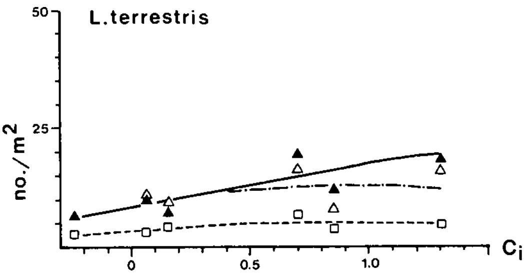

Figs. 12 and 13. Relationship between earthworm density and the temperature index, C_i, at different levels of farmyard manure (FYM). ▲100 tons / ha / year. △50 tons / ha / year. □Fertilizer, 80 kg N / ha / year. Fig. 12, ... 50 and 100 tons slurry / ha / year.

Thus all observations tend to confirm that A.longa prefer abundant organic matter of high quality and as a deep burrowing species is relatively well protected against desiccation and high temperatures, unless under extreme conditions as experienced during 1976. In plots with slurry application, 50 and 100 tons $ha^{-1}year^{-1}$, density of A.longa was very low (Fig. 12), because of the toxic effects of slurry (Curry 1976; Andersen 1980). For a species requiring a rich supply of organic material for food, like A.longa, the amount of energy spent in search for food may soon become critical, relative to what is necessary to maintain normal growth and reproduction, when the total supply of organic matter becomes less. If temperature increases in a system like this, the stress on available resources becomes still more serious for a species like A,longa, at least so long as the temperature is not high enough and moisture content has not become low enough to induce aestivation. In 100 tons FYM no decrease in population size was seen when C_i increased; but the sparser the food, e.g., 50 tons FYM and fertilizer, the sooner, i.e. at still lower C_i values, a decrease in population density did occur. The absolute level of population density over the whole range of C_i values from 1976-1981 is clearly determined by the level of organic matter supply. Likewise the negative effect of low C_i values is clearly demonstrated.

A.caliginosa

In A.caliginosa population maximum in 100 tons FYM, seemed to be reached at a relatively low C_i value = 0.4 (Fig. 14). In

50 tons FYM and fertilizer, maximum occurred at the same value. The question is, whether or not, the decline in population density at higher C_i values was due to a direct effect of temperature on behaviour, or food was becoming a limiting factor. Probably both mechanisms were operating. In the most fa -

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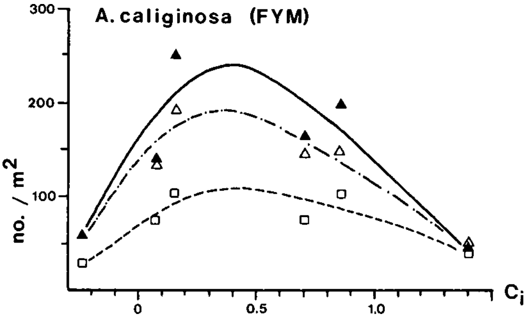
A.caliginosa (FYM)

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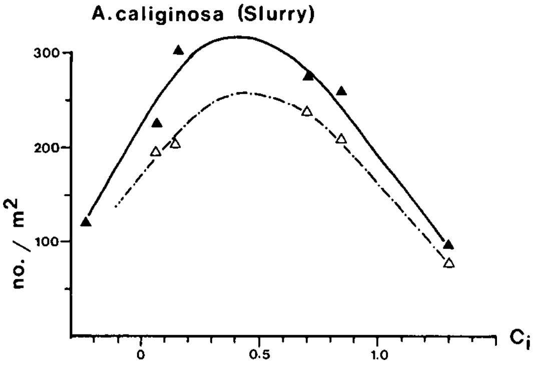
A.caliginosa (Slurry)

Figs. 14 and 15. Relationship between earthworm density and the temperature index, C_i, at different levels of farmyard manure (FYM). Fig. 14 and slurry, Fig. 15. ▲100 tons / ha / year. △50 tons / ha / year. □Fertilizer, 80 kg N / ha / year.

vourable C_i range, it seems obvious that food limitation must be important, but at both ends of the C_i range it is likely that climatic conditions are more important. In 1979 growth and reproduction were inhibited by low temperatures, and in 1976 hot and dry conditions were the causes. A shallow working species like *A. caliginosa* will soon begin to aestivate under conditions like in 1976, and under the prolonged drought mortality was probably greatly increased, desiccation affecting all developmental stages, including cocoons. The relative significance of food limitation and climatic conditions are difficult to study under field conditions, and therefore the offered explanations may be somewhat tentative. However, looking at *A. longa* at 50 tons FYM, food limitation seemed to become significant at a C_i value of approximately 1.0 (Fig. 12), whereas in *A. caliginosa* (Fig. 14), maximum population density occurred at $C_i = 0.40$, in both 50 and 100 tons FYM. From this it may be suggested that there was no serious competition between the two species for food, either because of different feeding behaviour, and or in conjunction with this, because the climatic optimum for the two species is not the same. That climatic factors are strongly influencing the performance of *A. caliginosa* may be seen from the fact that maximum population density in this species occurred at the same C_i value in the three different treatments, fertilizer, 50 and 100 tons FYM (Fig. 14). In slurry (Fig. 15), maximum population density in *A. caliginosa* was 300 and 233 individuals m^{-2} for 100 and 50 tons slurry respectively. This is somewhat higher than for the same levels of FYM. But slurry treatment greatly reduced the number of the two deep burrowing species A.longa and L. terrestris (Figs. 12 and 13), because of the toxicity of slurry, which easily infiltrate the burrows of these species. (Andersen 1980; Curry 1976). Therefore the higher maximum population density in slurry may reflect that some competition for food between A.longa and A.caliginosa does exist, however, never becoming significant for the reasons just mentioned. It is interesting to notice that maximum population density of A.caliginosa in slurry occurred at the same C_i value as in FYM. This again stresses the importance of temperature regime for the development of A.caliginosa, irrespective of food supply, the level of which of course in the end sets the limit.

A. chlorotica

This species (Figs. 16 and 17) showed a response somewhat similar to that of A.caliginosa, but with a population maximum occurring at a somewhat higher C_i value, close to 0.60. This was seen in all treatments, except in 50 tons FYM, where it was close to 0.40, as in A.caliginosa. In fertilizer (Fig. 16), population maximum was the same as in 50 tons FYM, but in 50 tons slurry (Fig. 17), it was lower. In other fertilizer experiments (Barnes and Ellis 1979) there has been a positive effect of increasing amounts of fertilizer on the number of A.chlorotica in comparison with A.caliginosa. This was attributed to a better performance of A.chlorotica at the slightly lower soil temperatures, being caused by the increased foliage coverage at high levels of fertilizer. This might as well have been a climatic effect, or have been caused by a negative influence of high fertilizer doses on A.caliginosa

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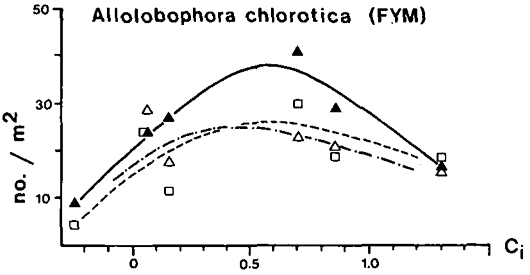

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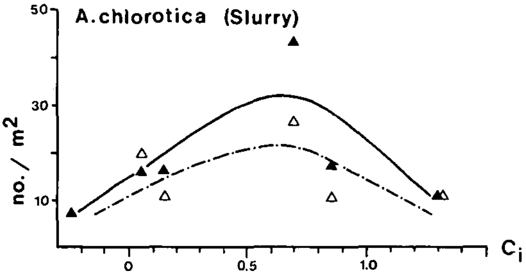

Figs. 16 and 17. Relationship between earthworm density and the temperature index, C_i, at different levels of farmyard manure (FYM), Fig. 16 and slurry, Fig. 17. ▲ 100 tons / ha / year. △50 tons / ha / year. □Fertilizer, 80 kg N / ha / year.

A. rosea

In A.rosea (Figs 18 and 19) there were indications of a population maximum at $C_i = 0.20$, and another at $C_i \geq 1.00$. In the range of C_i = 0.20 - 1.00, the number of A.rosea was probably reduced by competition from A.caliginosa and A.chlorotica. A.rosea seems to utilize roughly the same food resources as A.caliginosa and A. chlorotica, but because of its slow growth rate and reproduction (Phillipson and Bolton 1977), it appears to be sensitive to competition from these two species in their most favourable C_i range.

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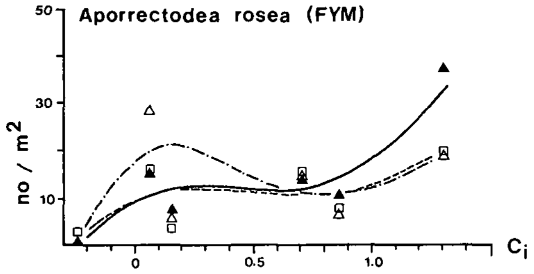

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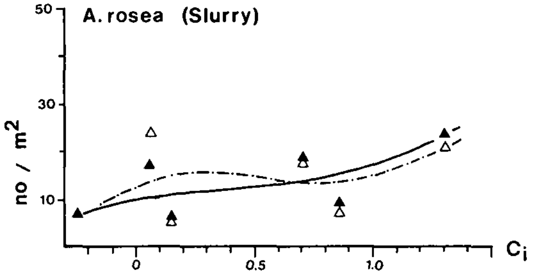

Figs. 18 and 19. Relationship between earthworm density and the temperature index, C_i, at different levels of farmyard manure (FYM), Fig. 18 and slurry, Fig. 19. ▲ 100 tons / ha / year. △50 tons / ha / year. □Fertilizer, 80 kg N / ha / year.

L. terrestris

L.terrestris (Fig. 13), which is deep burrowing and forages on the soil surface (anecique), never became very numerous. Like A.longa and A.rosea it seems to tolerate relatively high C_i values, and apparently there was no great competition for food between L.terrestris and the other species. But because the manures were ploughed into the soil, the endogeic species were favoured.

GENERAL REMARKS

In the beginning it might be thought that the influence of seasonal temperature variations on field populations of earthworms was relatively simple to describe, but when different species are living together, and different amounts of manures and fertilizers have to be taken into consideration as well, the interactions become extremely complex. Another limitation in studies of this kind, is the lack of relevant data, although in the present case a record of 6 years have been available. It might be suggested to include all available literature data in a similar analysis. This, however, will introduce still more variables, as different soil types, other crop rotations and a variety of mechanical treatments. In the present analysis extreme C_i values were encountered, ranging from -0.24 to 1.30, which probably make the suggested response of the different species to temperature variations more convincing. For the reasons mentioned earlier it has not been attempted to develop any sophisticated models for the behaviour of the different species. To be able to do so, would have required a continuous record of at least 10 - 15 years, with a fairly even distribution of C_i values over the entire range, which in the present set of data is not quite fulfilled. Nevertheless, the results obtained in the present analysis seem to stress the significance of temperature regime for the development of field populations of earthworms. The findings presented here should be further tested by detailed studies of the reproduction of the respective species at different temperatures.

As to the significance of temperature regime, it also appears that when food is limited, there may be an important interaction between these two parameters, e.g., A.longa. When food is abundant, the general effect of temperature regime is more easy to recognize, and species like A.longa, L.terrestris and also A.rosea seem to perform well at high C_i values, 1.30 or more, whereas A.caliginosa and A.chlorotica did best at intermediate values between 0.30 and 0.60. At extremely low C_i values, e.g., -0.24 in 1979, with a very cool summer after a very cold winter, the number of all species was seriously reduced. This effect persisted into the spring of 1980 (Fig. 52), but in the autumn, the population had recovered.

It could be supposed that at least the European distribution (North American distribution is here left out of consideration), of the species treated in this section, somehow reflects the different temperature range preferences, as exemplified by the temperature index C_i. The European distribution of lumbricids is considered to have been greatly influenced by the quaternar glaciations. This was treated in detail by Stöp-Bowitz (1969). Some species were able to recolonize North Europa after the las ice age (Würm), presumably possessing good spontaneous spreadi capabilities. These are generally referred to as "peregrine" species. The species treated in the present section all belong to the peregrine species. South of the border line of maximum glaciation (Riss), in South-, South East- and East Europa, the Middle East and into Asia, a vast array (incl. peregrine specie of other lumbricid species occur, referred to as endemic specie with presumably lesser spreading capabilities and more strict requirements against environmental variables, e.g., general habitat, food, temperature range and precipitation (stenobionts).

Among the perigrine species here under consideration, not all have penetrated equally far northwards. *Aporrectodea caliginosa* has a very wide distribution, from the Arctic Circle to North Africa, occupying a number of very different climates. *A.longa* is much less common in Norway, only a few records from South East Norway exist, which may be in agreement with a higher optimum C_i value $\geq 0.70 - 0.80$, in this species, in comparison wit *A.caliginosa* (optimum C_i value around 0.40). The distribution *Allobophora chlorotica* is somewhat similar to that of *A.longa*, and is considered occasionally to have been introduced by man Southern Norway (Stöp-Bowitz 1969). Optimum C_i value for *A.chl rotica* is around 0.60 - 0.70. An optimum C_i value for *A.rosea* was hard to recognize because of competition interactions from other species (p. 39), but would perhaps be within the range o

$C_i \geqslant 0.50$. *A.rosea* is common in South East Norway and goes also far eastwards into the USSR. *L.terrestris* with an optimum C_i value presumably similar to *A.rosea* is distributed in both western and eastern Southern Norway. Stöp-Bowitz (1969) recognized a number of distributional types, mainly with reference to Scandinavian lumbricids. *A.caliginosa*, *A.rosea* and *L.terrestris* belong to "The northerly advanced southern species". *A.longa* and *A.chlorotica* were considered to be "True South Scandinavian species".

An interpretation of the temperature index C_i, along these lines must of course be very cautious because of the very varying climates occupied by the worms, from north to south and west to east, with respect to distribution of precipitation and annual temperature range. It may here be suggested that perhaps species with an intermediate C_i optimum like *A.caliginosa*, or less well defined towards the higher end, e.g., *A.rosea* and *L.terrestris*, will be among the more wide spread. This, however, may also be dependent of other special requirements of the worms.

Other species with a very widely distribution are *L.rubellus* and *Dendrobaena octaëdra*. *L.rubellus* reaches very far north (North Cape). The same accounts for *D.octaëdra*, which is also found in Greenland (Stöp-Bowitz 1969). Both species are among the most pH tolerant species (Satchell 1967; Piearce 1972a, 1972b), and *D.octaëdra* is supposed (Stöp-Bowitz 1969) to have survived the last glaciation (Würm), in refuges in both Western Norway and Greenland.

The very variable C_i values recorded in Denmark (1976 - 1981) are due to the fact that Denmark lies in a somewhat transitory region between a western maritime and a more continental climate to the east. Thus it appears that the density distribution of the different species along the Danish C_i gradient (1976 - 1981) may indicate a general effect of temperature range (together with other environmental variables), also on the European distribution of peregrine lumbricids. This subject, however, needs much further study, i.e., in other climates (South Europa, hot and dry summers, mild and wet winters, vs. East Europa, hot and relatively dry summers and very cold winters), before a more comprehensive understanding of the distributional ranges may be achieved.

Soil moisture levels are important with respect to short term vertical migrations (p. 84), as well as during drought, occurring from time to time. Under more normal conditions, it may turn out that temperature regime is not less important than moisture conditions, especially with respect to variations from year to year. In the following section is looked upon the combined effect of temperature regime and precipiration on population development.

COMBINED INFLUENCE OF TEMPERATURE REGIME AND PRECIPITATION

Apart from temperature, the amount of precipitation is likely to affect population density through effects on both activity, reproduction and vertical distribution. In the following the three parameters, precipitation, (Table 4B), temperature and population density (Table 4C), have been taken together, their interrelationship being expressed in a three-dimensional manner as a topographic relief.

This has only been done for the two species A.longa and A.caliginosa, representing a deep burrowing and a shallow working endogeic species respectively. The population data, total number of individuals m^{-2}, or the proportion of newly hatched individuals (%), occurring in October month, has been plotted along the vertical, z- axis. Temp. index, C_i , and precipitation, mm, have been plotted in the horizontal plane, x- and y- axes. Precipitation data for the summer period (June - August) and spring (April - May) have been treated separately. The population data are from 100 tons FYM $ha^{-1}year^{-1}$ (Table 4C).

Precipitation during summer

Newly hatched individuals, which are recorded in October samplings, are probably derived from cocoons produced during the summer months. It may therefore be of considerable interest to establish how much emergence, as well as total no. m^{-2} is influenced by different combinations of temperature and precipitation, during this period (June - August). A pattern like the following could be suggested. If summer temperatures are low, activity is reduced and therefore fewer cocoons produced. Incubation time is prolonged and therefore emergence during autumn decreases. If precipitation is low this tendency is probabaly reinforced. On the other hand, if precipitation is extremely high, water logging and anaerobic conditiond may develop, increasing mortality. At higher temperatures, effects of desiccation may become significant, whereas the negative influence of excessive precipitation may become less pronounced because of increased evapotranspiration.

The combined effect of temperature and precipitation on the % of newly hatched individuals is visualized in Fig.20 for A.longa and in Fig. 21 for A.caliginosa. For both species it is seen that maximum % of newly hatched individuals at a given C_i value tend to lie within a certain range of precipitation, which, however, changes on moving from lower towards higher C_i values. Both excessive and low amounts of precipitation showed a reducing effect on the % of newly hatched individuals. In A.longa Fig. 20 it is seen that the maximum % of newly hatched individuals tended to increase with increasing C_i values, maximum 82% in 1976. At the same time maximum tended to occur at still decreasing amounts of precipitation. The summer of 1976 was the driest in a 102 years record, and severe drought phenomena occurred during late summer. Nevertheless the population size of A.longa in October

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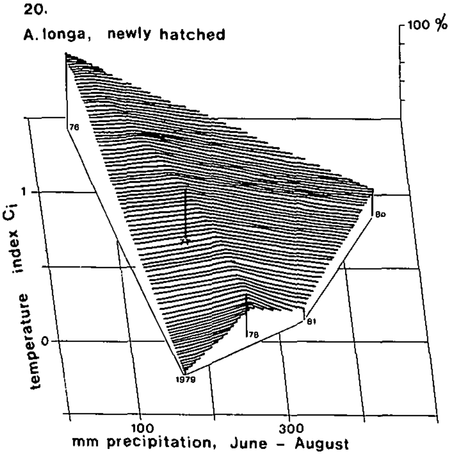

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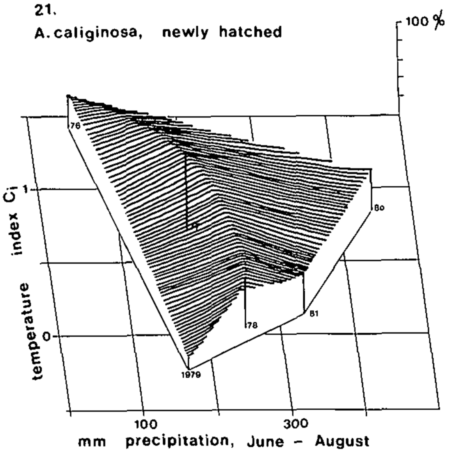

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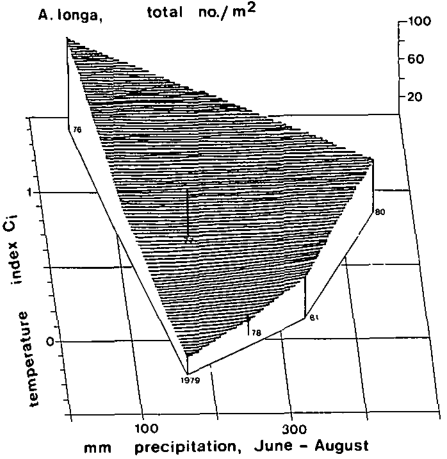

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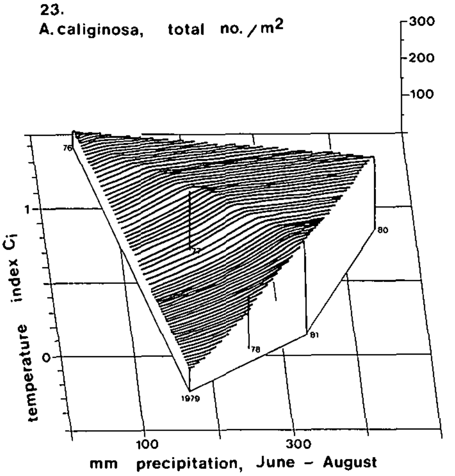


Figs. 20 - 23. Three-dimensional plots, showing the relationship between hatching (%), in October, or total numbers; the temperature index, C_i and the amount of precipitation during June - August (1976 - 1981) for the species A. longa and A. caliginosa, Askov.

1976 was the highest recorded during the study period. The summer of 1975 was also very hot, however without drought. This may have contributed to a high population density of A. longa before climatic conditions became severe, during the end of the summer 1976. The first half of 1976 (Fig. 1A). showed favourable climatic conditions, which probably favoured growth and reproduction, so that significant numbers of cocoons had been produced early during summer, and were able to hatch during October. In general it seems that hot summers are beneficial for A.longa, and it may be suggested that reduced incubation time for the cocoons and a somewhat deeper deposition of these at higher soil temperatures contributed significantly to the large proportion of newly hatched individuals (82 %) in October 1976.

In A.caliginosa (Fig. 21) the maximum % of newly hatched worms decreased at C_i values higher than 0.70 (1977), where the greatest % , 79 %, was recorded (Table 4C). The reproductive potential in A.caliginosa, however, is much bigger than in A. longa and very high densities were reached in 1980 and 1981, with 200 and 250 indiv. m^{-2} respectively (Fig. 23). The lowest record was from 1976 with only 61 individuals m^{-2}. In A.longa (Fig. 22) the total number of worms m^{-2} is positively influenced by increasing amounts of precipitation during the period June - August in a rather general way, while at the same time the positive influence of increasing C_i values is easy to recognize. These findings indicate that A.longa is well adapted to overcome high temperatures and dry conditions, and that it also performs very well at higher amounts of precipitation. A.caliginosa seems to perform better at intermediate C_i values and relatively high amounts of precipitation, which is in accordance with the more shallow working habit of this species.

It is interesting to notice that the maximum level, of percent newly hatched individuals tend to compose a ridge in the C_i - precipitation "landscape", turning somewhat to the left towards lower amounts of precipitation as C_i values increase. The position of the ridge probably in some way defines the maximum possible response of the species in question to the onset of relatively unfavourable combinations of temperature and precipitation. To the left of the ridge induction of aestivation and gross mortality of all developmental stages may increase, offsetting cocoon production. The temperature during summer may (in combination with soil moisture), determine the rate and depth of downward migration, which again gives a feedback on cocoon production. On the other side of the ridge probably only little aestivation occurs. Here population development is most likely controlled by pathogens and predators. As to the reason why the ridge is moving to the left when C_i increases, it could be suggested, that after a period with increasing temperatures, the worms may have accommodated somewhat deeper in the soil profile, which would require still more drying out and heating to produce a general decline. In the case of A.caliginosa, where the maximum values of percent newly hatched worms (Fig. 21) declined at C_i values greater than 0.70, a more limited burrowing capability than in A.longa is probably involved, together with a more superficial depositing of cocoons. The total number of A.longa (Fig. 22) was positively influenced by increasing amounts of precipitation in the whole range of C_i values. The combination of low precipitation and low temperatures in 1979 reduced the population size considerably. A. caliginosa was affected in the same manner, however with a steep slope in total number, when conditions become more dry (Fig. 23).

As mentioned before, a high percentage of newly hatched worms does not necessarily indicate that here are the most favourable conditions encountered; on the contrary. In A.longa the highest percent was associated with the most severe climatic stresses. In A.caliginosa the highest percent was found in 1977 at an intermediate C_i value and precipitation towards the lower end of the range, 0.70 and 195 mm respectively. But at higher amounts of precipitation, to the right of the ridge, the percent of newly hatched worms fell, whereas total population size increased. This may indicate that longevity in A.caliginosa is favoured by high amounts of precipitation, whereas cocoon production and survival does not necessarily increase simultaneously, or if reproduction increases, increased cocoon mortality may offset continued population increase. This can be seen from Fig. 23, where the total no / m^2 of A. caliginosa tend to become stabilized at the highest amounts of precipitation, 1980 and 1981. This may also apply to A.longa, although the population size of this species seemed less sensitive to precipitation.

From the foregoing discussion it becomes clear that the interactions of temperature regime and precipitation are rather complex. Generation of three dimensional topographic reliefs may greatly facilitate the biological interpretation of data of this kind. Perhaps the 6 data points of the present study is somewhat sparse, which makesthe conclusions more like suggestions to what kind of information 10 or more years would have been able to yield. The true causes as to the response of the worms, however, still remain somewhat speculative, because the fundamental biological processes involved are not easily observed under field conditions, unless a very close survey is conducted (Chapter III), and because realistic field conditions are very difficult to simulate in the laboratory with respect to annual variations of temperature and precipitation.

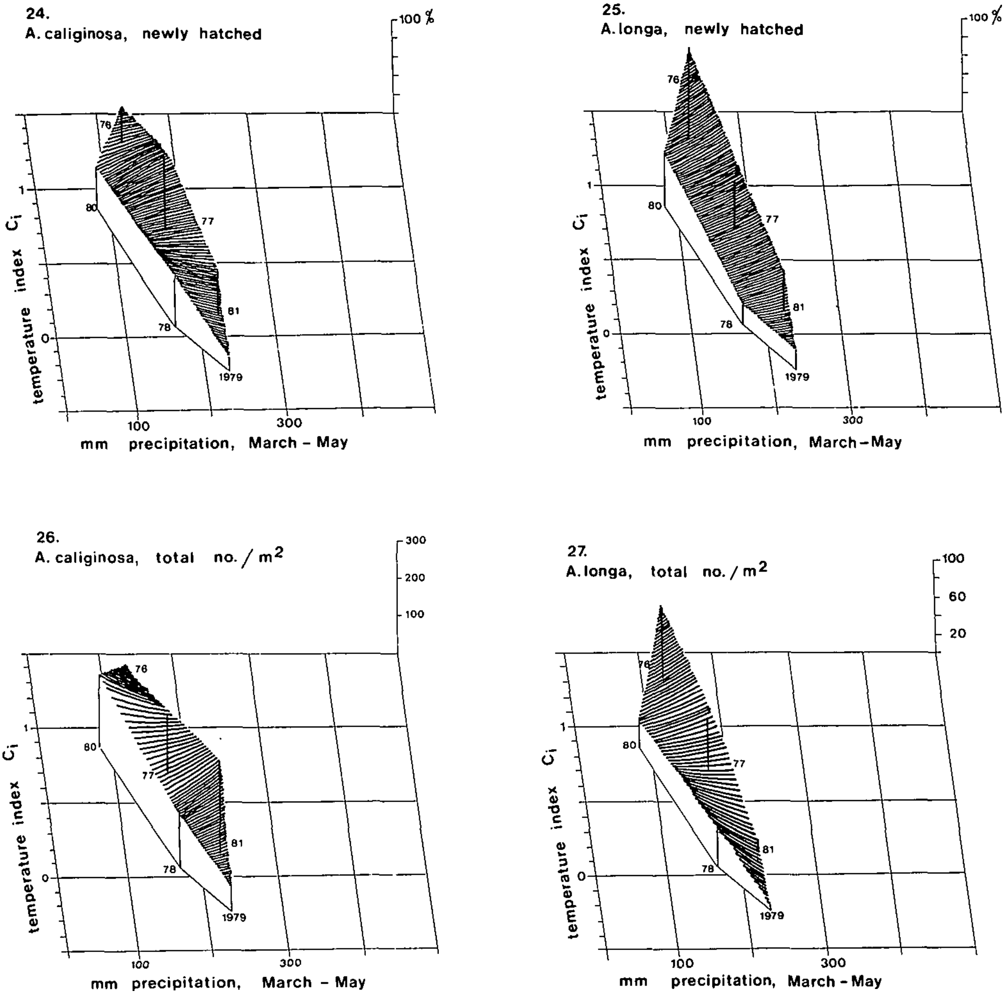
Below is given a short summary of the distribution of temperature and precipitation for the most critical years during the summer period (June - August), demonstrating the very variable pattern experienced during the study period.

It is seen that there were both very dry and very wet summers incombination with both low and high C_i values. This resulted in a relatively great area in the x- y- plane. Further it is noted that precipitation during the cool 1979- summer (C_i = -0.24) was relatively low (165 mm). This was caused by an unusual long period in July with cold air flowing down from the middle- and North- Atlantic. Furthermore the winter 1978 - 1979 was the most severe during the study period, also contributing to the low C_i value. The year 1980 was unusual by its very large amount of precipitation during summer, 443 mm (Table 4). The summer temperatures were not particularly low (C_i = 0.84) and the precipitation fell in combination with thunderstorms (warm air from SW and S in June) and frequent passages of low pressures (July-August) with colder, respectively warmer air masses from W and SW. The summer of the years 1978 and 1981 were relatively cold (Fig. 1A), with 1977 being somewhat warmer. 1976 was extremely dry and hot, with the summer precipitation being the lowest in a 102 years record. Thus it can be seen that the study period, 1976 - 1981, covered three years with three extreme types of summer weather: 1976 being hot and dry; 1979 being cool and dry and 1980 being wet and relatively warm. The two years 1978 and 1981 were towards the colder end, and 1977 somewhat intermediate, and not so wet as 1978 and 1981 (Table 4B).

From this it seems reasonable to believe that the response of the worms, as visualized by the three-dimensional plots within the triangular area defined by temperature regime and precipitation, is representative of what can ever be expected to occur. But of course a more extensive set of data would greatly increase the accuracy of the predictions supplied by the relief.

Precipitation during spring

The amount of precipitation during spring, March - May, probably enhances population development in a more general manner, being of importance when activity is resumed after the cold


24. A. caliginosa, newly hatched

25. A. longa, newly hatched

26. A. caliginosa, total no./m²

27. A. longa, total no./m²

Figs. 24 - 27. Three-dimensional plots, showing the relationship between hatching (%), in October or total numbers; the temperature index, C_i and the amount of precipitation during March - May (1976 - 1981) for the species A.longa and A.caliginosa, Askov.

season. This effect however, may be obscured by the climatic development during the summer months. It must also be kept in mind that soil moisture at the end of the cold season, in most years is relatively high after melting of snow and ice. The amount of precipitation during March - May, 1976 - 1981 (Table 4B) was much less variable than during June - August, which makes the area in the x- y- plane relative narrow and elongated (Figs. 24 - 27). This indicates that precipitation during spring probably did not contribute significantly to variations observable as changes in autumn densities. The effects which perhaps might be recognized by analysis of Figs. 24-27 are probably greatly overridden by the effects of summer precipitation.

CONCLUSIONS

The general impression of the effect of precipitation on development of field populations of earthworms, e.g., *A.longa* and *A.caliginosa* is that the amount of summer precipitation in conjunction with temperature regime is most critical. On *A.caliginonosa*, which is a shallow working species in comparison with *A. longa*, which is more deep burrowing, the influence of dry conditions seems more detrimental than wet conditions. For *A.longa* the influence on total number of summer precipitation appears to be less significant than for *A.caliginosa*. The effect of precipitation during spring cannot be considered alone, but may enhance population development in a general positive manner.

APPENDIX.
TEMPERATURE AND PRECIPITATION 1975-1981

1975

Earthworms were not sampled in 1975, but 1975 is included because the climate of one year may be of importance for the population size of the following. The beginning of 1975 was relatively mild with -9°C as the lowest temperature recorded. The spring was relatively cold, but in the beginning of June temperatures increased rapidly, and the summer period June-August was extremely hot, with maximum temperatures exceeding 30 °C during the last part of July. In the autumn there was a relatively cold period at the end of September, with minimum temperatures close to zero. Night frost began at November 1st. Precipitation was high in January. Until the middle of May it was moderate. June and July were very dry until the end of July. During August and October precipitation was somewhat higher than in spring.

1976

Temperatures during the winter were lower than in 1975, with absolute minimum temperatures of -13 and -10 °C in February and March respectively. April was warmer than in 1975 and there was a period during the middle of May with high day temperatures, 25 °C. Most of June, however, was cold in comparison with 1975, but at the end of June the weather became very hot, with maximum temperatures close to 30 °C. At the transition between July and August there was a cooler period, but during the rest of August and the first half of September, temperatures again were very high. After that, temperatures decreased gradually, and night frost began in the beginning of November. The lowest temperature of December was -10°C. Precipitation followed the same pattern as in 1975, however with severe drought during August.

1977

Winter temperatures were lower than during the two preceeding years, with an absolute minimum of -16 °C at the end of January, and -8 °C at the end of February. After a mild period during March, a period of three weeks with minimum temperatures close to -5 °C occurred during April. Temperatures increased slowly during May, and not until the middle of June, mean air temperatures exceeded 15 °C. Three warmer periods of shorter duration were encountered during summer, with intervening relative cold periods, mean air temperature, 14°C. Mean air temperatures were close to 10 °C during most of September and October. From November air temperatures decreased rapidly, reaching an absolute minimum of -5 °C. December was relatively mild. Precipitation was moderate to high during most of the year.

1978

During winter January was mild; but February and March very cold with absolute minimum temperatures going down to -22 °C and -13 °C respectively. Both April and May were relatively cold, with regularly night frost until the middle of May. During the end of May temperatures increased rapidly, with maximum temperatures reaching 27 °C. After the first week of June, the warm period was followed by a very cold period until the beginning of August, with temperatures considerably below normal. One week, beginning of July, mean air temperature was as low as 10.5 °C. During the first half of August, temperatures raised to the same level as during the first warm period. During the end of September a very cool period was encountered with night frost. October and November were relatively mild. From the beginning of December the weather became increasingly colder, with an absolute minimum temperature reaching -11 °C. Precipitation was high in January and March, and again in May - June. July and August were relatively dry. In September and November periods with higher percipitation occurred.

1979

January and February were very cold, several weeks with minimum temperatures below -10 °C, going down to -16 °C in both months. After a shorter mild period in the beginning of March another cold period was encountered, with minimum temperatures reaching -10 °C. April and most of May were also very cold with night frost persisting until the second half of May. Then temperatures increased rapidly to give a short warm period, after which the rest of the summer was very cold, with mean air temperatures below 15 °C. During September temperatures decreazed relatively rapidly, followed by a warmer period in the beginning of October. The second half of November was also very mild. During December an absolute minimum of -7 °C was reached. Precipitation was moderate most of the year. Only in May and November - December precipitation was high.

1980

The lowest temperatures during January and February were -10 °C and -12 °C respectively, with the rest of the winter being relatively mild. Temperatures increased during April, however, with a colder period with night frost in the second half of May. The first half of June was relatively warm, followed by a cool period until mid July. The rest of July and August were warm. Also September was relatively warm. During October temperatures decreased rapidly and night frost began during the middle of October. November was cold in the beginning and milder towards the end. During the first part of December minimum temperatures went down to -13 °C, again followed by a milder period. Precipitation was relatively low until the beginning of June, where larger amounts of precipitation were encountered. Also July and August were relatively wet. October and November were extremely wet.

1981

In January the lowest temperature recorded was -12 °C. March was relatively mild, followed by a cold period in April. In the beginning of May temperatures increased rapidly, and there was a short warmer period with mean air temperatures of 16 °C. The rest of the summer was cool until August, with mean air temperatures below 15 °C. August was warm, mean air temperatures reaching 19 °C. In the beginning of September mean air temperatures decreased to 14 °C. During October temperatures decreased more rapidly, with night frost beginning at the end of the month. During November temperatures again decreased more slowly, followed by a very cold December, with an absolute minimum temperature of -15 °C. February and March were relatively wet, April and May more dry. During the rest of the year, there were alternating periods with large amounts of precipitation and more dry periods.

CHAPTER II
RESPIRATION OF EARTHWORMS

INTRODUCTION

In descriptions of whole ecosystems, great emphasis has been laid upon energy and nutrient cycling, resulting in an increased focusing on decomposers, among which the earthworms play a fundamental role. Earthworm activity is an important factor in soil development, mixing of mineral soil and organic matter, including stimulation of microbial activity (Barley and Jennings 1959). Already Franz (1951) and Macfadyen (1961) suggested that invertebrate metabolism was directly related to soil fertility. Therefore a lot of work has been devoted to the study of the metabolism of different groups of soil invertebrates, in order to quantify the relative significance of their contribution to the total soil respiration and turnover of organic matter. Respiration of earthworms has been studied by several authors, and important reviews were given by Mendes and Almeida (1962) and Laverack (1963) in the monograph on earthworm physiology. The most important recent studies are those of Byzova (1965) and Phillipson and Bolton (1976).

The following account deals with the respiration (O_2 consumption) of three species of earthworms common in arable soil, <u>Aporrectodea</u> <u>caliginosa</u>, <u>A</u>.<u>tuberculata</u> and <u>A</u>.<u>longa</u>, and different developmental stages of these. Here the technique used has been carried a little further than in previous studies, allowing the worms to stay in a natural burrowing medium of sandy loam. Measurements were also made on aestivating *A.tuberculata* at low temperature.

MATERIAL AND METHODS

Oxygen consumption was measured in a Gilson Differential Respirometer with 14 channels. One channel was accommodated with a reference flask, and usually three were reserved for zero calibrations. Measurements were made in the dark at 12 °C, the water bath being covered with black plast foil. The respiratory chambers were of a modified cylindric type made of acryl, 65 x 35 mm (inner dimensions). Carbon dioxide was absorbed in 1 ml 1 normal KOH on a filter paper strip in a small cylindric glass. The worms used were adult, juvenile and newly hatched *Aporrectodea caliginosa* (Sav.), adult and juvenile *A.tuberculata* (Eisen) and subadult *A.longa* (Ude). Respiration during aestivation at low temperature, 2.5 °C, was measured on subadult *A.tuberculata*. It was found that lowering of the temperature was not enough to induce aestivation, with the worms rolled up into a ball, as they are found in the soil during winter. But when the chambers were subjected to partial drying out, the worms went readily into aestivation.

One series of measurements was made on *A.caliginosa*, with the worms lying in the chambers without burrowing medium in only 1 ml water. All other measurements were made with the worms in a burrowing medium of unsterilized sandy loam, approximately 3o g soil (water content 20 %) per respiration chamber and 1 g biomass. The worms used for the measurements had been reared in the laboratory at 12 °C constant darkness, and were transferred to the chambers 24 hours before the beginning of the measurements, allowing the worms to establish a burrow system and to maintain normal feeding behaviour during the measurements. Chambers containing burrowing medium without worms were run simultaneously. The difference between the two series, with and without worms, was then calculated, and is the oxygen uptake of the worms. Measurements were made over a period of 2½ hours.* It is well known that earthworm activity stimulates microbial activity, and some of the oxygen uptake, taken as earthworm respiration, could therefore be believed to result from this stimulating effect. But owing to the relatively short duration of accomodation before measurements were made (24 hours) and the relatively low temperature, 12 °C, this effect has been ignored. After the experiment all the worms were counted and weighed to make sure that none had died since introduction into the respiration chambers. The oxygen consumption of the worms was then calculated, reduced to STP conditions and expressed as $\mu l \; O_2 \; g^{-1} h^{-1}$, the respiratory rate.

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* During the six series of measurements with worms in respiration chambers with burrowing medium, five chambers with burrowing medium excl. worms were run simultaneously with five chambers with burrowing medium + worms. The total amount of oxygen respired by the burrowing medium and the worms, respectively, was of the same order of magnitude, i.e., about 200 $\mu l \; O_2$ over 2½ hours. Thus the statistics of the calculated worm respiration (by subtraction) was not essentially affected by this procedure. The variability of the respiration of the burrowing medium was only slight. The mean standard error of the six series was 5.3%. The variability of the worm respiration was somewhat greater, the mean standard error, being 8.0%.

OXYGEN CONSUMPTION OF DIFFERENT SPECIES

Earthworms are negatively phototropic, and may exhibit either positive or negative thigmotactic reactions, depending on the environmental conditions, during measurements. The two series of measurements of oxygen uptake on A.caliginosa, without, and with access to a natural burrowing medium, clearly demonstrates this effect.

In Table 5 - 6 , the mean respiratory rates of the different developmental stages are given as obtained directly from the measurements, i.e., Table 5A for A.caliginosa without burrowing medium, and Table 5B, with burrowing medium. In Table 6 A - C, the same data are given for A.tuberculata and A.longa respectively. The respiratory data of aestivating subadult A.tuberculata are given in table 6B. The mean respiratory rate at 2.5 °C: 8.5 μl O_2 $g^{-1}h^{-1}$ was 36% lower than the value obtained by correction from 12 °C to 2.5 °C, of the respiratory rate of subadult worms of the same weight, taken from line 3) Fig. 28. Thus it appears that a physiological adaptation takes place in connection with the onset of aestivation. From the series made on A.caliginosa, without burrowing medium, (Table 5A), it is seen that the respiratory rate in subadults and juveniles was lower than in adults. In the series with burrowing medium, the respiratory rates were at a somewhat higher level, and more consistent with the general priciple, of becoming lower with increasing body weight.

In Fig. 28, the figures from Table 5-6 have been plotted against the individual weights of the worms, and two straight li-

Table 5. Respiration of *Aporrectodea caliginosa*. μl O_2 $h^{-1}g^{-1}$ (live wt) at 12°C

A. Without burrowing medium 1)

	worms/ chamber	mean wt./ worm g.	respiration 1	2	3	4	5	6	mean resp.	variance	standard error	SE %
Adults	2	0.518	30.4	28.7	33.1	55.4	79.2	36.9	43.95	326.21	7.37	17
Subadults	3-4	0.338	39.4	26.5	40.1	35.8	51.2	40.2	38.87	53.00	2.97	8
Juveniles	6-10	0.123	35.5	30.7	-	43.6	38.2	33.6	35.32	19.23	1.96	5
Newl. hatch.	21-23	0.022	47.8	48.3	-	56.2	68.7	-	55.25	71.40	4.22	8

1) (1-3) and (4-6) were run on separate occasions

B. With burrowing medium of unsterilized sandy loam 1)

	worms/ chamber	mean wt./ worm g.	1	2	3	4	5	mean resp.	variance	standard error	SE %
Adults	3	0.416	45.9	51.4	46.1	22.0 2)	53.5	49.22	10.96	1.66	3
Juveniles	7-8	0.128	62.5	63.2	54.9	73.7	64.2	63.61	34.32	2.62	4
Newl. hatch.	14-22	0.019	55.8	66.1	64.8	-	-	62.20	21.05	2.64	4

1) (1-5) all run together, for each of the developmental stages

2) Discarded; leakage in the tubing system

Table 6. Respiration of *Aporrectodea tuberculata*. µl O_2 $g^{-1}h^{-1}$ (live wt) and *A. longa*

A. 12°C.

	worms/ chamber	mean wt./ worm g.	1	2	3	4	5	6	mean resp.	variance	standard error	SE %
Adults	1	1.279	36.5	33.6	37.0	-	-	-	35.69	2.32	1.08	3
Juveniles	2-3	0.328	60.7	48.8	52.9	49.9	60.4	56.1	54.80	21.76	2.08	4
B. 2.5°C.												
Aestivating subadults	1	0.596	7.6	10.6	7.3	-	-	-	8.47	2.21	1.05	12

C. Respiration of *Aporrectodea longa*. µl O_2 $g^{-1}h^{-1}$ (live wt) at 12°C

	worms/ chamber	mean wt./ worm g.	1	2	3	4	5	mean resp.	variance	standard error	SE %
Subadults	1	1.731	27.9	27.2	26.5	38.0	28.1	29.54	18.14	2.13	7

nes fitted to the plots by linear regression. Now it can better be seen that the respiratory rates apply to the general rule, becoming smaller with increasing body weight. It is also seen that the respiratory rates recorded in the series without burrowing medium (line 1) were at a somewhat lower level than those recorded in the series with burrowing medium present ($p < o.o5$; t- test) line 2). It is also noted that the results from the series without- were much more variable than those in the series with burrowing medium (Table 5), although the relationship was still significant ($p < o.o2$). Therefore, from an ethological point of view, it seems likely that the behaviour of *A.caliginosa* in the chambers with burrowing medium was close to normal field behaviour. The activity in the chambers without burrowing medium appears to have been abnormally low, however, with intermittent burst of activity, producing the higher variability in the measurements. The straight line 3) Fig. 28, represents juvenile and adult *A.tuberculata*, including subadult *A. longa*, because on inspection of the plots it became apparent that the *A.longa* measurements fitted the same straight line as *A.tuberculata*. The relationship between respiratory rate and body weight of these two species was similar to that of *A.caliginosa* and highly significant ($p < o.ool$) Table 8). Thus it appears that respiratory rate in earthworms is related to individual weight and not to a specific developmental stage.

Considering the significant relationship between respiratory rate and body weight it may be convenient, in large field surveys, where it is impossible to weigh worms individually, to take the respiratory rate from the regression lines of the mean body weight of the different developmental stages, thus also overcoming the variability of the direct measurements. This has been done in Table 7, which also gives the range of the body weights of the respective developmental stages. For adult, subadult, juvenile and newly hatched A.caliginosa, the respiratory rates thus obtained were: 45.8, 53.o, 6o.3 and 65.o μl O_2 $g^{-1}h^{-1}$ (live wt). The corresponding figures for A.tuberculata were: 37.5, 45.o, 54.o and 59.o. For subadult A.longa the respiratory rate was 29.5. All the above figures refer to experiments with burrowing medium.

If the general relationship between respiration and body weight is expressed as a double logarithmic plot of caloric output (1 ml O_2 = 4.775 calories; Heilbrun 1947) and body weight, a straight line appears, the equation of which takes the form: $R = W^n + y$; or $\log R = n \times \log W + \log k$. The slope of the line, n, is a fractional power of the body weight, W, and log k a constant. Hemmingsen (1960), calculated a standard poikilotherm line with $n = 0.751$, from literature data on a wide variety of poikilotherm animals, including also plants and microorganisms. n was slightly different for the different groups of organisms, but always between $n = 1$ for a direct respiration-weight relationship, and $n = 0.67$ for a direct respiration surface area relationship. The present respiratory data have been treated in the same manner, and in Fig. 29, regression lines with n- values of o.864, o.821, and o.866 are shown for: 1) Data with- and without burrowing medium combined, 2) combined data with burrowing medium, and 3) A.caliginosa without burrowing medium. The correlation coefficients for the respective lines were all highly significant (Table 8). Line 2) is probably more representative for the active worms in comparison with line 3), which may be closer to the standard conditions, the difference, however, being only o.o89 log decades (1.22 times).

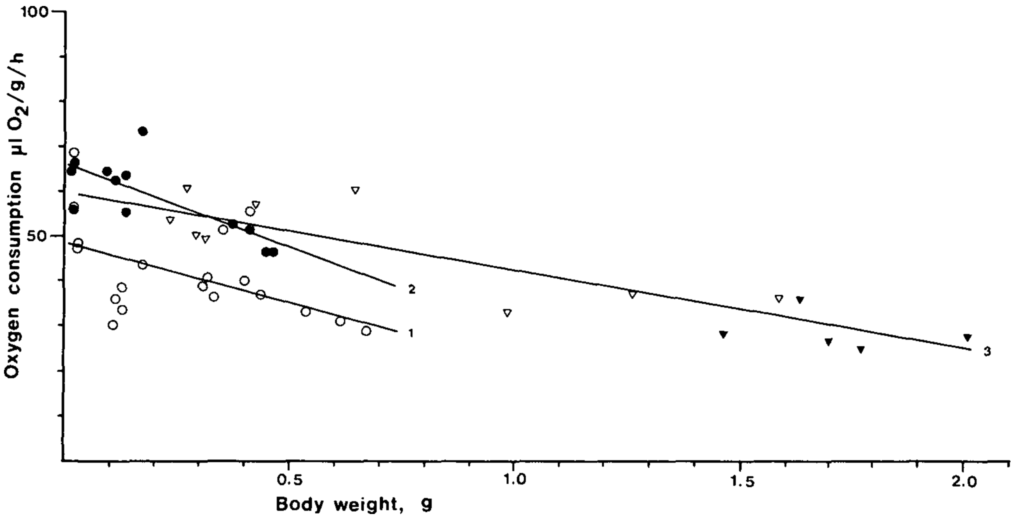

Fig. 28. Correlation between respiratory rate and body weight. 1) ○A.caliginosa without burrowing medium. 2) ●A.caliginosa with burrowing medium. 3) ▽A.tuberculata / ▼A.longa with burrowing medium,

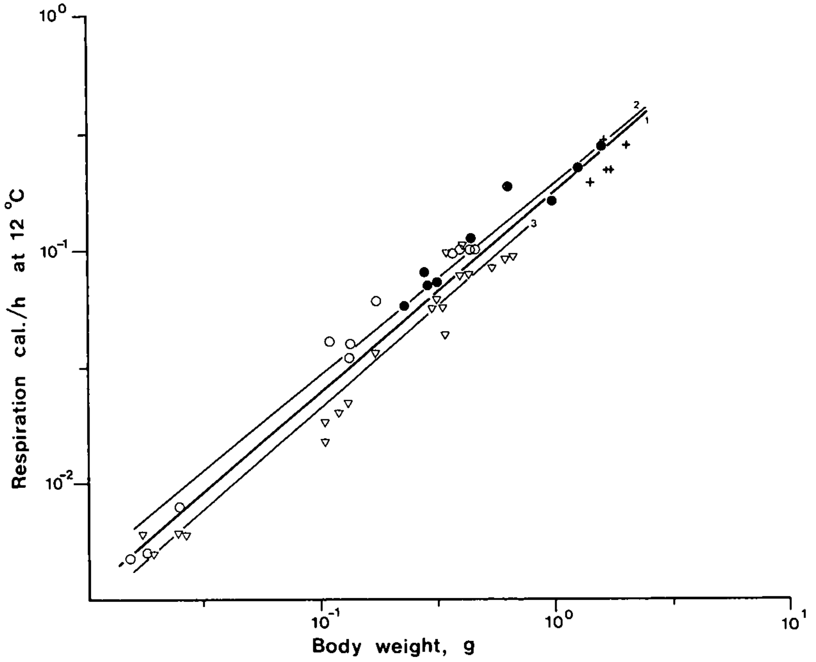

Fig. 29. Correlation between caloric output and body weight. + A.longa, ●A.tuberculata, ○A.caliginosa. 1) All data. 2) Exclusive data without burrowing medium. ▽A.caliginosa without burrowing medium, 3).

Table 7. Respiratory rate, µl O_2 $g^{-1}h^{-1}$ of different developmental stages of the earthworms Aporrectodea caliginosa, A. tuberculata and A. longa taken from linear regressions. Respiration measured at 12°C.

A. caliginosa	range of body weight g	mean body wt. g	with burrowing med.	without burrowing medium
Adults	0.4 - 0.7	0.55	45.8	34.0
Subadults	0.3 - 0.4	0.35	53.0	39.3
Juveniles	0.02 - 0.3	0.15	60.3	44.3
Newly hatch.	0.02	0.02	65.0	48.0
A. tuberculata				
Adults	1.0 - 1.6	1.30	37.5	
Subadults	0.7 - 1.0	0.85	45.0	
Juveniles	0.03 - 0.7	0.35	54.0	
Newly hatch.	0.03	0.03	59.0	
A. longa				
Subadults	1.75	1.75	29.5	

In fig. 30, the authors data have been combined with most of the available literature data, corrected to 12 °C, to yield a common lumbricid relationship between caloric output and body weight. The line (Fig. 30) represents data on the following species: *Lumbricus terrestris*, *L.rubellus*, *L.castaneus*, *Aporrectodea caliginosa*, *A.tuberculata*, *A,longa*, *A.rosea*, *Eisenia fetida*, *Eiseniella tetraëdra*, *Octolasion lacteum*, *O.cyaneum*, *Dendrodrilus rubida* and *Dendrobaena octaëdra*. The following sources were used: Konopacki 1907, Davis and Slater 1928, Raffy 1930, Krüger 1952, Byzova 1965 and Phillipson and

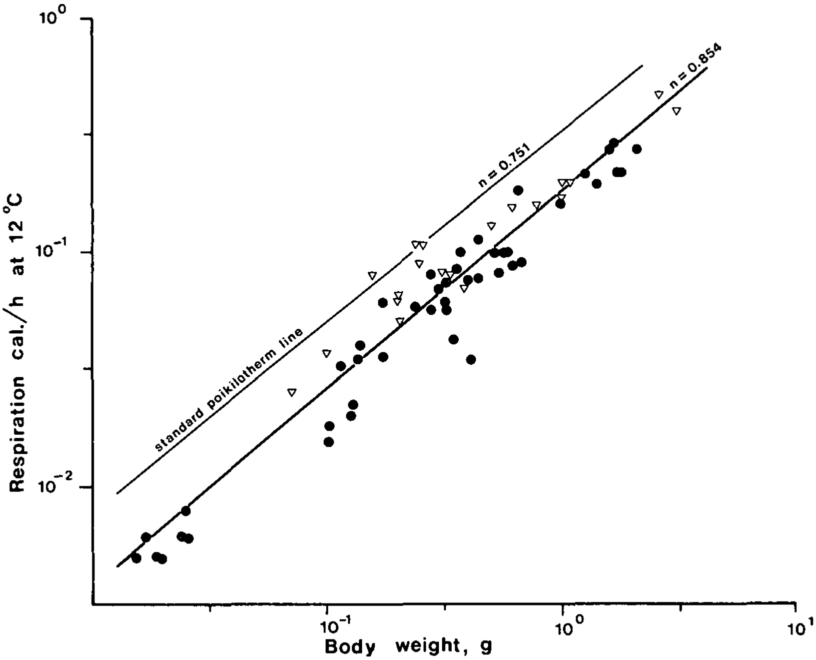

Fig. 30. Correlation between caloric output and body weight. ●Combined lumbricid respiratory data, inclusive, ▽litterature data, at 12 °C.

Table 8. Correlations on respiratory data

		slope n	constant log k	correlation r	significance p<	degrees freed. f	reference to figure
A.	A. caliginosa (-)	-	-	-0.4926	0.02	18	Fig. 28 line 1)
	A. caliginosa (+)	-	-	-0.7456	0.01	10	- - 2)
	A. tuberculata/ A. longa (+)	-	-	-0.8832	0.001	12	- - 3)
B.	A. caliginosa (-)	0.866	-0.822	0.9813	0.001	18	Fig. 29 line 3)
	A. caliginosa/ A. tuberculata A. longa (+)	0.821	-0.733	0.9867	0.001	23	- - 2)
	Combined (- and +)	0.864	-0.762	0.9799	0.001	43	- - 1)
	Combined data incl. available litt.	0.854	-0.725	0.9999	0.001	62	Fig. 30
	Stand. poikilotherm	0.751	-0.480	-	-	-	Hemmingsen 1960

A: Correlation between respiratory rate (µl O_2 $g^{-1}h^{-1}$) and body weight (g) at 12°C.

B: Correlation between respiratory output (cal. h^{-1}) and body weight (g) at 12°C.

(+) and (-): With, respective without burrowing medium.

Bolton 1976. The slope of the regression line was, n = 0.854, which is not far from from the standard value of n = 0.751. The relationship was highly significant (Table 8). The lumbricid line lies 0.28 log decades below the standard poikilotherm line, corresponding to a difference of 1.9 times, which should not be too surprising, taking the relative sluggishness of earthworms into consideration.

DISCUSSION

Various factors may influence the results obtained during respiratory measurements, e.g., nutritive state of the worms, composition of the atmosphere in the respiratory chambers, acclimatisation of the worms before measurements and in particular the presence of a suitable burrowing medium in the respiratory chambers. The significance of a burrowing medium in terms of thigmotactic reactions, emerges from the fact, that if worms of the genus *Aporrectodea* used in the present study are put into a small box provided with moistened layers of thin paper cloth, they will quickly establish themselves between the layers, and if kept cool be in good condition after more than three weeks, except for the effect of starvation. If the worms are kept in a similar box without paper cloth, only in a small amount of water, they may soon become relatively motionless, somewhat flaccid and elongated, however moving around from time to time. If a number of individuals of, e.g., *Eisenia fetida* are kept in water alone, they will aggregate to form bundles, thus exhibiting an elevated state of activity to maintain these. Either type of thigmotactic response is likely to influence the respiratory measurements.

In a comparative study of different respirometry techniques, Wightman (1977), tried to vary the environmental conditions, using a heat sterilized soil as a burrowing medium for the test animals, larvae of the scarabaeid beetle, Pachnoda ephippiata, which is a predator. In other studies (Newell et al. 1974; Petrusewicz and Macfadyen 1970 and probably also Phillipson and Watson 1965) noted an excited phase before accommodation to the respiratory chambers had taken place. In P.ephippiata larvae, this excited phase lasted longer if the larvae were accommodated in soil. This implies that the higher rate of oxygen consumption is closer to what happens under natural conditions. Wightman confirmed this by observing individuals in petri dishes. When no soil was present, the larvae moved around in the dishes for 1 - 2 hours and then lay stationary, with intermittent bursts of activity. Yet when there was sufficient soil to cover the larvae, they were in almost continuous motion, which conforms with the observation that P.ephippiata larvae tend to move through the soil until they find food. The oxygen consumption after the end of the excited phase is therefore most representative of the standard condition. Thus normal behaviour of an animal must be carefully judged before respiratory data are included in an energy budget.

The respiratory techniques studied by Wightman (1977) were constant pressure respirometer (O_2), Gilson Differential respirometer (both O_2 and with a CO_2 modification for RQ determination), Infrared Gas Analyzer IRGA (CO_2), gaschromatograph (O_2 and CO_2) and a Kipp Zonen Diaferometer, KZD. Statistical similar results were obtained with the different techniques, except for the KZD, which proved unsuitable for measurements on small invertebrates. Further he found that heat sterilization had not removed all microbial activity and had to make allowance for this.

Phillipson and Bolton (1976), used IRGA to measure the CO_2 output of the species Dendrodrilus rubida, Lumbricus castaneus, Aporrectodea rosea and Octolasion cyaneum. In the respiration chambers they also used a burrowing medium, consisting of a mixed, coarse and fine textured, sandy material, which had been heat sterilized and buffered to pH = 6.5. They conducted an initial 48 hour study of the accommodation in terms of CO_2 output of the worms after introduction into the respiration chambers. Lumbricus castaneus showed a high initial output, which became stabilized after 30 hours, however still remaining at a high level. D.rubida also showed a very high CO_2 output in the beginning. After 30 - 36 hours, however, it became stabilized at a much lower level than in L.castaneus. In A.rosea, a high initial output became stabilized already after 4-6 hours at approximately half the initial value. The response of O.cyaneum was similar to that of A.rosea, stabilization occurring after 12 hours. These striking differences in accommodation patterns probably reflect the nature of the burrowing medium in relation to the normal habitat of the respective species. This, however, was not discussed by the authors, although they decided to use only the last 12 hours in a 48 hours period. *A.rosea* and *O.cyaneum*, which showed the fastest accommodation belong to the endogeic group and the short accommodation time of these two species is thus consistent with their mainly mineral soil dwelling habit. *L. castaneus* and *D.rubida* belong to the epigeic group, and the longer accommodation time of these two species indicates that the burrowing medium was somewhat unpalatable for mainly litter dwelling species like these. Findings like those mentioned above seem further to stress the importance of creating environmental conditions as close to natural as possible in experiments of this kind. Using the post excited phase as mentioned above is probably representative of natural conditions, when the worms are monitored in a system with burrowing medium present. But in the case of *L.castaneus*, where the burrowing medium was very far from the natural habitat of this species and the post- excited level of CO_2 output was considerably above what was found in the other species, the CO_2 output of the last 12 hours was probably not representative of respiration during natural activity. Therefore it should be kept in mind that eventual burrowing media must be selected with due regard to the normal habitat of the investigated species.

Phillipson and Bolton converted their CO_2 figures to oxygen consumption, using RQ values obtained by Warburg technique. They found a seasonal trend in RQ values, which however tended to fall below the expected range of o.7o - 1.oo, except in D.rubida and A.rosea. Therefore it is here suggested that for comparative purposes a standard RQ = o.82 for average foodstuffs (Peterusewicz and Macfadyen 1970) should be used until further studies on this subject have been conducted.

Effects of the burrowing medium probably also obliged Phillipson and Bolton to introduce relatively large correction factors for gut content, from 16 - 25 % to 50 % in O.cyaneum. In comparison with Byzova (1965), using 10 % for endogeic species and none for epigeic, these values seem much too high to warrant general use. The high correction factors of Phillipson and Bolton may have been due to a very low organic matter content in the burrowing medium, inducing an abnormally long residence time. Byzova made her measurements of O_2 consumption in a Warburg apparatus. As long as no standard correction factors for earthworms are available, except for what can be done to create so near natural conditions as possible, this procedure seems relatively unsafe. The alternative is to create "standard" conditions, i.e., post absorbtive and resting conditions in combination with special adaptations or use of drugs, to exclude unwanted behaviour. Most similar to standard conditions in the present study is probably line 3 (Fig. 29), which was approximately 1.2 times below line 2), representing worms exhibiting normal field activity. In the present study no correction factors have been applied. In any case correction factors may represent artefacts, arising from varying experimental conditions, as far as earthworms are concerned.

The epigeic species are said to be representative of r- strategists, in comparison with the endogeic, being K- strategists (Satchell 1980), exhibiting a lower metabolic rate than the former. Introduction of unreliable correction factors may tend to obscure this concept, which probably is a real phenomenon.

One interesting question, which has not yet been answered, is how earthworm metabolism compares with that of other groups of poikilotherm animals, clustering around the standard line (fig. 30). This can be done from Hemmingsens work (1960). Lower invertebrates such as turbellarians, hirudineans and nematodes, e.g., Ascaris lumbricoides have a metabolism approximately 1.9 times below the standard poikilotherm line, which fit nicely with the combined earthworm metabolism also being 1.9 times below the standard poikilotherm line. In molluscs, slugs and snails, metabolism is from 1.7 - 2.5 times below standard poikilotherm metabolism, however, being 2.1 times above in various cephalopods, which are the most advanced and active molluscs. In various groups of crustaceans the metabolism is slightly above or below the standard line. In insects the metabolism is close to the standard poikilotherm line, but in various groups also considerably above (up to 4 times). In fishes the metabolism is generally close to the line, however (Boëtius, pers. comm. unpublished data), in benthic fishes such as pleuronectiforms, the metabolism is approximately 2 times below that of more active groups, i.e., pelagic or semipelagic forms. In reptiles the metabolism is close to the standard line, however, somewhat above in tortoises. In amphibians it is approximately 2 times below the standard line. The general impression is that in invertebrates with a rather low level of organisation, metabolism is also towards the lower end of the range, but higher in more advanced groups, e.g., insects and cephalopods. The same seems to be true for poikilotherm vertebrates. Earthworm metabolism fit very well into this pattern, reflecting that a comparatively low metabolism in sluggish animals is an inherent feature laid down during the course of evolution in the respective groups.

CHAPTER III

ECOLOGY OF A. TUBERCULATA (EISEN)

INTRODUCTION

The systematic position of *A.tuberculata*, together with that of the other members of the "*caliginosa*" complex (*turgida*, *trapezoides*, *nocturna* etc.), has been much debated over the years. A solution to these problems has recently been suggested by Zicsi (1982) and Sims and Gerard (1985).

The species *A.caliginosa* is considered a very plastic one, encompassing a variety of mostly phenotypic morphs. The *tuberculata* morph is considerable larger than the ordinary *A.caliginosa* sensu stricto (syn. *turgida*), i.e., 90-150 mm vs. 60-85 mm. Formerly these four "morphs" were commonly treated as separate species (Gates 1972). They may be distinguished on a varying development of tubercula pubertatis and genital tumescences. These variations are considered associated with larger size and increased sexual activity (Sims and Gerard 1985). The "*trapezoides*" is male sterile with a more feeble development of tubercula pubertatis and genital tumescences, following from heavy infestation by the protozoan parasite *Monocystis* spp. in the seminal vesicles.

The authors collections consist of more or less equal parts of *caliginosa* s.s. and *tuberculata*, from several sites in Denmark. "*trapezoides*" was very rare in the material collected.

In the present material it was very easy to distinguish between adult *caliginosa* and *tuberculata* on size and configuration of genital tumescences, e.g., Gates (1972). Genital tumescences in setal lines ab, segments: xxx, xxxii and xxxiv, are typical of *tuberculata*. Genital tumescences in segments xxx and xxxii - xxxiv are typical of *caliginosa*.

To operate with "morphs", being that different and constant may be disputed; also the concept itself seems somewhat intriguing. This, however, is a very delicate matter, which may still not be settled. From the present investigations it appears that the larger morph, i.e., *tuberculata* (*nocturna* has not been recorded from Denmark), is no more sexually active than the smaller *caliginosa* (syn. *turgida*)as suggested by Sims and Gerard (1985). This is also contradictory to the presumably more K- strategic-like behaviour of the larger *tuberculata* and *nocturna*. It appears that sexual activity (=reproduction), apart from climatic causes, is controlled more or less exclusively by organic matter input.

It has not been documented, e.g., by electrophoretic studies, whether or not reproductive isolation is established between *caliginosa*, *tuberculata* and *nocturna*. By electrophoresis it was found (Jaenike 1982; Øien and Stenersen 1984), that there was complete reproductive isolation between *Eisenia fetida* and *E.andrei*, which otherwise may only be separated from each other by the colour pattern. Consequently, it may as well be advocated, taking the greater morphological differences into account, that an electrophoretic study might show the *caliginosa* morphs to be reproductive isolates, and thus good species after all. In the present studies, either caliginosa or tuberculata was dominating, which may not easily be explained. This perhaps may be the only thing in favour of the "morph" concept. That caliginosa and tuberculata, however, are physiologically different may be indicated by the growth experiments (p.134), and so long as no conclusive evidence to the contrary has been produced, it is felt more safe to consider A.tuberculata a good species. Hence, this has been done throughout the present work.

METHODS

A large population of A.tuberculata has been studied at Roskilde Experimental Station from August 1980 to December 1981, by weekly samplings of one 0.5 m^2 quadrate. Sampling was performed by digging and handsorting the layers, 0-10, 10-30 and 30-60 cm. The worms were sorted into developmental stages, adults, subadults, juveniles and newly hatched individuals. At the same time the activity state of individual worms was noted. Soil temperatures were recorded at the time of sampling, at 5, 20 and 40 cm depth, generally at 10 am, using a Grant continuous temperature recorder. Other meteorological data for the station were obtained from the Danish Meteorological Institute. Respiration of A.tuberculata (adults and juveniles) was measured as oxygen consumption in a Gilson Differential Respirometer at 12 ^{o}C (p. 61). The field data have been evaluated in terms of general biology in relation to climatic factors and popu-

6

lation development. The population data (number and biomass) were gathered from undisturbed surfaces, except for winter ploughing in 1980, after sugar beets, and seed-bed preparation in spring 1981 for oil rape.

CLIMATIC CONDITIONS AUGUST 1980- DECEMBER 1981

Precipitation and temperatures during the study period are given in Fig. 31. Precipitation is the weekly rainfall measured at the station, and the temperatures are given as mean weekly air temperatures, including also the absolute minimum and maximum temperatures. During spring and summer, temperatures and rainfall tend to follow each other, and with respect to the response of the earthworms, this is best interpreted from the records of precipitation. During autumn and early winter the worms respond to the general lowering of temperatures, and in lesser degree to precipitation, which during that period in general is sufficient to keep an adequate level of soil moisture for earthworm activity. In the following the overall climatic development during the study period is summarized, and after that, the response of the earthworms is treated.

Temperature

From the beginning of September 1980, mean air temperatures steadily decreased from 15 °C to a minimum of 1 °C in the middle of the first half of November, with night frost occurring from the last week of October. Then there was a milder period until the middle of November, with mean air temperatures reaching 7 °C, however still with night frost during some nights. From the beginning of December real winter conditions were encountered. Milder periods occurred during the second half of December, and likewise during the beginning of February 1981. In the beginning of March 1981 mean air temperatures gradually rose from 0 °C to 7 °C in the first half of April, which was without night frost. This was followed by a temperature drop with night frost in the second half of April. From the beginning of May, temperatures increased rapidly, and summer conditions with mean air temperatures of 15 - 16 °C prevailed until the middle of August. From then, until the middle of the first half of October, mean air temperatures decreased slowly until 10 °C was reached. Then mean air temperatures decreased more rapidly to 5 °C in the middle of October. Night frost began around the first of November, however, with a mild period during the second half of November. Thereafter temperatures decreased rapidly and reached a minimum of -10 °C mean air temperature in the middle of December, with an absolute minimum of -22 °C.

Precipitation

After a dry week in the beginning of September 1980, there was a rainfall of 42 mm in the middle of the first half of September followed by a mean weekly rainfall of 10 mm until the end of October, which was more wet. During winter precipitation was moderate, with a weekly precipitation between 10 and 30 mm. Relatively dry periods were encountered during the end of January and February. March 1981 was relatively wet with a total precipitation of 85 mm. April was relatively dry, and also the first half of May. Then rainfall increased, reaching a maximum of 65 mm in the last week of May. Relatively dry periods were encountered in the middle of June, beginning and middle July, the two first weeks of September, middle of the second half of September, middle of October and in the beginning of November.

VERTICAL MIGRATION

Newly hatched

In September 1980, 100 % of the newly hatched *A.tuberculata* (Fig. 32D) were found in the upper 10 cm; but from the beginning of October, with decreasing temperatures, there was a rapid downward movement, and from November until December, 70 - 100 % of the newly hatched were found in the 10 - 30 cm layer. The mild second half of November seemed to cause a small upward movement. During winter approximately 50 % of the newly hatched individuals were found below 30 cm depth, but they did not move so deep as the larger individuals. At

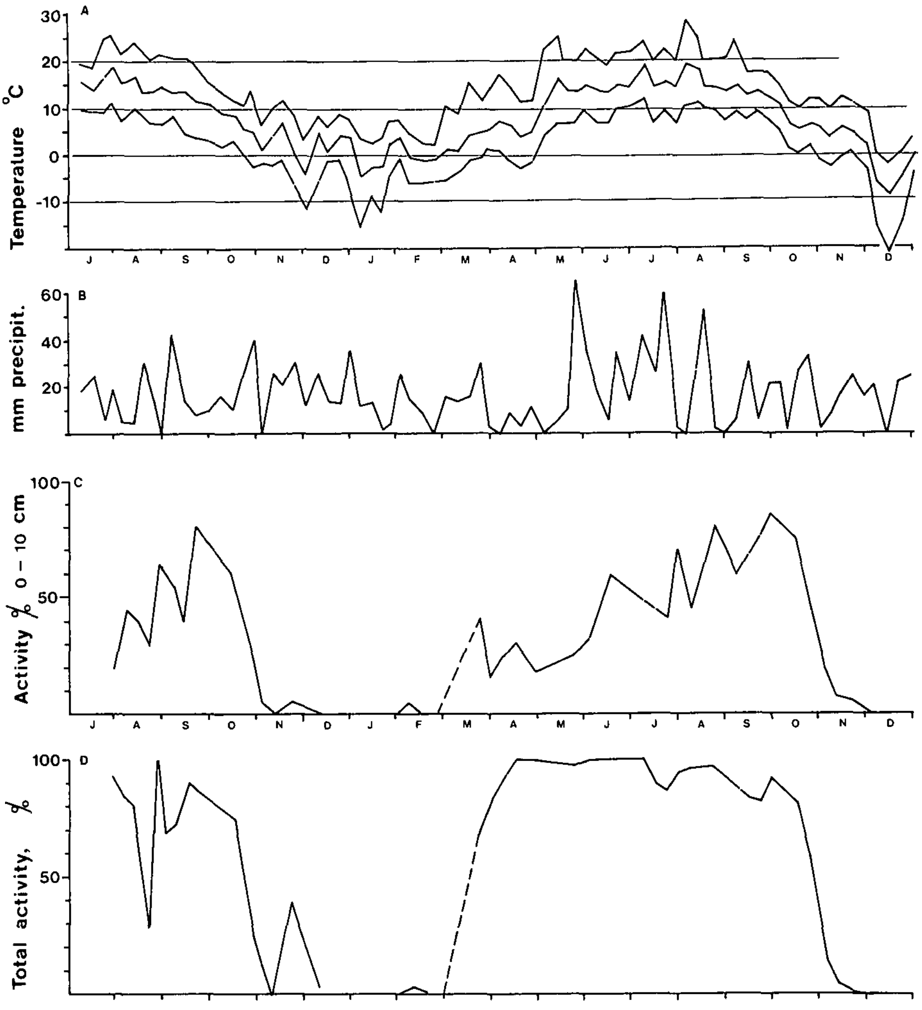

Fig. 31. A. Weekly mean air, absolute maximum and absolute minimum temperatures, ^{o}C, at Roskilde Experimental Station, 1980 - 1981. B. Weekly precipitation, mm. C. Activity %. Percent active worms (not rolled up and aestivating) present in the 0 - 10 cm layer. D. Toal activity %. Percent active worms (not rolled up), 0 - 60 cm.

the end of March 1981, upward migration had already started, and newly hatched individuals were again found in the upper 10 cm layer. The worms which were found here, probably consisted of both overwintering, and worms which had just been hatched. As a result of the low precipitation during April and most of May, there was a new downward migration from the upper 10 cm, so that at the middle of the second half of May, all of the newly hatched A.tuberculata were found in the 10 - 30 cm layer. Then following the heavy rainfall at the end of May, there was a general upward migration, and during summer nearly all of the individuals were found in the 0 - 10 cm layer. Just after the middle of July, there was some downward migration from the upper 10 cm. This was most likely caused by a high evapo-transpiration by the oil rape relative to rainfall, resulting in a decrease in soil moisture, and also by a significant part of the precipitation being intercepted by the now very dense foliage, which had developed. The same effect could by seen on the other size classes as well. From the end of July, following heavy rainfall, until the middle of September, 100 % of the newly hatched worms could be found in the upper 10 cm layer. Around the middle of September, again some movement down to 30 cm was observed, followed by a renewed upward migration until the middle of October, after which rapid downward migration as a result of lowering temperatures was observed. At the middle of November 50 % of the newly hatched worms were found between 10 and 30 cm depth. Later on migration to depths below 30 cm

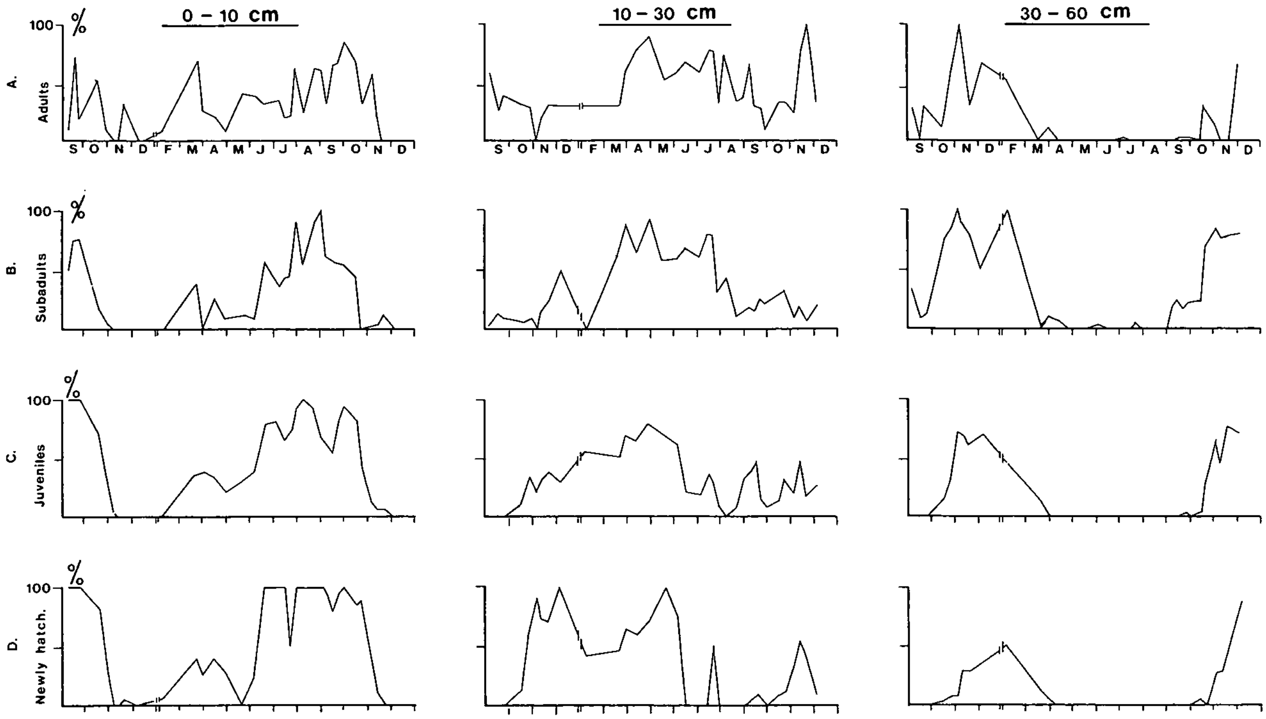

Fig. 32. Vertical distribution of *Aporrectodea tuberculata*, 1980 - 1981, at Roskilde Experimental Station, measured by weekly samplings of the 0 - 10, 10 - 30 and 30 - 60 cm layers. The percent distribution between the respective layers are given for: A, adults, B, sub - adults. C, juveniles and D, newly hatched individuals.

was seen, and in the beginning of December 90 % of the worms were found here.

Juveniles, subadults and adults

The vertical migrations of the other developmental stages followed the same general pattern as for the newly hatched. However, probably as a result of better burrowing capabilities, they seemed to respond more quickly to changing weather conditions. It also seemed that the fastest reaction was found among adults, and in decreasing order among subadults and juveniles. This was in particular seen with regard to migration between the 0 - 10 cm layer and the 10 - 30 cm layer from June until November, with alternating periods of rainfall and more dry conditions. In all the size classes (adults) subadults and juveniles), there was an upward migration during March, followed by a downward migration during April and May as a result of low rainfall and a cold period during the end of April. Downward migration accelerated from the middle of October, interrupted by a short period with upward migration during the mild second half of November. (Fig. 32 A - C). The final upward migration before winter was not so pronounced in the juveniles and subadults, as in the adults.

POPULATION DEVELOPMENT

Emergence of newly hatched

Newly hatched individuals of the species Aporrectodea tuberculata weigh from 30 - 50 mg and rapidly gain weight. 14 days after emergence the weight is from 100 to 150 mg, and from then they are classified as juveniles. In order to estimate the total emergence of newly hatched worms during a given period, a smoothed curve was constructed, each plot representing the mean of two successive catches. From this curve, a new curve was constructed by interpolation, with a time interval between each plot of 14 days, showing the calculated emergence (Fig. 33). Only active worms were plotted, i.e., worms which were not aestivating, rolled up into a ball. Under the assumption that worms which were recorded as newly hatched in a given 14 days interval had passed on to the juvenile stage at the advent of the following interval, a cumulative curve of plots of newly hatched individuals present in each 14 days interval, as described above, will then be a measure of the hatching which has actually taken place. This was done for the emergence of new individuals from August 1980 until December 1981 (Fig. 35C). From the cumulative curve the hatching during a given period can easily be found.

From (Fig. 33) it is seen that there exists a bimodal pattern of emergence of new individuals in A. tuberculata, with peaks during spring and autumn. The hatching thus recorded seems to

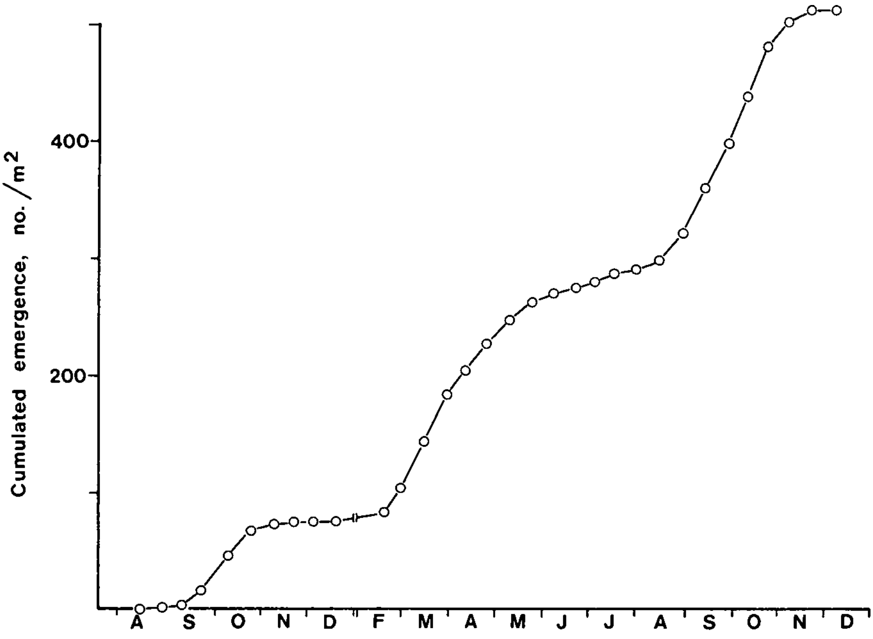

Fig. 33. Cumulative emergence of newly hatched individuals of A.tuberculata. Roskilde, 1980 - 1981.

be derived from cocoons produced approximately three months before. Therefore, from the mean number of adults present at that time, it should be possible to calculate the mean cocoon production per worm per month during a given time interval of the year.

Development time of cocoons

From the cumulative curve of hatching (Fig. 33) it is seen that from the second half of August 1981, there was an increased rate of hatching of new individuals, which again decreased from the end of October until the end of November. Likewise in spring, an increased hatching began already at the end of February, slowing down at the end of April. From the end of May until the end of August only a few new individuals emerged. In this way the emergence pattern is clearly divided into two distinct periods, each of approximately three months length, which indicates a developmental period of three months for cocoons produced during spring and summer. Overwintering cocoons produced during the autumn appear to require 6 months for development.

Number of cocoons produced

If the mean number of cocoons produced is estimated from the mean number of adult worms present during successive periods of three months length (Fig. 34) it is found that the reproductive rate was highest during autumn (1980), i.e., 2.7 cocoons/worm/month , and lowest during spring (1981), only 0.5 cocoons/worm/month . During the summer (1981), cocoon production was somewhat higher than in in spring, 1.1 cocoon/worm/month. This gives a total of 13 cocoons/worm during a 9 months active period. The rate of cocoon mortality and the rate of cocoon predation are not known, but should be added to the above mentioned figures, which thus are considered minimum estimates. Compared to other species (Edwards and Lofty 1977) it appears that A.tuberculata reproduces at a relatively slow rate, K- strategy (Satchell 1980b).

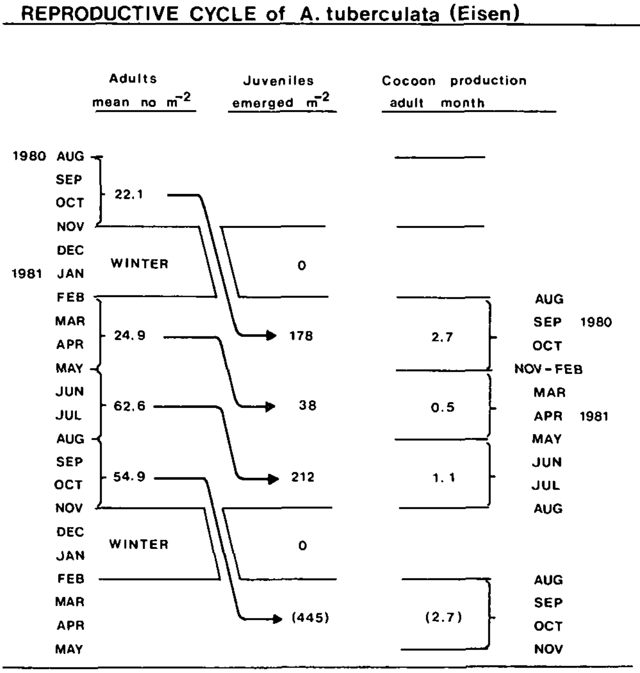

Fig. 34. Reproductive cycle of A.tuberculata. Roskilde, 1980 - 1981.

Juveniles

An increased emergence of new individuals is expected to be followed by increased numbers of juveniles afterwards. This is very nicely demonstrated in the autumn 1981 (Fig. 35B), where there was a rapid increase in the number of juvenile individuals approximately 14 days after the increase in the number of newly hatched individuals recorded (Fig. 35C). However, in the middle of October, there was a marked decrease in the number of juveniles present, which continued until sampling ceased in the beginning of December. The decrease was not caused by soil tillage, but must be attributed to the combined effect of pathogens and predators. The decline coincided with a drop in mean air temperature to about 5 °C (Fig. 31), with soil temperatures in the 0 - 10 cm layer of 6 - 8 °C. The relationship between decreasing temperatures and increased suspectibility to certain pathogens is not known, but could be brought into consideration.

The most important predators are probably found among centipedes and ground beetles. The most common ground beetles are, _Pterostichus_ _melanarius_, _Agonum_ _dorsale_ and _Bembidion_ _lampros_, constituting 90 % of the population (Schieller, pers. comm.). These however, cannot contribute to any significant mortality among the worms during November - December, when also ground beetles become inactive. Between March and September they may be more important.

From about mid February until the end of March 1981, there was some increase in the number of juveniles, which then tended to become stabilized at mid April after a decrease of 50 %. The increased number in the beginning of March could be a result of overwintering newly hatched individuals now entering the juvenile stage, together with increased hatching of cocoons. The 50 % decrease observed from the beginning of April was most likely caused by predation and seed-bed preparation for the oil rape, including cultivation between the rows after emergence of the seedlings.

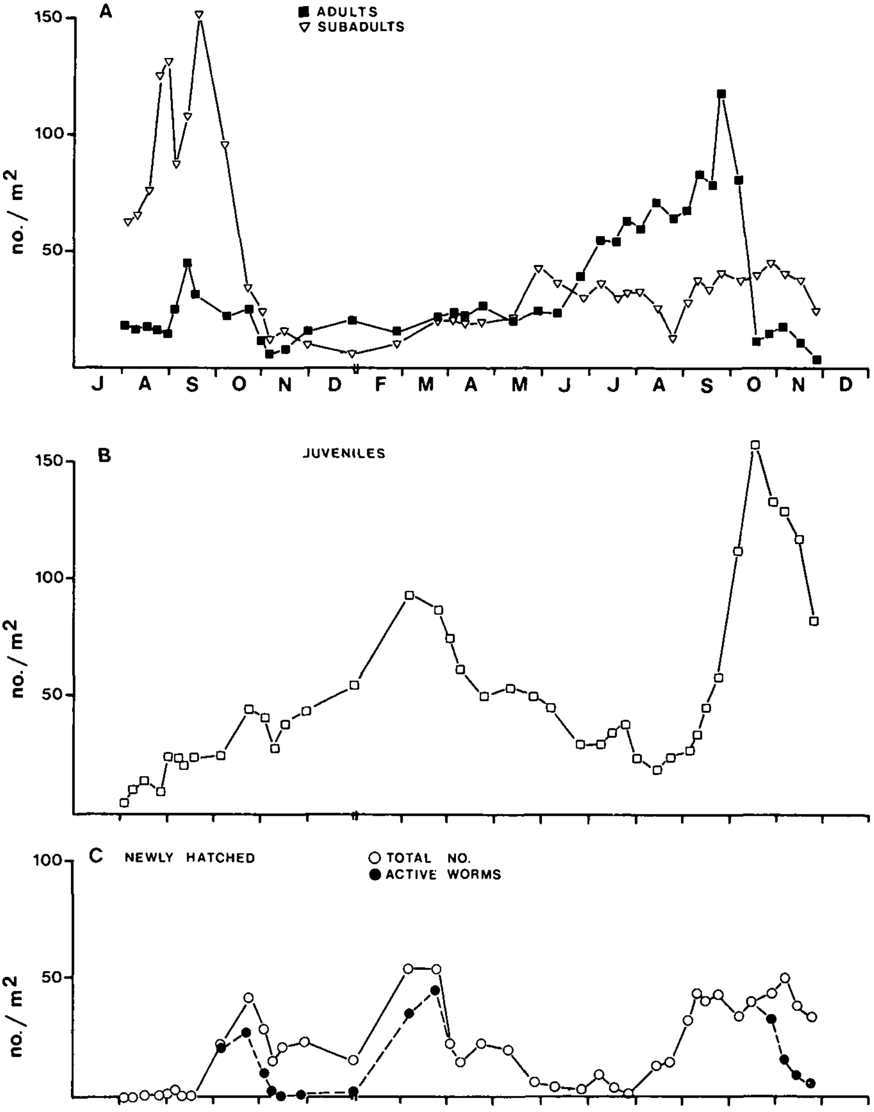

Fig. 35. Seasonal dynamics of A.tuberculata, Roskilde, 1980 - 1981. A. adults and subadults. B, juveniles. C, newly hatched.

Subadults and adults

During August and September 1980 (Fig. 35A), quite large numbers of subadults were found, 130 individuals/m^2 in comparison with the number found at the same time in 1981, being only 4o-5o individuals/m^2. The reason for this difference may have been the very hard winter between 1979 and 1980, being followed by a relatively cold spring (Met.1980), retarding development. This is also indicated by a low number of adults in August - September 1980 and a relatively high number in August - September the next year, 1981. The winter between 1980 and 1981 was not so cold as the preceding one.

After a cold period during the second half of April 1981 (Fig. 31), temperatures increased rapidly during the beginning of May, in contrast to 1980, when the temperature did not rise significantly until the beginning of June (Met. 1980). During October 1980, there was a rapid decrease in the number of subadults until the beginning of November, which is not readily explained; neither by climatic conditions nor soil tillage. Samples were taken on undisturbed surfaces and the temperature was only gradually decreasing, although night frost began during the last week of October. Again mortality from various pathogens must be taken into consideration. However, this side of earthworm ecology has only been little studied. During spring until June 1981, the number of subadults increased relatively slowly, ending with a sudden peak (Fig. 35A), after which the level was fairly constant until the end of October, however, with a decline at the end of August. During the same period the number of adults was also relatively constant until the end of June, At this time the number of adults increased rapidly (Fig. 35A) from about 25 individuals / m^2 until the middle of October, where the number of adults reached a maximum of 125 individuals / m^2. The onset of the increase in adult numbers was 2-3 weeks delayed with respect to the occurrence of the maximum of subadults at the end of May, which may indicate that the time for transition from the subadult stage to the adult stage is about the same duration. The number of juveniles was highest in early spring, after which there was a constant decrease in juvenile numbers until the middle of August. This is consistent with a continuous recruitment of juveniles to increase the number of subadults and adults. The decline in the number of juveniles, however, is much more steep than the corresponding increase in the number of adults and subadults, indicating a high mortality among the juveniles. The number of juveniles did not increase until after the beginning of the autumn hatching in the beginning of September.

After the occurrence of the maximum number of adults in late September 1981, there was an extremely rapid decrease in numbers during October, to about 20 individuals / m^2. The reason for such a rapid decrease may in part be related to dying off of older individuals, perhaps in combination with increased mortality from pathogens. The effect of predation is difficult to assess, but on the larger worms the influence of bird predation is probably more significant than that of insects.

General population development

In Fig. 36 biomass and density has been plotted together, and it is seen that during winter, both biomass and density was low. During March and the beginning of April after activity had been resumed, including emergence of new individuals, both density and biomass increased. This tendency was interrupted because of a cold and dry period during late April. By the end of May the spring hatching ceased, and during summer until the end of August, there was a slight decrease in density. Because of continued growth, biomass however, still increased. When the autumn hatching began in late August, density again began to increase.

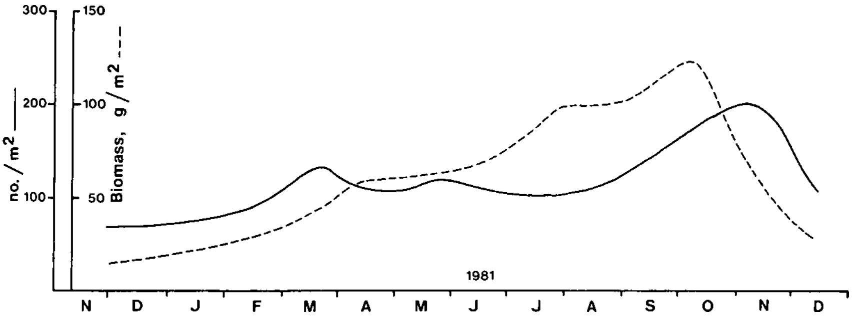

Fig. 36. Seasonal dynamics of total number and biomass of A.tuberculata at Roskilde Experimental Station, 1981.

From June and during the rest of the summer (Fig. 31), most worms could be found in the 0 - 10 cm layer, where food is most abundant, and from August until the middle of October, biomass increased rapidly (Fig. 36). At the end of August autumn hatching began, and density increased steadily until the beginning of November. At the middle of October there was a sudden decrease in biomass, related to a great mortality among adults (Fig. 36). However, density continued to increase because of continued hatching until the middle of November, whereafter also density decreased rapidly, becoming close to the situation at the same time the previous year.

DISCUSSION

Seasonal activity has been studied by Nordström (1975) as part of an extensive study of lumbricid associations in a variety of habitats in Southern Sweden (Nordström and Rundgren 1973, 1974), yielding results more or less similar to the present. It was found that Allolobophora and Aporrectodea spp. became inactive more readily than do Lumbricus spp. Fewer A. caliginosa were inactive in July (1966), with very low soil moisture in permanent pasture and elm - ash-wood than in beech wood, where soil moisture was not so low. At Roskilde the lowest activity recorded was in August 1980, 3o % (Fig. 31), after a period with weekly rainfall between 10 and 22 mm. This is almost the same as was found for July in Southern Sweden (1966) in permanent pasture and elm - ash wood. At Roskilde weekly rainfall in 1981 was between 2o and 40 mm during June and July, and activity only fell to 85 % at the end of July. The following week rainfall was 60 mm and activity increased to about 95 %. During the second half of August and the first half of September, rainfall was relatively low, below 10 mm per week and one week with 30 mm. During this period activity fell to 80 % (Fig. 31). During October weekly rainfall was from 20-30 mm, and a short period with increased activity was observed, but because of decreasing temperatures, activity decreased rapidly from the end of October until December (Fig. 31 and 32), when activity ceased. These reults tend to confirm that _Aporrectodea_ / _Allolobophora_ spp. respond relatively quickly to rainfall in terms of activity / inactivity, i.e., the % rolled up and aestivating in a small chamber. This response is still more easily recognized when the migration between the 0 - 10 cm layer and deeper layers (Fig. 31 and 32) is considered. Vertical migration has been studied by Rundgren (1975) in the same biotopes as Nordström (op.cit.). Here sampling was performed every sixth week, and the same general trend was observed as in the present study, but owing to the greater time interval between samplings, vertical migration could not be followed so closely as in the present study, where weekly samplings were taken. Gerard (1967) also studied vertical distribution and seasonal activity in a permanent pasture, with the same general conclusions, however, based on fewer samplings than in the above mentioned studies. He also made some conclusions on mortality of worms in the field, and stated that only a small part of the total mortality could be attributed to parasites and predators, and that most deaths were among newly hatched individuals in June and July, where the top 10 cm layer dried out on several occasions. From Fig. 36, it can be seen that in 1981, the lowest record of newly hatched worms was found also during June and July. However, during this period no drying out of the soil took place, and the low density of newly hatched worms is here attributed to a low hatching rate. Almost all the dead worms found by Gerard, were found in a rolled up state in the top soil. In the study by Gerard a significant part of the population during June - July consisted of newly hatched worms, which is in contrast to the present study, where the greatest density of newly hatched worms was found from March to May, during spring.

Apart from mortality caused by desiccation, directly observable in the field, causes of mortality seem difficult to analyse and quantify, and may as mentioned before be attributed to either adverse climatic conditions, pathogens, parasites, predation or senescence, which is discussed in the following. In both 1980 and 1981, the most marked mortality was observed from October to November, and any combination of the parameters mentioned above may be brought into consideration. In the autumn 1980, there was a very large proportion of subadult individuals in the population (Fig. 36A), and a great mortality among these, in comparison with other size classes, was observed. In the autumn 1981 there was a large proportion of adults and juveniles, and a great mortality was observed among both size classes during October and November. First among adults during October, and later, during November, among the juveniles. The proportion of subadults was relatively low in the autumn 1981, but also some mortality was observed in this size class. Cuendet (1979) found that black-headed gulls following the plough could remove up to 20 % of the earthworm population, but in the present investigation, on undisturbed surfaces, bird predation could be expected to be less important, and thus cannot account for the great mortality observed during the autumn 1980 and 1981. Therefore one could think of a combined action of pathogens and parasites and a greater suspectability to these at the beginning of aestivation as a major cause of mortality, and not so much of climatic conditions and predation. For the adults also senescence may be important at this time of the year. The reason for the large proportion of subadults in the autumn 1980 could have been the long and hard winter 1979 / 1980, as discussed in the earlier section (p. 95), and if senescence was of some importance for mortality among adults, this was not easily observed at the low densities in 1980. In 1981, increased mortality among adults began at the end of September, extending into October, but no significant number of aestivating adults was observed until the middle of November. Therefore it could be argued that senescence was a major cause of mortality in the beginning, and that later on mortality from pathogens and parasites took over, after the adults began to aestivate. For the other size classes the major cause of mortality would then also be the action of parasites and pathogens, in combination with aeativation. Significant downward migration of juveniles was seen from the middle of October (Fig. 32C), simultaneously with a rapid decrease in density. As proposed before, it seems unlikely that climatic parameters could have been a major cause of mortality at that time, where soil temperatures (Fig. 37) were still from 7 - 8 °C at all depths. Unfortunately dead earthworms go very rapidly into dissolution in wet soil, and they possess no hard parts, which can be used in the identification of dead worms later on, and practically no worms in an advanced state of dissolution were recovered on handsorting. Virtually nothing is known about which specific pathogens and parasites may actually cause the death of earthworms. Here a large work still remains to be done. A study of this kind would also require a very accurate timing with the onset of aestivation of the different size classes.

Also Rundgren (1977) has studied the seasonal emergence of earthworms in Southern Sweden, and he found that the greatest emergence of A.caliginosa during spring took place from April to June. This was a little earlier than was found by Gerard (1967) at Rothamsted, but still a little later than was found at Roskilde for A.tuberculata. This may be attributed to a real difference between *A.caliginosa* and *A.tuberculata* in this respect, although the two are very closely allied; but also differences in soil temperatures may contribute. At Roskilde, soil temperatures were between 5 and 6 °C in the 0 - 30 cm layer in March, which was somewhat high (owing to a mild winter) in comparison with soil temperatures in Southern Sweden in 1966, which were only from 2 - 4 °C down to 50 cm during April. In Southern Sweden the emergence pattern was similar for *A.caliginosa* and *A.rosea*, with the greatest hatching during spring, occurring from April to May. Another peak was observed during the autumn. In *L.terrestris* the greatest hatching took place from May to June. Gerard (1967) found a somewhat different emergence pattern for *Allolobophora chlorotica*, where most hatching took place from June to August, however, with a marked decrease during September, because of severe desiccation. Thus it appears that there are differences in emergence pattern between the different species, and that precipitation and temperature may cause significant variations from a more general pattern from one year to another in this respect, as well as to distribution of size classes.

CHAPTER IV

FIELD RESPIRATION OF APORRECTODEA TUBERCULATA

INTRODUCTION

Several workers have reported on density and biomass of earthworms in habitats ranging from moorland, coniferous forests, deciduous woodland to arable soil, Andersen 1980b, 1983; Lofs-Holmin 1983a, 1983b; Persson and Lohm 1977; Phillipson et al. 1978; Reichle et al. 1975; Satchell 1967, 1980a and Wilke 1962, including many others. In comparison, relatively few have tried to estimate their energetical importance in terms of contribution to total soil respiration or turnover of organic matter, measured as oxygen consumption, carbon combustion or nitrogen turnover. Some of the most detailed studies in this respect are those of Persson and Lohm 1977; Phillipson et al. 1978; Satchell 1967 and Andersen 1983. Calculations are generally based on measurements of respiration compiled from various sources, and in the case of turnover rates of nitrogen and carbon, directly from measurements of growth and excretion, or often more indirectly by application of McNeil and Lawtons (1970) equation for productivity. Different techniques of respirometry have been used (p. 72) at different temperatures. Also conditions for the worms in the respirometers have been very variable, ranging from respiratory chambers without a burrowing medium (Warburg technique) to chambers with seminatural - to as near natural conditions as possible. In the following is given an analysis of the oxygen consumption of a field population of Aporrectodea tuberculata in arable soil, where the population consisted almost exclusively of this species. This is the same population at Roskilde Experimental Station, which was treated in the previous section.

METHODS

The calculations are based on 27 samplings from November 1980 to November 1981, and because only one 0.5 m^2 was sampled on each occasion, the biomass figures used are the means of two consecutive samplings. The same procedure was adopted for the temperature data for the three depths, 0-10, 10-30 and 30-60 cm, also taking the temperatures as mean temperatures of the respective strata. The oxygen figures used in the calculations are representative of resting, but non aestivating A. tuberculata at 12 ^{o}C (Table 7), and were 45.0 and 54.0 μl O_2 g^{-1} $hour^{-1}$ for adults and juveniles respectively. Oxygen consumption of aestivating worms is based on measurements on aestivating subadults at 2.5 ^{o}C, i.e., 8.5 μl O_2 g^{-1} $hour^{-1}$. The O_2 consumption of the two size classes being present in the respective strata was corrected to mean soil temperature by

Krogh's curve (1914) for each time interval. Finally the respective O_2 figures were summarized to yield the annual oxygen consumption.

In the following oxygen consumption is discussed in relation to vertical migration, seasonality and feeding biology.

RESULTS AND DISCUSSION

Annual oxygen consumption

The annual oxygen consumption of the A.tuberculata population is shown in Table 9, and amounted to 25.5 l O_2 $m^{-2}year^{-1}$. A further analysis of this result seems to reveal some interesting features concerning the ecology of both A.tuberculata and earthworms in general, at least with respect to the endogeic, the group to which A.tuberculata belongs. The annual oxygen consumption of the active worms was 24.0 l O_2 m^{-2}, and it is seen (Table 9), that this part amounts to 94 % of the total annual consumption, and that only 6 % was used during aestivation. This probably has a twofold cause. Firstly there was a general decline in population density towards the advent of winter, and secondly there was a change in the physiological status of the worms during aestivation, the respiration being reduced by approximately 36 %, as an adaptation to the low winter temperatures, and perhaps also to a lower oxygen tension in the more or less water filled

Table 9. Field respiration of Aporrectodea tuberculata at Roskilde Exp. Station

A. Adult and juvenile respiration in different depths.

Active worms:		l O_2 m^{-2} annually	%
Adults	0-10 cm	6.30	51.5
	10-30	5.86	47.8
	30-60	0.09	0.7
Total adults		12.24	
Juveniles	0-10 cm	6.20	52.6
	10-30	5.19	44.0
	30-60	0.39	3.3
Total juveniles		11.79	
Total active		24.03	
Aestivating worms:			
Adults	0-10 cm	0.00	0.0
	10-30	0.02	14.2
	30-60	0.14	85.8
Total adults		0.17	
Juveniles	0-10 cm	0.03	2.2
	10-30	0.34	27.1
	30-60	0.89	70.6
Total juveniles		1.26	
Total aestivating		1.43	
Total annual resp.		25.46	

B. Respiration of total active and aestivating worms in different depths.

Active worms:	l O_2 m^{-2} annually	%
0-10 cm	12.51	52.0 of active resp.
10-30	11.05	46.0 -
30-60	0.48	2.0 -
Active total	24.03	94.4 of total annual resp.
Aestivating:		
0-10 cm	0.03	2.0 of active resp.
10-30	0.37	25.6 -
30-60	1.03	72.4 -
Aestiv. tot.	1.43	5.6 of total annunal resp.

soil in the deeper layers. This fits very well with the fact that earthworms possess a very low lipid content, 6 - 8 %, and thus seem unable to store significant energy reserves to be used during the cold season. The endogeic worms are generally said to conserve energy (K- strategy), i.e., low metabolic rate, relatively low reproduction and greater longevity than the epigeic, which mostly rely on a greater cocoon production to overcome adverse seasons. As to metabolism and reproductive rate, _A.tuberculata_ conforms with the endogeic concept, but in terms of longevity, this seems not to be very pronounced, according to the relatively great mortality before winter in both 1980 and 1981 (Figs. 35-36). This seems to indicate that survival of the adverse winter season, to a relatively great extent must depend on overwintering cocoons. This is also consistant with the greatest cocoon production, taking place during the autumn, which is rather similar to what has been said about the epigeic, which are r- strategists (p.11).

The conclusion is that among small sized endogeic species, at least in habitats with extreme exposure likely to occur, e.g., arable soil, longevity appears to be limited in comparison with larger species, such as _A.longa_ and _Octolasion_ spp. But in more protected habitats with a litter layer, continuous grassland, parks and deciduous woodland, longevity of small endogeic species may probably be greater. However, sufficiently detailed studies of population structures over the seasons, being able to clarify this have not yet been performed. There may also be considerable variation among individual species within the frames of the endogeic concept, e.g., according to Phillipson and Bolton 1977, A.rosea takes more than 2 years to reach maturity, and thus exhibits extreme longevity and development time.

Oxygen consumption and vertical migration

If the attention is drawn towards where in the soil profile the greatest energy expenditure takes place (Table 9), it is not surprising, that during the active period, more than 50 %, i.e., 52 %, takes place in the 0 - 10 cm layer, and 46 % in the 10 - 30 cm layer, but only 2 % below 30 cm. This distribution seems clearly related to search for food, food being most abundant in the ploughing layer, 0 - 25 cm. Looking at the oxygen consumption during the inactive period (aestivation), it is seen that for adult worms, which retreat deepest into the soil during winter, 86 % of the oxygen consumption takes place in the 30 - 60 cm layer and only 14 % in the 10 - 30 cm layer, whereas for juvenile worms the corresponding figures were 70 and 27 % for the 30 - 60 and 10 - 30 cm layer, respectively. The time distribution of the energy expenditure in relation to depth is seen to be somewhat skewed during the active season, so that during spring and early summer, most energy is used in the 10 - 30 cm layer, being allocated to the top 10 cm during late summer and autumn. This is illustrated in Fig. 32 A - D, for the time distribution of the worms in the respective soil layers. The development of soil temperatures seemed to be the most important factor governing this distribution in conjunction with precipitation, i.e., drought. However, moisture throughout the study period seemed to be adequate, except during the end of April (Fig. 31), and no large scale downward migration and onset of aestivition as a result of lack of precipitation was recorded during summer. From the end of March / beginning of April, there was a relatively warm period, which seemed to coincide with the onset of a rapid upward migration from below, being reversed, however, during the second half of April. During this period, with dry clear weather,

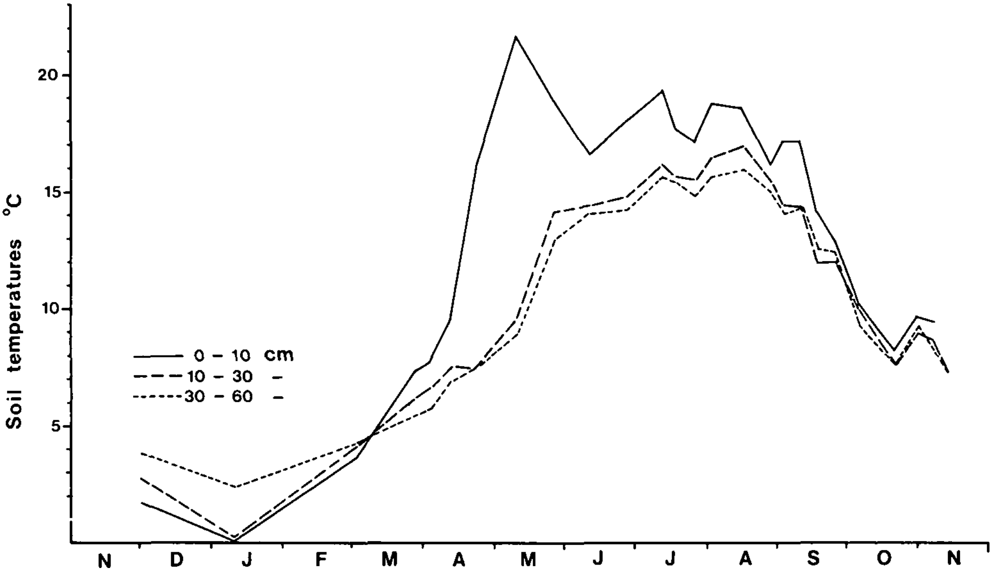

Fig. 37. Mean temperatures of the soil layers, 0-10, 10-30 and 30-60 cm at Roskilde, measured at 10 am. 1981.

there was a great insolation during the day, and a great irradiation during night time (night frost), At the same time there was a slow increase in the temperature of the deeper layers. The highest temperature of the year in the 0 - 10 cm layer was reached around May 1st, and during the following period the insulating effect of the developing crop, oil rape, became more and more significant. This resulted in a slow decrease in the temperature of the 0 - 10 cm layer, until the beginning of September, whereas temperatures of the deeper layers reached a maximum in the middle of August (Fig. 37), after a steady increase. During the same period there was a generally increasing population density in the upper 10 cm. Thus it appears that food resources in the upper 10 cm layer are being increasingly exploited during the season, until the middle of October, which is consistent with cocoon production also being greatest during the second half of the active period (Fig. 34).

CHAPTER V

PILOT STUDIES ON THE GROWTH OF A. CALIGINOSA, A. TUBERCULATA, A. LONGA AND O. CYANEUM

INTRODUCTION

Growth of a number of lumbricid earthworms has been studied by different authors to clarify various aspects of ecology, e.g., the effect of heavy metals (Neuhauser et al. 1984), pesticides (Lofs-Holmin 1980, 1982). Other studies have dealt with growth and reproduction in relation to suitable systems and media for rearing worms in greater quantities.

Only a few studies have been made under as near natural conditions as possible, in order to produce data applicable to field conditions (Satchell (1967), on _L.terrestris_ and Phillipson and Bolton (1977), in a very comprehensive study on _A.rosea_).

The present account deals with the growth of three species, which are very common in arable soil, _A.caliginosa_, _A.tuberculata_ and _A.longa_, including a fourth species, _Octolasion cyaneum_, the occurrence of which is more sporadic. In the present study it was attempted to set up a seminatural system with respect to feeding and temperature regime, including minimal disturbance on weighing occasions.

At this point it must be stressed that the experiments reported on here are of somewhat preliminar nature, because of the relatively low number of individuals used for each of the species. However, with the experimental technique developed here, it nevertheless seems possible to obtain a reasonably degree of accuracy, because environmental variables may be easily controlled. From other studies it appears, that although large numbers of individuals were employed, it has been difficult to obtain reliable results on growth rates, e.g., in studies on Eisenia fetida (Satchell pers. comm.). The results reported on here, being based on rather few individuals of the respective species, are by no means contradictory to what is known on the general ecology of the different species, but obviously needs confirmation in a more extensive survey, which must be kept in mind. However, it can also be said, that if the utmost care is taken to standardize and control routines, as in the present experiments, using suitable small containers and mostly isolated individuals, the worms indeed seem to perform very well.

MATERIAL AND METHODS

The worms used were newly hatched individuals of the species Aporrectodea caliginosa (Sav.), A.tuberculata (Eisen) (p. 79), A.longa (Ude) and Octolasion cyaneum (Öerly), emerging from cocoons isolated from laboratory stocks of the respective species.

The experiments were performed in cylindric 350 ml PVC- jars, each containing approximately 300 g sandy loam (arable field topsoil, Tåstrup), passed through a 5 mm mesh screen. The jars were lined with a loose polythene tube, fitting the inner diameter of the jars, which made it possible to remove the whole content of the jars (inside the polythene tube) as intact soil cores, except for some loose surface material. This design made it very easy to split individual soil cores into a few pieces and isolate the worms for weighing. After weighing, the soil cores were reassembled, wrapped with new polythene foil and put back into the jars. The worms were guided back into the soil through burrow openings on the surface. Any loose material remaining was put back on the top.

This procedure caused minimal disturbance of the worms and allowed weighing on each 14 day. Later during the experiments, when the worms had become larger, the disturbance caused by taking out the soil cores, would make the worms crawl out by themselves, or stimulation of the head or tail ends would make them crawl out of the still intact soil core. In the bottom of the jars were drilled three 1 cm holes for drainage, sealed with nets (0.5 mm mesh size) to prevent the worms from escaping. The cultures were maintained in constant darkness at 12 °C, and regularly watered to field capacity. Before weighing, the worms were submerged into tap water to remove adhering soil, and then gently rolled on blotting paper. Weighing took place in a small plastic box with closed lid to minimize evaporation during the weighing procedure. On handling, the worms sometimes voided some gut content, which so far as possible was collected and weighed together with the worms.

A. longa Experiment

Six individuals were kept in separate jars for a period of 45o days. The worms were fed ad libitum with a mixture of crushed Ulmus spp. and Tilia spp. litter, distributed in the top 2 - 3 cm of the soil cores.

A.tuberculata

Three individuals were kept separately under the same conditions as for A.longa. Instead of leaf litter as food, 5 g ground barley straw, particle size, 0.2 - 0.8 mm, was mixed into the total soil volume. The experiment lasted for 150 days.

A.caliginosa

1) One individual was kept alone for 150 days under the same conditions as for A.tuberculata.

2) One individual was kept alone, under the same conditions as for A.longa for 450 days.

3) In this experiment several worms were kept together in the same type of jars as before, using both leaf litter and ground barley straw as food. During the course of the experi-

ment, the number of worms in the cultures was reduced. Weighing intervals were weekly during the first 5 weeks, thereafter with 3 weeks intervals, and finally with approximately monthly intervals. The whole series lasted for 456 days.

3a) 6 juveniles, mean weight, 280 mg, were kept on *Tilia - Ulmus* litter (10 g) in the same jar. After 118 days, three individuals (adults) were transferred to a new culture with 10 g ground barley straw added / 300 g soil. The original culture was continued on leaf litter, with addition of 10 g, also on day 118. On day 138, one individual was removed from the leaf litter culture, and one more on day 220, thus leaving one worm for the rest of the period. In the barley straw culture, one worm was removed on day 350, leaving two worms for the rest of the period.

3b) Eight individuals, mean weight, 124 mg, were kept in the same jar, with addition of 10 g ground barley straw / 300g soil. On day 118 another 10 g was added. On day 31, 87, 118 and 370, respectively, one worm was removed, leaving four worms for the rest of the period. Between day 370 and 401, the soil was renewed in all the cultures (3), without addition of new food. Only data from exp. 1) and 2) on *A. caliginosa* were used to construct the growth curve. In experiment 3) the environmental conditions were very variable, and the results originating from this experiment were only used for tracing more general effects of these.

O. cyaneum

The course of this experiment was similar to that of experiment 3) for A.caliginosa. 7 smaller juveniles of somewhat varying size, mean weight, 224 mg, were introduced into the same jar, containing 300 g soil, mixed with 10 g barley straw. After 136 days, the size of the worms, however, had become markedly different, and the culture was split into two, one containing two larger worms, and the other, four smaller worms. At the same time the culture medium was renewed, with addition of 10 g ground barley straw. During the rest of the experiment, the soil was renewed with approximately 3 months intervals, without addition of ground barley straw. Accidentally two periods with partially drying out of the cultures occurred, resulting in aestivation with zero-growth or weight loss. The experiment was finished after 517 days.

Treatment of growth data

To illustrate the growth pattern of the different species, growth curves were constructed for each of these. The growth curves were typically s- shaped (logistic growth), the ordinary formula for which is of the form $W = A / (1 + B^{\rho x})$ (Snedecor and Cochran 1967). This type of growth requires somewhat complex methods of curve fitting, which has not been attempted here. More interesting, it is to look at the relative specific growth rates of the different species (weight gain per day per unit body weight; in the following denoted v′). v′ is often used in productivity estimates of animal populations (Petrusewicz and Macfadyen 1970; Andersen 1983).

v′ is likely to change with increasing body weight and age of a particular species. v′ has been calculated from the original growth data, for each interval between weighings. This could also have been done by means of the growth curves, which however, would have precluded assessment of the actual rates, v′. When the calculated v′ figures were plotted against body weight, it was seen that an exponential decline of v′ might be assumed. Therefore the v′ figures were log transformed, and a straight forward linear regression performed (least squares method). The accuracy of the fit of the straight line then determines the degree to which v′ declines exponentially with increasing body weight.

In ecological literature is often referred to the respiration / production ratio (R/P), from which it may be calculated how much of the assimilated energy (A); A = R + P, is converted into growth. R was estimated from the standard respiratory line for earthworms (Chapter II, Fig. 30), using average biomasses and v′ figures calculated from the growth curve of the most common species A. caliginosa at successive 10 days intervals. Calorific equivalents for the biomass data were obtained, using 17 % for dry matter content (excl. gut content) and 4.52 Kcal g $^{-1}$ (Phillipson et al. 1978). On plotting R/P against body weight, a curve of the exponential type appears, which was treated similar to the v′ - body weight curve. This procedure gives an idea of the utilization of the assimilated energy.

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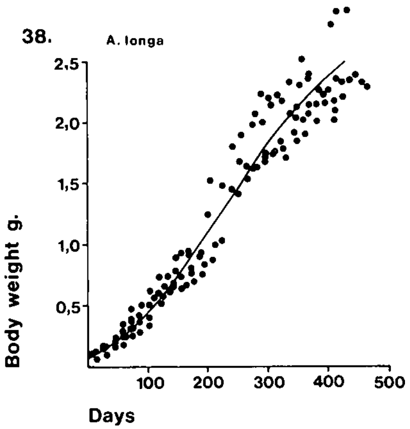

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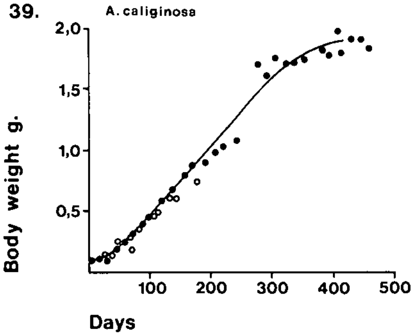

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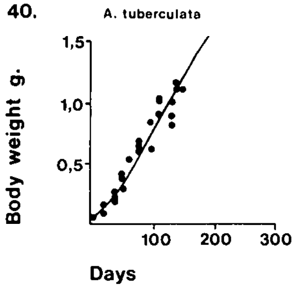


Figs. 38 - 40. Growth curves of three species of earthworms. 38, *A. longa*. 39, *A. caliginosa*. 40, *A. tuberculata*.

RESULTS

The growth curves for the different species are shown in Figs. 38 - 42, and are all of the logistic type. In most cases the duration of the experiments was long enough to estimate, with only little extrapolation, the maximum weight obtainable under the specific environmental conditions for the respective species. Maximum weight may be maintained for a longer period, before senescence begins, several years have been reported for some species, followed by weight loss and death.

A.longa (Fig. 38) reached a mean body weight of 2.5 g after 450 days, apparently without having reached maximum weight, which from extrapolation of the growth curve would probably be close to 3 g under the specific environmental conditions encountered in the present experiment. Tubercula pubertatis appeared after approximately 300 days, at a mean weight of 1.75 g. After this the worms became clitellate during the following 2 - 3 weeks, thus becoming sexually mature in less than one year. Moisture content of the cultures seem to be the environmental factor, which has to be most carefully monitored during experiments of this type. Although uniform conditions were attempted at the beginning of the experiments, individual jars seemed to lose moisture at different rates after some time, which may cause the worms to go into aestivation. Worms which had gone into aestivation were easily revitalized by putting them into ordinary tapwater for 15 - 20 minutes.

A. caliginosa

Experiment 1)

The single specimen, which was kept on Tilia - Ulmus litter, reached a body weight of 1.85 g after 45o days, which is probably close to the upper limit for this species. Adult specimens from field samples rarely exceed 0.70 g. This particular specimen became clitellate at a weight of 0.80 g after 200 days.

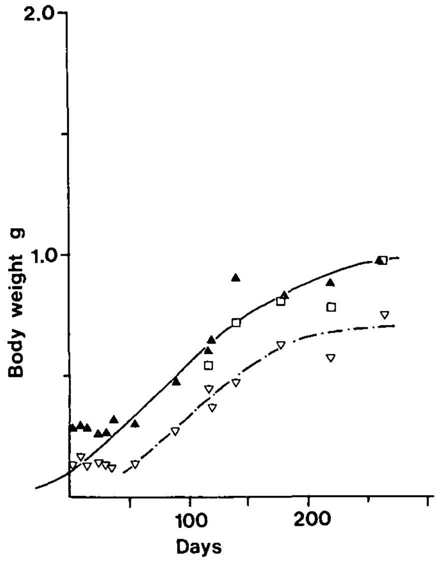


Fig. 41. Growth of A.caliginosa. ▲Tilia - Ulmus litter. □ Straw powder, after splitting of the culture on leaf litter. ▽Straw powder alone.

Experiment 2)

The single specimen kept on ground barley straw reached a body weight of 0.85 g after 150 days. Clitellum appeared after 135 days at a weight of 0.57 g. The growth data from both experiment 1) and 2) seemed to fit the same curve and were used to construct the growth curve Fig. 39.

Experiment 3)

This experiment showed that the worms were unable to gain weight when the burrow systems were destroyed by weighing with weekly intervals (Fig. 41). Not until the "minimal disturbance " method was adopted after the first 5 weeks, the worms were able to gain weight. The worms which were kept on leaf litter (Fig. 41), reached maturity after 120 days, at a mean weight of 0.66 g. In those, being continued on this diet, growth began to decrease after 150 - 200 days (Fig. 41). When the experiment was finished after 456 days, the single worm left weighed 1.10 g.The worms which were transferred to a ground barley straw medium, however, seemed to grow somewhat better and reached a final weight of 1.50 g after 456 days. In the culture with 8 individuals, being kept in one jar on ground barley straw (Fig. 41), weight gain was somewhat slower than in the leaf litter culture. The final weight was 0.80 g. At this time 4 worms remained in the culture. Maturity, however, was not reached until after inflexion of the growth curve between day 340 and 370, at a body weight of 0.65 g. Up to this time 5 worms were present in the culture. The delayed appearence of clitellum under these conditions may indicate that food had become limited. The difference between the litter culture and the barley straw culture, where fewer worms were present, may have been caused by the ground barley straw being more readily attacked by microorganisms in comparison with the leaf litter, which was only crushed and not mixed homogeneously into the total soil volume.

A. tuberculata

This experiment lasted only for 150 days. The growth curve was more steep for this species (Fig. 40) than for A.longa and A.caliginosa. Maturity was reached after approximately 120 days at a body weight of 0.90 g. At the end of the experiment the mean body weight of the worms was 1.20 g.

O. cyaneum

Fig. 42 shows two growth curves of typically logistic shape, each representing slightly different environmental conditions. After 136 days it was decided to distribute the worms between two cultures. In culture 1), two worms were introduced, and 4 in culture 2). The mean weight of the 4 worms in culture 2) was fitted onto the common growth curve for the first 136 days of the experiment as the starting point for culture 2). During the course of the remaining period, two periods where the cultures dried out were encountered. This resulted in zero growth and weight loss in both cultures (Fig. 42). When these data points are omitted, two well defined growth curves appear, 1) and 2), representing 2, respectively 4 worms in the same culture. It is seen that with 4 worms in the culture, the worms tended to grow more slowly than with only 2 worms in the same culture. At the end of the experiment (after 517 days) the mean weight was ap-

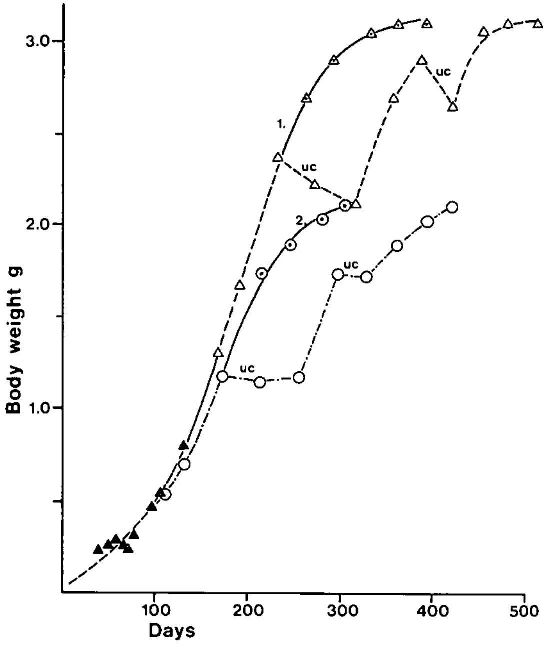


Fig. 42. Growth of Octolasion cyaneum. ▲Before splitting of the culture (7 worms). △After splitting (2 worms). ○After splitting (4 worms in a single jar). ◬Data corrected for inactivity, culture 1. ⊙Same correction, culture 2. UC, unfavourable conditions in the cultures.

proximately 1.0 g lower than in 1). In the culture with two worms present, maturity was reached after approximately 200 days at a body weight of 2.0 g. With 4 worms in the culture, the corresponding figures were 250 days and 1.8 g respectively. The extrapolated maximum body weight in culture 1) was 3.2 g and 2.2 in culture 2). The relevant growth data for all the investigated species are summarized in Table 10.

Table 10. Growth data on different species of earthworms

Species	Worms/ jar	Dev. of clitellum		Maximum weight		Food	Food g/jar	Duration of experiment
		days	wt. g	days	wt. g			
A. longa	1	320	1.90	600	3.00 ×	Litter	Unlimited	450 days
A. caliginosa	1	200	0.80	400	1.90	Litter	Unlimited	450 -
-	1	135	0.57	300	1.20	Straw	5	150 -
-	6 → 1	120	0.66	250	1.00	Litter	10	456 -
-	3 → 2			250	0.90	Lit.→Str.	10	456 -
-	8 → 4	350	0.65	250	0.70	Straw	10	456 -
A. tuberculata	1	120	0.90	300	1.80 ×	Straw	5	150 -
O. cyaneum	7 → 2	200	2.00	400	3.20	Straw	10	517 -
-	7 → 4	250	1.80	400	2.10	Straw	10	517 -

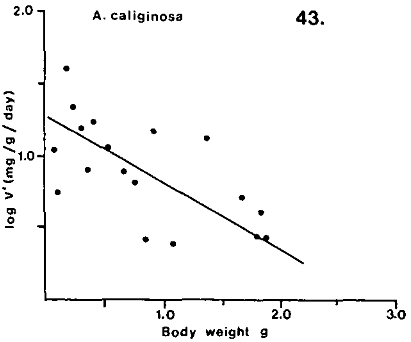
×: Data obtained by extrapolation of the growth curve.
Litter: Crushed *Ulmus* and *Tilia* leaves.
Straw: Ground barley straw (0.2 - 0.8 mm particle size).

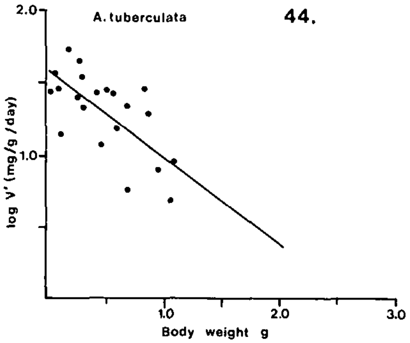
Arrows indicate that the number of worms was changed during the experiment.
See text for further details.

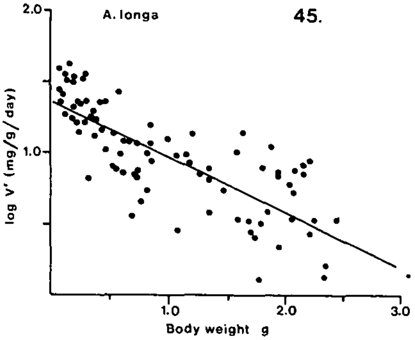
Relative specific growth rate

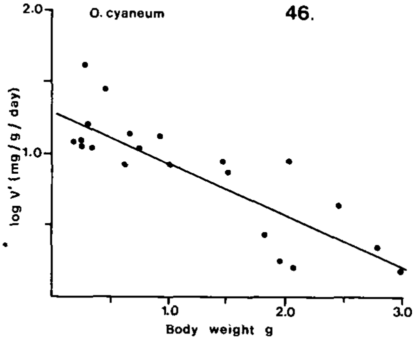
The linear regressions on log v′ and body weight are reproduced in Figs. 43 - 46. The slope of the regression lines, y- intercept, correlation coefficient and significance are given in Table 11. The correlation coefficients lie between -0.72 and -0.84, which for all species give p- values of less than 0.001, which seem to confirm that v′ declines exponentially with increasing body weight. It is noticed that the data points are relatively scattered, which may indicate a non uniform growth pattern. In A.longa there were 5 replicates of isolated individuals, giving 83 data points (negative growth rates omitted). The correlation coefficient for A.longa was -0.77, which is in the middle of the range, indicating that correlation may only be improved by very large sampling. In A.tuberculata, the data originated from three isolated worms and in A.caliginosa only from a single individual. In O.cyaneum a number of worms were kept in the same jar (7), and later 2 and 4 together in two separate jars, which seemed to smoothen out differences in individual growth rates. Here the correlation coefficient was as high as -0.84. Therefore the apparent scatteredness of the data points is probably a real biological phenomenon, which may be due to an alternating burrowing-feeding behaviour.

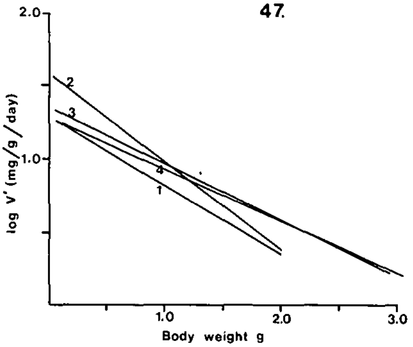
The slopes of the regression lines are given in Table 11, and the respective lines are shown in Figs. 43 - 46. The steepest slopes were found in A.tuberculata and A.caliginosa, -0.609 and -0.457 respectively. The slope of the regression lines for A.longa and O.cyaneum were less steep, -0.382 and -0.354 respectively. Thus the steepest slopes were found in the two smaller species. The Y- intercept gives the order of magnitude of the initial relative specific growth rate (v′).











Figs 43 - 46. Relationships between relative specific growth rate and body weight.

Fig. 47. The regression lines of Figs. 43 - 46 shown together. 1) A.caliginosa. 2) A.tuberculata. 3) A.longa. 4) O.cyaneum.

Table 11.

Relationships between log growth rate, mg $g^{-1}day^{-1}$ and body wt g

Species	Slope	Intercpt.	r Correl.	Signif. of r	n
A. tuberculata	-0.6089	1.6021	-0.7508	0.001	22
A. caliginosa	-0.4574	1.2785	-0.7238	0.001	18
A. longa	-0.3818	1.3592	-0.7678	0.001	83
O. cyaneum	-0.3543	1.2833	-0.8429	0.001	21

The initial log v′ for A.tuberculata was 1.602, which is much higher than for any of the other species, where the values of log v′ (initial) lie between 1.28 and 1.36. Similar initial log v′ figures were found in both A.caliginosa and O.cyaneum, log v′ = 1.28. In A.longa it was a little higher, 1.36. Both A.longa and O.cyaneum may reach a body weight of 3 g or more, which as it appears from the present study is achieved in slightly different manners. A.longa sets out at a greater pace than O.cyaneum with respect to v′, which however declines more rapidly in this species than in O.cyaneum. This leads to the interesting fact that A.longa is "overtaken" by O.cyaneum, which as can be judged from the growth curves (Figs. 38 and 42), reaches maximum body weight in shorter time than A.longa , 400 days vs. 600 days (Table 10). The ecological significance of these differences is further developed in the discussion. A.tuberculata and A.caliginosa are relatively small sized in comparison with the two just mentioned, A.tuberculata, however, being somewhat larger than A.caliginosa. The ranges of maximum body weights in field samples of the two species are approximately from 0.6 - 0.8 and 1.2 - 1.5 g respectively. The high initial growth rate of A.tuberculata, makes it possible for this species, although the slope of the regression line is rather steep (-0.609), to reach maximum body weight in the same, or shorter time than A.caliginosa (Figs. 39 and 41). In A.caliginosa the slope was only - 0.457. The ecological implications of these differences are further treated in the discussion.

Respiration/production ratio

The R/P ratios of various developmental stages have been calculated for A.caliginosa, which is probably the most common species in arable soil in Denmark. In Table 12, the mean R/P ratios for a number of body weight ranges are given, together with the proportion of assimilated energy (P %), which is converted into tissue production. To this comes mucus production and reproductive production. From Table 12, it is seen that the P % of assimilated energy declines steadily with increasing body weight. In small juveniles 75 % of the assimilated energy is used in tissue formation, declining to 20 % or less, when body weight becomes close to maximum. From the regression on log R/P vs. body weight (Fig. 48) it is seen that the R/P ratio increases exponentially during most of the life time of A.caliginosa. The R/P

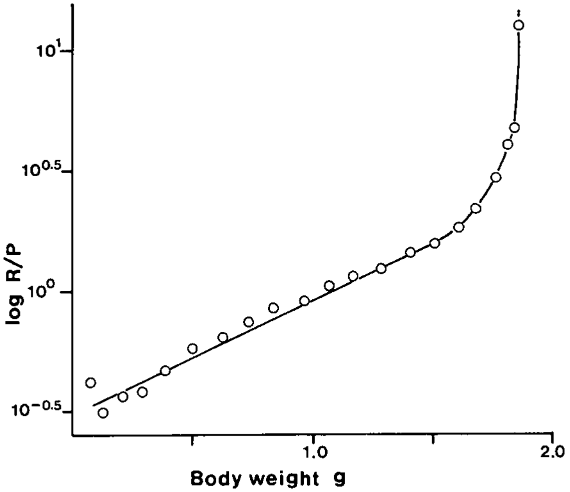


Fig. 48. Relationship between respiration/production ratio, R/P, and body weight in A. caliginosa.

Table 12.
Respiration/production ratios for A. caliginosa

Body weight, g	R/P ratio	Production, % of assimil.
0.050 - 0.200	0.35	75
0.200 - 0.400	0.43	70
0.800 - 1.000	0.82	55
1.500 - 1.800	2.65	35
1.850 -	-	20

ratios may be used to convert respiratory figures into production estimates, when the time distribution of biomass on different developmental stages are known from field sampling (Andersen 1983).

DISCUSSION

One of the most recent studies on earthworm growth is that of Lofs-Holmin (1982), who studied the growth of several species, including also those of the present study, except for A.tuberculata. The culture medium was a 50 % mixture of clay and farmyard manure in 0.25 - 1.0 l jars, depending on the size of the species in question. Weighing intervals were 1 - 2 weeks in the beginning, with greater intervals later on. The number of worms / jar was from 2 - 5. The growth on this medium, 50 / 50 % clay and FYM at 15 °C, was much faster than in the present study at 12 °C, using leaf litter or ground barley straw as food. On the FYM diet A.caliginosa and A.longa became mature after 45 and 60 days respectively, corresponding body weights being 0.5 and 1.5 g. In the present study A.caliginosa became mature after 150 - 200 days at body weights of 0.6 - 0.85 g. A.longa became mature after 320 days weighing 1.8 - 1.9 g. Differences of the same order of magnitude were seen for O.cyaneum. This clearly demonstrates that earthworms are able to grow very fast on a high quality diet as, e.g., FYM. In the present study, however, the environmental conditions were probably closer to field conditions, where food resources are generally limited. The temperature in the present study, 12 °C, was probably also closer to the mean temperature during the active period of the worms from March - November. The study af Phillipson and Bolton (1977) on A.rosea under field conditions, also revealed a much longer development time (2.5

years to reach maturity), in comparison with those recorded by Lofs-Holmin 1982, under optimal laboratory conditions. From the present figures it appears that individuals of *A.tuberculata* and *A.caliginosa,* emerging during spring, may just be able to reach maturity during the autumn of the same year and contribute to the population of the next year, if environmental conditions are favourable. This seems also to be confirmed by the field data (Fig. 35) for *A.tuberculata*.

In the present study, the relative specific growth rates of the four species were analysed by linear regression. The results, which showed that the relative specific growth rates declined exponentially, at least until close to maximum body weight, may give an idea of the evolutionary strategies of the worms with respect to growth pattern in relation to general ecology. All of the investigated species belong to the endogeic group (p. 11). The two larger species, *A.longa* and *O.cyaneum*, both reach a maximum body weight of about 3 g. But in *A.longa*, the initial growth rate (v′) was a little higher than in *O.cyaneum*, and the slope of the regression line also somewhat steeper. This tend to indicate that *A.longa* probably utilizes more high grade food than *O.cyaneum*. *A.longa* makes surface casts, *O.cyaneum* does not, pointing into the direction that *A.longa* is more surface active (to the extend permissible by environmental factors), in a somewhat richer environment than is *O.cyaneum*. This was also suggested in the section on climatic influence (p. 16). *A. longa* is brown pigmented, whereas *O.cyaneum* is without such pigments, which also indicates more surface activity in A. longa than in O.cyaneum, which then probably does not utilize exactly the same food resources as A.longa, but depends on relatively more low grade food deeper in the soil profile, still however, requiring relatively nutrient rich food. The dependency of O.cyaneum on relatively more low grade food than A.longa, is counterbalanced by a less steeper decline in relative specific growth rate with increasing body weight. In this way competition between the two species may be reduced. In undisturbed nature, e.g., in the garden of the Royal Veterinary- and Agricultural University, Copenhagen, under large Ulmus spp. with a dense cover of undervegetation of various herbaceous plants, the two species coexist in about equal numbers, together with also large numbers of L.terrestris, which belong to another ecological group (the anecique), with a different feeding biology. In arable soil, however, O.cyaneum is only sporadic, which may be due to the fact, that this species is very sensitive to mechanical treatment in comparison with A.longa. A.longa may be quite numerous in arable soil recieving farmyard manure (Table 1 and 21). This is in good agreement with the authors personal experience, that O.cyaneum is much less tolerant to any kind of handling during laboratory routines than most other species. As an example, O.cyaneum is very sensitive to sunlight and tends to die after less than one hour's exposure to diffuse daylight. Also the body wall musculature seems relatively week. As to the r- and K- selection principles developed by Satchell (1980b), it thus appears that O. cyaneum is one of the most typical representatives of the K- strategists.

Of the two smaller species studied, *A.caliginosa* and *A.tuberculata*, which are very closely related, *A.tuberculata* showed a remarkable high initial growth rate, $\log v' = 1.602$, in comparison with the 1.280 of *A.caliginosa*. Similarly the slope of the regression line was different, -0.61 vs. -0.46 in *A.caliginosa*. This appears to be somewhat similar to the *A.longa* - *O.cyaneum* situation. In contrast however, *A.tuberculata* probably needs less time to reach maximum weight than does *A.caliginosa*. Both species may be found together in arable soil, but never in equal numbers, one of the species is always dominating strongly over the other. This indicates that the two species may somehow be competing for food. However, it has not yet been established, which mechanisms are actually operating. Inherent features as well as a number of environmental factors may be interacting, e.g., crop rotation, mechanical treatment and soil type, but for the moment nothing finite can be said about this. A better understanding of these phenomena may not be achieved until the physiological mechanisms, underlying the observed differences in growth patterns have been studied in more detail, and set in relation to feeding biology of earthworms in general. A clue to part of the solution of these problems could be found by measurements of the area of the absorbtive gut-surfaces relative to body weight, notably typhlosole differentiation, which is known to vary among species. Until now, only gross morphology of the typhlosole is known, and sometimes used as a systematic character in a number of keys, e.g., Martin (1977).

From the regressions on specific growth rates and body weight, it seemed possible to suggest some basic ecological mechanisms for the individual species. The reliability greatly depends on the variability of the data. The correlation coefficients for the respective species were from 0.72 - 0.85, but owing to the large number of observations, 20 - 80 per species, the significance of the respective correlation coefficients were as high as $p < 0.001$. Yet, only from 2 - 7 individuals per species were used in the experiments. This of course warrents the need for series of experiments with a higher number of individuals. This would allow an assessment of the variability between individual worms (if kept single throughout the experiments), as well as making the biological interpretations more convincing. But an increase in general accuracy is probably hard to achieve. It is the impression, given proper control of environmental variables, that the performance of individual worms is reproducable. If something does go wrong, the immediate response of the worms is arrest of growth or weight loss. Contributing to varability is probably also the source of the worms, e.g., whether the worms originate from different sites, or from laboratory stocks kept for a long time before use in experiments, as in the present study.

PART II

EARTHWORMS AND AGRICULTURAL PRACTICE

This part summarizes the main results of a number of previously published papers (preface, references 1)-4)), in order to give a general impression of the influence of agricultural practice on earthworms under Danish conditions. In addition are presented some results not previously published, concerning reduced tillage (rotavation during spring) with catch crops of leguminous plants and ryegrass, including direct drilling without catch crops.

CHAPTER I

DIFFERENT MECHANICAL TREATMENTS AND CATCH CROP OF WHITE MUSTARD *Sinapis alba*

The results presented here have been published in a technical report (Andersen 1981a), and originates from a study of the earthworm fauna, carried out at "Ørritslevgård", Fyn (1977-1980), as part of a major study on reduced tillage and catch crops, also covering investigations of soil structure, energy consumption, crop yield, weeds and soil nematodes (1972-1980).

Two different trials were investigated. A, comparison of ploughing without catch crop and rotavation with white mustard as catch crop. In experiment B, five different soil treatments were investigated likewise with mustard as catch crop, i.e., the following implements: Rotavator, stubble cultivator, spade-roller harrow, disc harrow and stubble cultivator + plough. Experiment B was initiated in 1976, and thus followed from the beginning, whereas in A, the experimental treatments had been conducted for five years before earthworms were investigated.

The soil was a fine textured sandy soil with clay (8.2 - 8.7 %; 15-35 cm depth), with a great content of stones. There were no significant differences between the two experimental fields, A and B.

Plot size in A, was 3 ha for rotavation and ploughing, respectively, and 1 ha for each of the different treatments in B, where there were two replicates. In both A and B a number of eight samples per treatment were taken at random. Sampling was done by combined formalin extraction and digging / handsorting.

EXPERIMENT A. ROTAVATION WITH- AND PLOUGHING WITHOUT CATCH CROP

The total number of earthworms is given in Table 13 and is seen to vary considerably from one year to another. It is seen that density in spring 1977 was lower than in the autumn, which is normal, however. The rest of the samples were autumn samples, and October 1978 is seen to be much lower than October 1977. This trend compares nicely with what was found in the Askov samples (Table 2B), i.e., decreasing values of the temperature index C_i from 1976-1979. The C_i value for 1978 was 0.06, which is close to the lowest record, -0.24 for 1979. In 1980 climatic conditions were much better, with a C_i value = 0.84, resulting in a strong increase in earthworm density in both treatments (Table 13). Now excactly the same temperature conditions were probably not encountered at both sites, Ørritslevgård (island Fyn) and Askov, Jutland, but nevertheless somewhat comparable. No samples were taken in 1979. The high density in October 1980 seems to reflect the recovery potential of the dominating species, *A.tuberculata*, when temperature conditions became favourable after a period with adverse conditions. In all the years there was a significant effect of catch crop with rotavation, as compared with conventional tillage, ploughing without catch crop. Mean densities for the two treatments were 109.8 and 43.1 individuals / m^2respectively.

In this experiment it was not possible to discriminate between the effect of rotavation and catch crop separately. This is better seen in experiment B and the experiments described in chap-

Table 13.
Density of earthworms, no./m^2, Experiment A, Ørritslevgård

	1977		1978	1980	
	spring	autumn	autumn	autumn	mean
Plough (-)	17.6	41.0	9.6	104.2	43.1
Rotav. (+)	40.2	141.6	41.2	216.4	109.8

(-) without catch crop
(+) catch crop of white mustard

Table 14.
Population structure in October 1980, Experiment A, Ørritslevgard

	Rotav. with catch crop		Plough without catch crop
	A. tuberculata	A. chlorotica	A. tuberculata
Adults %	24	62	28
Subadults -	5	27	6
Juveniles -	31	8	30
New. hatch.-	40	3	36

Biomass	Rotav. with catch crop	Plough without catch crop
g/m^2	62.7 ± 4.9	45.4 ± 5.7

ter II. One effect, which seems to be recognizable is that a catch crop may increase species diversity (Table 14). In the conventionally tilled field, A.tuberculata was solely dominating, whereas in the field with catch crop and rotavation about 30 % of the population consisted of Allolobophora chlorotica. In Table 14, the population structure in October 1980 has been given, and for A.tuberculata it is seen that the population consisted of 71 and 66 % juveniles in catch crop (rotavation) and without catch crop (ploughing), respectively. This is very much in contrast to A.chlorotica, where only 11 % of the population consisted of juvenile individuals. This together with results presented in previous sections also point in the direction that A. tuberculata is more of an r- strategist than expected, whereas A.chlorotica appears to be a typical K- strategist, similar to O.cyaneum and A.rosea. This is also indicated by the reputation of A.chlorotica as being rather sluggish in comparison with other species. Annual cocoon production is towards the lower end of the range, 25 (Evans and Guild,1948) in comparison with a species like Lumbricus rubellus, with an annual cocoon production of 79. Other species quoted by Evans and Guild exhibit a still lower cocoon production, A.longa and A.rosea , 8 coccoons per annuum. These figures, however were obtained under laboratory conditions. The annual cocoon production of A.tuberculata, 13, p.51, was obtained during the year 1981, with a relatively low C_i value = 0.15 where also not mortality among newly hatched is included. Apparently cocoon production in A.tuberculata may be much higher.

EXPERIMENT B

FIVE DIFFERENT SOIL TREATMENTS AND CATCH CROP

The field used for experiment B, had been under conventional tillage until the autumn 1976, when the experimental plots were laid out. The development of earthworm populations from spring 1977 until October 1980 is shown in Fig. 49. Although annual variations in density were great, as envisaged already in experiment A, a clear trend could be observed, during the three years.

Firstly, the introduction of catch crop (Sinapis), had a general stimulating effect, and secondly the effect of the different implements became visible (Fig. 49). Thus three groups may be recognized. 1) The most beneficial was the spade-roller harrow on its own. 2) Disc harrow and stubble cultivator + plough and 3) rotavator and stubble cultivator. The three groups may also be characterized by the intensity of the mechanical treatment. 1) Only slight interference. 2) Somewhat more intensive, with a final turnover of the soil, ploughing being prece ble cultivation before sowing of the Sinapis. In 3) a more effective disintegration of soil particles takes place, without

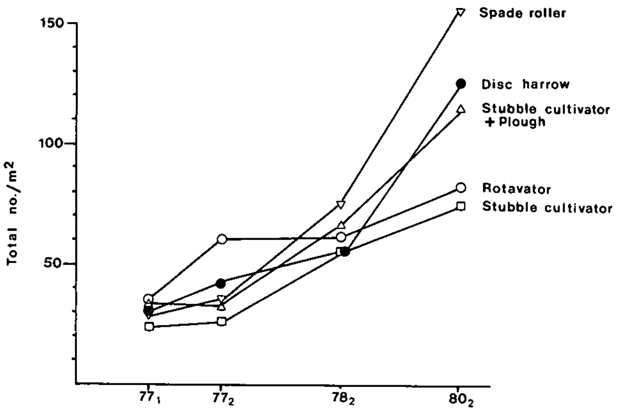


Fig. 49. Number of earthworms after 5 different mechanical treatments in plots with catch crop of white mustard, Sinapis alba L. Ørritslevgård, 1977 - 1980. I, spring. II, autumn.

Table 15.
Influence of five different implements on population structure of *Aporrectodea tuberculata* after three years with catch crop

		Sp.r.	D.h.	St.+P.	Rot.	St.
Adults	%	20	21	31	26	37
Subadults	-	12	11	7	13	20
Juveniles	-	52	56	43	50	38
New.hatch.	-	16	12	19	11	5
Biomass g/m^2		66.5	50.3	52.7	39.4	41.9

Sp.r. = spade roller harrow
D.h. = disc harrow
St.+P. = stubble cultivator + plough
Rot. = rotavator
St. = stubble cultivator

significant turning over, The influence on population structure, October 1980 is given in Table 15. The general tendency, going from left to right, is that the percentage of juvenile stages decrease and that the percentage of adult stages increase. It is remarkable that stubble cultivation after harvest, followed by winter ploughing, is only little different from disc harrowing, which may indicate that stubble cultivation at that time is not detrimental. Two passes were made by the stubble cultivator before sowing the *Sinapis*. The exposure on the surface of cocoons and small worms, which may be expected, thus may not be so significant as later in the season, when the catch crop is incorporated during November - December. Both disc harrow and plough turn the catch crop into the soil, whereas rotavator and stubble cultivator have a more disintegrating mode of action, which perhaps may be suggested to leave cocoons mainly, exposed more superficially in the soil profile, where they may be destroyed by freezing. During November a significant proportion of the population has moved deeper into the soil profile (Fig. 31), where they seem more protected against the different implements during incorporation of the catch crop. At this time of the year (Fig. 35), it also appears that there may be a significant mortality among adult worms, which together with destruction of cocoons has a negative influence. However, addition of organic matter in the catch crop apparently is able to compensate for this, by making the worms grow faster and produce more offspring. The negative influence of rotavation in this experimental design is probable also due to the mode of sowing the Sinapis, which is performed by a combined rotavation - sowing machine. At this time of the year, immediately after harvest, significant numbers of worms may be present in the upper soil layers if the soil is moist, where they may be hit directly by the rotavator.

CHAPTER II

CONTINUOUS BARLEY WITH CATCH CROP, PLOUGHING AND ROTAVATION

This series of trials was conducted from 1979 - 1982 on a number of different soil types, with the earthworm population being assessed during 1980 - 1982 (Andersen et al. 1983), together with other soil biological parameters, i.e., microbial biomass and activity (Eiland) and nitrogen fixation (Vinther). Also the morphology of barley plants, soil physical conditions and yield, including weed populations were investigated.

Earthworm populations were investigated at four research stations, Jyndevad (coarse sandy soil), Roskilde (sandy loam), Rønhave (clay) and Højer (clay, marsh). The catch crop was white mustard, Sinapis alba L. and the mechanical treatments ploughing and rotavation (with and without catch crop, respectively). The mean number of earthworms for the different treatments are given in Table 16. From Table 16, it is immediately seen that almost no earthworms were present in the coarse sandy soil. Those being present belonged to the species A.caliginosa. The species composition at the other stations were all different from from each other (Table 17). At Roskilde the population consisted of A.tuberculata and A.rosea, at Rønhave of A.caliginosa and L.terrestris, and at Højer of A.caliginosa and A.chlorotica. From Table 16, it is seen that there was a significant effect

Table 16.
Mean number/m^2 and biomass, g/m^2 of earthworms (1980-1982)

	Jyndevad	Roskilde		Rønhave		Højer	
	no.	no.	g	no.	g	no.	g
Plough -	2	32.1b	11.9	4.8a	3.9	27.0a	4.5
Plough +	2	45.1c	19.3	25.1b	23.2	50.4b	9.1
Rotav. -	2	13.0a	5.6	8.2a	12.0	24.9a	4.9
Rotav. +	2	27.0b	11.9	39.9c	45.8	41.8b	8.0

+, Catch crop of Sinapsis alba. -, Without catch crop.
Same letter in columns indicates that figures are not significantly different.

on earthworm density of the catch crop at all the stations except at Jyndevad, irrespective of ploughing or rotavation. At Jyndevad (coarse sandy soil, 3.5 % clay), the almost complete absence of earthworms, indicates that in soils of this type the earthworms are very sensitive to agricultural operations. However, in the hedgerows surrounding the experimental fields, earthworm densities averaged 30 - 50 individuals /m^2. In undisturbed clover / grass plots (2 - 3 years, Table 17B), it was quite surprising to find a well established population of L.terrestris and A.caliginosa, which demonstrates that catch crops of plants with symbiotic nitrogen fixation may have a marked beneficial effect on L.terrestris. Differences in density between stations at individual treatments cannot immediately be explained. Looking at the densities at individual stations may give an idea of the influence of the mechanical treatment, but also the soil type seems important as to the response of the earthworms to a given agricultural practice. Thus it may be suggested that a general effect of increasing clay content is a dampening of the mechanical impact.

Table 17.

A. Species composition, no./m^2 in spring barley with catch crop, ploughing and rotavation

	A. caliginosa				A. tuberculata				A. chlorotica				A. rosea				L. terrestris			
Station	Plough		Rotav.		Plough		Rotav.		Plough		Rotav.		Plough		Rotav.		Plough		Rotav.	
	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
Roskilde (10)	-	-	-	-	25	46	12	26	-	-	-	-	6	10	2	3	-	-	-	-
Rønhave (15)	2	10	3	11	-	-	-	-	-	-	-	-	-	-	-	-	2	11	4	26
Højer (18)	24	51	25	41	-	-	-	-	10	9	6	11	-	-	-	-	-	-	-	-

B. Species composition at Jyndevad, no./m^2 in clover/grass without mechanical treatment

Jyndevad (3.5)	A. caliginosa	L. terrestris
Clover/grass, 2 years	2.6	0.5
Clover/grass, 3 years	12.1	11.4

Claycontent % is given in brackets behind the name of the station.

A.caliginosa was found at both Rønhave and Højer (14 and 17 % clay) respectively, and there was a significant effect of the catch crop (Table 17A), but there was no difference between ploughing and rotavation. However, A.caliginosa was much less abundant at Rønhave.

At Roskilde the closely related A.tuberculata was found (Table 17A), but here density was about the double in the ploughed plots in comparison with the rotavated. Also A.rosea was found at Roskilde (Table 17A), and here a similar response was observed. At Højer also A.chlorotica was found, but there were no significant differences between treatments for this species.

The only place where significant amounts of L.terrestris were found was at Rønhave. Here the same general effect of catch crop was seen, But L.terrestris was more abundant in the rotavated plots than in the ploughed (Table 17A). This may be caused by L.terrestris not being able to retreat fast enough into its vertical burrow, when the plough cuts loose the topsoil at 20 - 25 cm depth. The working depth of the rotavator was 6 - 8 cm only. Other circumstances may also be contributing to the observed differences in density. Owing to the fact that the final treatment and incorporation of the catch crop took place in November/December, it seems likely that most earthworms probably had retreated to deeper layers at that time. Therefore only little direct damage may have been done to the worms, although it is not known at which time L.terrestris becomes inactive during winter. As it was shown (p. 13), L.terrestris was not severely affected by extreme drought, which in part may be due to coccoons being deposited deeper in this species than in *A.caliginosa*. Thus ploughing in fact may tend to expose *L.terrestris* coccoons to a greater extend than does rotavation. There are however, indications of *L.terrestris* being somewhat winter active during milder periods, which suggests that a combination of the two hypotheses may account for the observed response of *L. terrestris*. As to the response of the smaller species, the more heavy the soil, the less mechanical impact to the worms seems to be the rule.

CHAPTER III

SPRING BARLEY WITH UNDERSOWN GRASS AND LEGUMES

This experiment, in which earthworm densities were assessed in 1983 - 1984 was initiated in 1982 as a long term experiment to study the nitrogen dynamics under field conditions, see e.g., Nielsen and Jensen (1985). The experiments were laid out in a split - split plot design with two replicates, including the following treatments. Six levels of fertilizer (ammonium nitrate), 0, 30, 60, 90, 120 and 150 kg N/ha. Three levels of catch crop; no catch crop, Italian ryegrass (*Lolium multiflorum*) and *Medicago lupulina*. Two levels of irrigation; no irrigation and irrigation to field capacity at a soil water deficit of approximately 35 mm. Catch crops were incorporated by rotavation during spring.

Earthworms were sampled in irrigated plots at 0 and 150 kg N/ha and at no catch crop; *Medicago* (1983 and 1984), and ryegrass (only 1984). There were 8 samples per treatment (0.25 m^2 quadrats), by combined formalin extraction and digging/handsorting.

One of the reasons for examining this particular experiment was the presumed beneficial effect of catch crop of leguminous plants with symbiotic nitrogen fixation, especially on *L.terrestris*. The experiments were conducted in the fields of the Royal

Veterinary- and Agricultural University, Tåstrup. The soil was a clay soil (15 % clay, 0 - 15 cm, increasing to 23 % in 70 - 100 cm.

TOTAL NUMBER OF EARTHWORMS. 1983-1984

The development of the total earthworm population is given in Fig. 50, and it is seen that without catch crop earthworm densities were at a low level, 5 - 15 individuals / m^2 in both 0 N and 150N. With a catch crop of undersown Medicago there was a general increase from spring 1983 until autumn 1984 (Fig. 50). There was no difference between the two levels of fertilizer, except in spring 1983. The Medicago had a marked influence on earthworm density, reaching 92 and 75 individuals / m^2 in October 1984, 0 N and 150 N respectively. In ryegrass density was approximately 60 individuals / m^2.

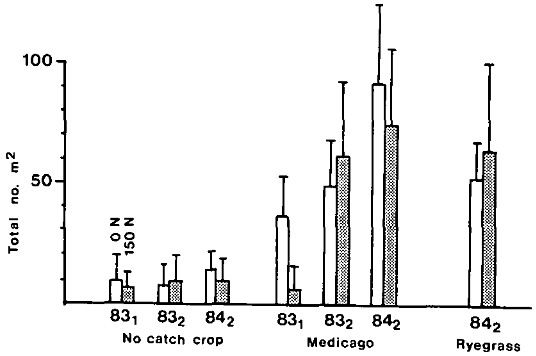


Fig. 50. Total number of earthworms/m^2 (± SD). Tåstrup, 1983 - 1984. 1) spring. 2) autumn. Catch crops, Medicago and Italian ryegrass.

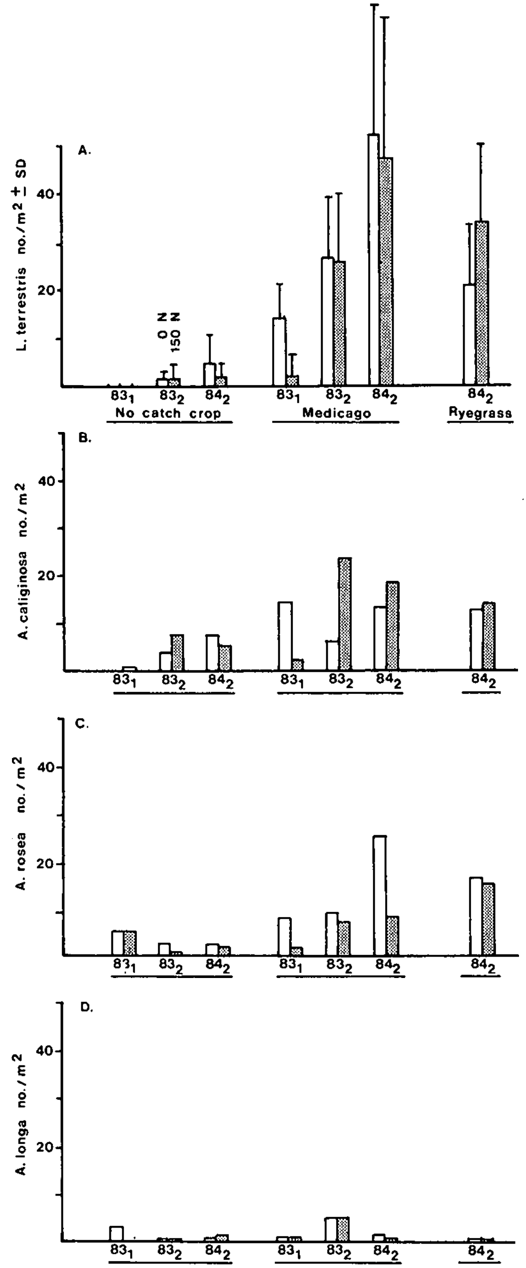


Fig. 51. Number / m^2 of different species at Tåstrup, 1983 - 1984. A, *L.terrestris*. B, *A.caliginosa*. C, *A.rosea*. D, *A.longa*. Legends as Fig. 50.

SPECIES COMPOSITION

The dominating species were *A.caliginosa*, *L.terrestris* and *A. rosea* (Figs. 51 A-C), with only small amounts of *A.longa* (Fig. 51 D). In *L.terrestris* there was no difference between the two fertilizer levels, except in spring 1983, with the lowest level in 150 N. In *A.caliginosa* there was a trend towards a higher density in 150 N, whereas the opposite was seen in *A.rosea*.

EFFECTS OF CATCH CROPS AND FERTILIZER

The mean earthworm densities (1983 - 1984) for the different levels of catch crops and fertilizer, including the two fertilizer doses combined are given in Table 18, except for *A.longa*. When the total density is considered, it is seen that for 0 and 150 N, there was no difference between *Medicago* and ryegrass, which however, both were significantly different from no catch crop ($p < 0.001$), t- test. Looking at the two levels separately, it is however seen, that density in *Medicago* at 0N was significantly greater than in ryegrass ($p = 0.05$). At 150 N there was no significant difference between the two catch crops.

The difference between the two levels of fertilizer (Table 18B), is seen to be caused by a higher density of *L.terrestris* in *Medicago* at 0 N, in comparison with the other treatments. The main reason for this, as expected, thus seems to be the nitrogen fixation by the *Medicago* at low levels of fertilizer ($p < 0.05$). At 150 N in ryegrass, the density of *L.terrestris* (Ta-

Table 18.

Influence of catch crops, *Medicago* and ryegrass, fertilizer and rotavation on earthworms in spring barley. No./m^2 ± SE.

A. Effect of catch crop

Total no.	Without	Medicago	Ryegrass
N combined	10.5 ± 1.6a	69.8 ± 5.7b	59.2 ± 6.9b
0 N	9.5 ± 2.4a	70.6 ± 8.6b	52.5 ± 5.3c
150 N	11.5 ± 2.3a	68.9 ± 7.7b	66.0 ±12.7b
L. terrestris			
N combined	2.3 ± 0.6a	38.1 ± 4.1b	27.5 ± 3.9c
0 N	3.0 ± 1.2a	39.4 ± 6.7b	21.0 ± 4.3c
150 N	1.5 ± 0.7a	36.8 ± 5.0b	34.0 ± 5.9b
A. caliginosa			
N combined	5.5 ± 1.3a	15.0 ± 2.1b	13.5 ± 2.3b
0 N	5.0 ± 2.5a	9.8 ± 2.0b	13.0 ± 2.7b
150 N	6.0 ± 2.1a	20.5 ± 3.3b	14.0 ± 3.9b
A. rosea			
N combined	2.1 ± 0.6a	12.6 ± 2.2b	15.8 ± 2.2b
0 N	2.3 ± 1.0a	17.3 ± 3.3b	16.5 ± 2.3b
150 N	1.3 ± 7.9a	7.9 ± 2.4b	15.0 ± 3.8b

B. Effect of fertilizer and catch crop. No. and g/m^2

	Without		Medicago		Ryegrass	
	0 N	150 N	0 N	150 N	0 N	150 N
Number/m^2 1)	3.0a	1.5a	39.4b	36.8b	21.0c	34.0b
Tot. biomass 2)	8.5a	5.0a	26.0b	20.6b	9.5a	24.4b

1) *L. terrestris* only. 2) All species. Same letter in rows indicates that figures are not significantly different.

ble 18B), was significantly higher ($p < 0.05$), than at 0 N.

Ross and Cairns (1982), studied the interaction between *A.caliginosa* and ryegrass (*Lolium perenne* L.) in subsoil, after topsoil removal, and found a significant increase in soil enzymatic activity, when both worms and ryegrass were present, in comparison with either worms or ryegrass being present alone. This shows that presence of organic matter is a prerequisite for the general stimulation of soil biochemical activity and nutrient cycling by earthworms. The beneficial effect of legumes on crop growth- and yield is well document
ther enhanced by the stimulating effect on the earthworm fauna, which has been shown here.

CHAPTER IV

DIRECT DRILLING

Only preliminary investigations of the influence of direct drilling have been carried out in Denmark. In a newly established (1982) experiment at Ballum, western Jutland, winter wheat with ploughing and direct drilling, earthworm density and biomass was assessed during October 1983 (Table 19). The same year, October 1983, earthworm populations were investigated (also winter wheat) in a field which had been direct drilled for at least 8 years by a local farmer at Heininge, western Zealand (Table 19). Both soils were clay soils.

BALLUM

After one year of direct drilling (Table 19), there was no difference between direct drilling and ploughing. *A.caliginosa* and *A.chlorotica* were the dominating species, 92.0 and 38.8 individuals / m^2 by ploughing and 79.3 and 53.8, respectively in the direct drilled plots. The total biomasses were 17.3 and 14.8 g/m^2 in direct drilled and ploughed plots respectively. There seemed to be a tendency towards more *A.chlorotica* in the direct drilled plots. *L.terrestris* occurred only sporadically.

Table 19. Earthworm density and biomass after ploughing and direct drilling (1983) ±SE

	BALLUM, 1 year				HEININGE, 8 years	
	Ploughed		Directly drilled		Directly drilled	
Species	no./m^2	biomass	no./m^2	biomass	no./m^2	biomass
A. longa	-	-	-	-	18.3 ± 3.8	7.9 ± 1.4
A. caliginosa	92.0 ± 14.8	8.2 ± 1.4	79.3 ± 11.3	9.2 ± 1.7	-	-
A. tuberculata	-	-	-	-	54.5 ± 8.1	17.3 ± 2.0
A. rosea	-	-	-	-	18.0 ± 4.4	1.9 ± 0.5
A. chlorotica	38.8 ± 8.6	4.5 ± 1.6	52.7 ± 8.5	8.1 ± 1.7	24.0 ± 4.5	2.7 ± 005
L. terrestris	2.0 ± 2.1	-	-	-	1.0 - -	0.2 - -
Total	132.8	14.8	132.0	17.3	115.7	30.0

HEININGE

After 8 years of direct drilling a somewhat balanced population of earthworms had developed, with five different species occurring, A.longa, A.tuberculata, A.rosea, A.chlorotica and L.terrestris, the latter being of sporadic occurrence at this site also. The other species seemed well established (Table 19). As to numbers, there was no difference between Ballum and Heininge. But because A.longa and A.tuberculata are of greater size than A.caliginosa, the biomass being supported at this site was 30 g, which was the double of what was found at Ballum (Table 19).

DIRECT DRILLING AND OTHER SYSTEMS

The conclusion on earthworm densities in direct drilled soils (mostly heavy soils), from experiments in England (Barnes and Ellis 1979; Gerard and Hay 1979; Edwards and Lofty 1982) is, that if ploughing is substituted by direct drilling, this will be most beneficial for the deep burrowing species, A.longa and L.terrestris, whereas the smaller endogeic species seem less affected. This seems consistent with the preliminary results presented here, as well as the results on the effect of ploughing in the previous sections. Thus when the mechanical treatment is minimized, e.g., direct drilling, the soil may support up to 100 g /m^2, which is several times more than in conventional systems (Gerard and Hay 1979). A similar order of magnitude may be obtained by heavy dressings of animal manure in ploughed fields, which is treated in the following chapter. It may also be mentioned that it is possible to sustain very large earthworm populations in systems with catch crop and rotavation if additional organic matter is introduced as animal manure. Two systems of this type were investigated by Andersen (1979) in Jutland (1977 - 1978) at local farms.

At one site (Herning), A.caliginosa was dominating with 200 - 300 individuals / m^2 and biomasses of 60 - 120 g / m^2. At the other site (Bryrup), A.longa was dominating,with approximately 125 individuals / m^2 and a biomass of 90 g / m^2.

A general effect of continued arable cropping, regardless of type of mechanical treatment (Edwards and Lofty 1982), is a decline in earthworm populations, which can only be counterbalaced by increased input of organic matter, animal manures or chopped straw in combination with a less intensive mechanical treatment. The beneficial influence on the deep burrowing species, A.longa and L.terrestris is very important because the soil tend to become more compacted when it is no longer ploughed. There is good evidence of earthworms improving soil aeration and drainage

(Russell 1973; Edwards and Lofty 1977; Ehlers 1975; Baeumer and Bakermans 1973; Barnes and Ellis 1979). In direct drilled soils the worm burrows tend to extend well into the subsoil without interuption as in contrast to ploughed land. In this respect *A.longa* and *L.terrestris* are particular important, but also the smaller species may be important in this function because of their seasonal vertical migrations (p. 84). Further it has been demonstrated that earthworm channels enhance root growth of cereals (Edwards and Lofty 1978, 1980), because these are lined with more available numeral nutrients, as well as, because a significant part (75 %) of the soil inhabiting, non symbiotic nitrogen fixing microorganisms are associated with the walls of earthworm burrows (Locquet et al. 1977).

CHAPTER V

EFFECT OF FARMYARD MANURE AND SLURRY IN TRADITIONAL SYSTEMS

The effect of animal manures, farmyard manure and slurry has been studied (1976 - 1981) in experiments at Askov Research Station (Andersen 1980b, 1983). The experiments are the same from which the climatic effects were evaluated in part I, p. 14. In the above mentioned papers only results, covering the period 1976 - 1979 were published. In the following results for the whole study period are summarized, together with statistical analyses of the 1976 - 1979 results, not previously published. The doses of manures, farmyard (FYM) and slurry (SLU) were 50 and 100 tons / ha / year, 200 tons / ha each second year and 400 tons / ha each fourth year. As controls were used plots recieving 80 - 90 kg N / ha (NPK- fertilizer).

EFFECTS OF MANURES AND YEAR ON DENSITY AND BIOMASS

These effects were evaluated for each dose and species separately in a two- factorial analysis of variance. For each species total numbers and juveniles were treated separately as well. The trend of this analyses, covering the period 1976 - 1979 is summarized for each species below. (See Fig. 52).

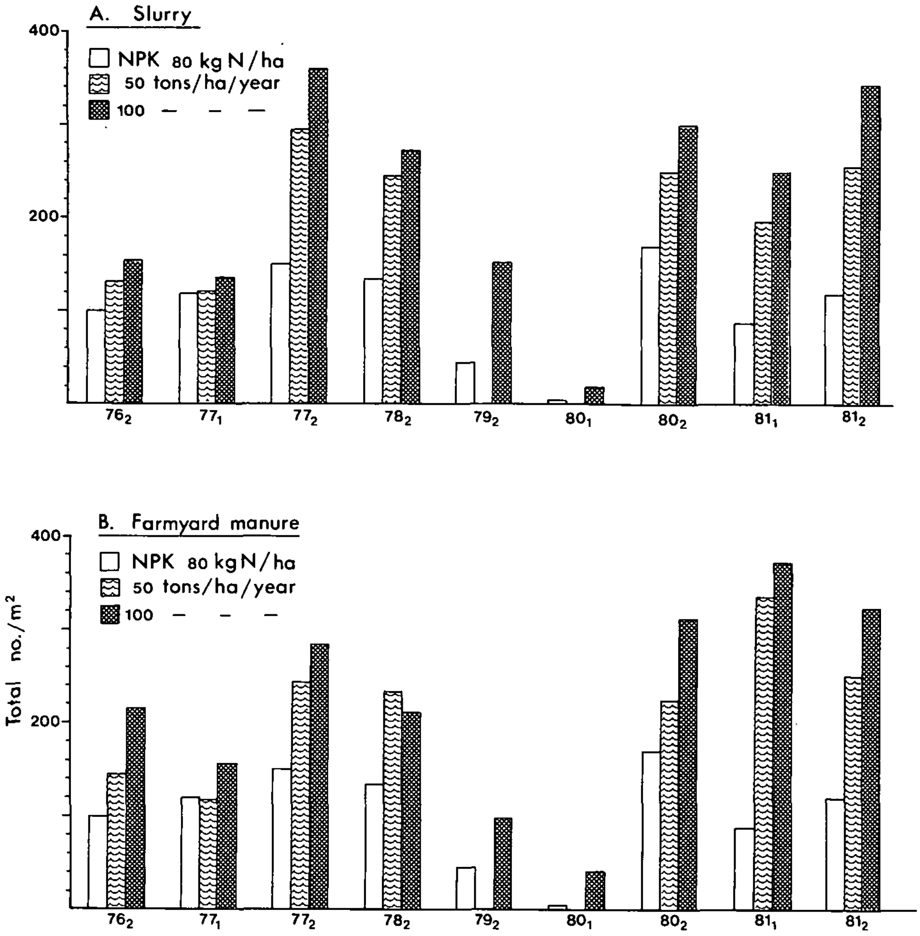


Fig. 52. Number of earthworms/m^2, Askov Research Station, 1976 - 1981. I, Spring. II, autumn. A, Slurry. B, Farmyard manure.

A.longa. There were significant differences ($p < 0.01$) between manures at all levels,as well as years, except in 50 tons. The effect of years at the levels, 200 and 400 tons may in part be due to manures not being given each year, and thus not to climatic factors only.

A.caliginosa. The response of this species was similar to that of *A.longa*

A.rosea and *A.chlorotica*. These two species were not very much influenced by the two types of manures, and were also not very numerous. The effect of years was significant. Also here interaction between year and the mode of application (2 and 4 years intervals) may be important. This cannot be established by this type of analysis.

L.terrestris. The response of this species was similar to that of *A.longa*.

All species. When all species were taken together there was no difference between manures irrespective of level. Some of the explanation of this may be that differences between species tend to cancel out, when absolute numbers are considered. However, the effect of years was still significant, both with respect to total numbers and juveniles. The effect on biomass followed the same pattern as for numbers.

COMBINED EFFECT OF MANURE DOSE AND YEAR ON DENSITY

The combined effects were evaluated in a three- factorial analyses of variance (Table 20), 1976 - 1978. The trend in the effect of manure and year was similar to that mentioned above. There were significant effects of dosis on *A.longa*, *A.caliginosa* and *L.terrestris*, but not on *A.rosea* and *A.chlorotica*, which apparently are unable to compete successfully with the other spe-

Table 20. Significance (p<) of the influence of manures, dosis and year on the number of earthworms. Analysis of variance, three-factorial. f- test (1976 - 1978).

Species Variable	A. longa	A. caligin.	A. rosea	A. chlorot.	L. terrest.	Total	degr. of frd.
Manures	0.01	0.01	-	-	0.01	-	1/280
Dosis	0.01	0.01	-	-	0.02	0.01	4/280
Year	0.01	0.01	0.01	0.01	0.01	0.01	3/280

-, not significant. Manures: Slurry and farmyard manure. Doses: 80 kg N/ha (NPK-fertilizer), 50 and 100 tons manure /ha/year. 200 and 400 tons manure each 2nd and 4th year, respectively. Years: October 1976, May 1977, October 1977 and October 1978.

cies (Edwards and Lofty 1982). However (Part I, p. 38), it appears that *A.rosea* becomes more numerous at the higher end of the C_i range, when the number of *A.caliginosa* and *A.chlorotica* tend to become reduced. The same tendency is seen at the lower end.

The combined data for the whole period, 1976 - 1981 are given in Table 21, total no. / m^2 for 50 and 100 tons FYM and slurry, respectively. The data for 200 and 400 tons are more suited to demonstrate short term effects, which has been treated by Andersen (1980b), From Table 21, it is seen that the deep burrowing species *A.longa* and *L.terrestris* are favoured by FYM in comparison with slurry, and that *A.caliginosa* is favoured by both types of manures, and becomes very numerous in comparison with fertilizer. The number of *A.chlorotica* and *A.rosea* was not very much influenced by the manures in comparison with fertilizer, which as mentioned above may be caused by competition phenomena, it may also be contributing to the low numbers, that these two species may be more extreme K- strategists than the others found.

Table 21. Number of earthworms/m^2. Mean autumn densities, 1976 - 1981 (±SE)

Treatment	Total	A. longa	A. caliginosa	A. rosea	A. chlorotica	L. terrestris
2 NPK	117.9 ± 17.1	18.9 ± 3.2	67.2 ± 11.8	10.9 ± 2.8	16.8 ± 3.2	4.1 ± 0.7
SLU 50 t	229.4 ± 27.1	12.6 ± 1.1	181.0 ± 27.2	15.9 ± 3.0	15.9 ± 3.0	4.5 ± 1.0
SLU 100 t	264.3 ± 37.3	13.9 ± 1.2	215.0 ± 34.8	13.7 ± 2.9	18.5 ± 5.2	3.2 ± 0.9
FYM 50 t	218.9 ± 19.0	37.8 ± 3.6	133.0 ± 22.4	14.7 ± 4.3	20.9 ± 2.2	12.4 ± 1.7
FYM 100 t	242.3 ± 35.0	48.2 ±12.0	144.0 ± 32.3	14.4 ± 5.1	24.4 ± 4.4	12.3 ± 2.2

2 NPK: 80 kg N/ha

Table 22. Mean biomass (g/m^2 ±SE) of all treatments and species, 1976 - 1981.

Treatment	Total	A. longa	A. caliginosa	A. rosea	A. chlorotica	L. terrestris
2 NPK	25.1 ± 3.2	9.0 ± 1.5	10.5 ± 1.7	1.3 ± 0.3	1.8 ± 0.3	2.5 ± 0.5
SLU 50 t	27.3 ± 4.8	4.7 ± 1.1	18.7 ± 3.9	1.2 ± 0.3	1.4 ± 0.3	1.3 ± 0.2
- 100 t	32.8 ± 5.4	5.7 ± 0.9	22.3 ± 4.4	1.3 ± 0.4	1.4 ± 0.2	2.0 ± 0.4
- 200 t	24.6 ± 4.1	4.8 ± 1.0	16.1 ± 3.4	0.7 ± 0.2	1.3 ± 0.4	1.5 ± 0.2
- 400 t	22.5 ± 4.7	4.8 ± 0.8	14.0 ± 3.7	1.0 ± 0.2	1.5 ± 0.4	1.3 ± 0.4
FYM 50 t	41.1 ± 7.6	14.4 ± 3.6	18.5 ± 6.8	1.2 ± 0.3	1.8 ± 0.5	5.2 ± 0.9
- 100 t	50.0 ±11.2	17.3 ± 3.7	21.6 ± 6.9	1.5 ± 0.3	2.5 ± 0.6	7.1 ± 1.0
- 200 t	43.7 ±11.1	12.6 ± 2.8	20.1 ± 7.6	1.3 ± 0.3	2.4 ± 0.6	7.3 ± 1.4
- 400 t	37.3 ± 8.5	11.2 ± 2.6	17.7 ± 5.2	1.1 ± 0.3	1.7 ± 0.4	5.5 ± 1.0

In Table 22, the biomasses are given for all of the treatments and species, and it is seen that the trend given by the statistical analysis for the 1976 - 1978 data seems to hold for the whole study period. It is seen that FYM is able to sustain a greater biomass than slurry, which in part may be due to a greater dry matter content, 15 % vs. 6.5 in slurry. This is in particular beneficial for the larger species, *A.longa* and *L.terrestris*. The mean total biomass, e.g., 50 g / m^2 in 100 tons FYM, and the other biomasses as well, are somewhat greater than those given by Andersen (1983), which is caused by the very favourable year, 1980, the effect of which continued into spring 1981. However, because 1981 was less favourable (Table 3B), the autumn population was much lower than the spring population, a phenomenon which is rarely encountered. Thus extremely high biomasses were recorded in spring 1981, 120 g / m^2 in 100 tons FYM.

TURNOVER OF ORGANIC MATTER

A biomass of approximately 30g / m^2 (Andersen 1983) represented a nitrogen turnover of about 13.3 kg N / ha in tissues, faecal and non- faecal excreta. For a mean biomass of 50 g / m^2, this amounts to 22 kg N / ha annually, all of which is readily mineralizable. At the maximum biomass recorded, about 53 kg N / ha is turned over. The greater part of this is of course immobilized by microorganisms and colloidal adsorption; and crop uptake only takes place during a short period of the year. However, it must also be taken into consideration that the earthworms process large amounts of organic matter, which accelerate microbial decomposition and mineralization. Thus a popualtion of 50 g / m^2 will be able to ingest approximately 6.8 tons organic matter (dry wt)/ ha / year, which corresponds to about 190 kg N / ha / year flowing through earthworm guts, an amount which cannot be without meaning in terms of plant production.

A positive effect on crop growth of earthworms is easy to demonstrate in pot experiments under laboratory conditions, and has been done several times (Barley and Jennings 1959; Edwards and Lofty 1978, 1980). Under field conditions, however, this is not so easily achieved. The reasons for this are probably many, and climatic interactions may be among the most important, e.g., climatic conditions which may affect crop yield and earthworms, positively or negatively, may not coincide temporally, or work in opposite directions. Nevertheless, all evidence taken into consideration, there remains no doubt that on a long term basis, earthworms are among the major contributors to soil fertility in our latitudes.

Total soil respiration in 100 tons FYM (0 - 20 cm) was of an order of magnitude of 500 g C / m^2/ year, figure based on Eiland (1985), being somewhat higher than that of, e.g, Roskilde soil, 320 g C /m^2/ year (Andersen et al. 1983), owing to the high input of organic matter. Earthworm respiration in 100 tons FYM amounts to approximately 12,3 g C / m^2/ year, which is about 2 % of the total soil respiration. This figure is in close agreement with results from other studies. The carbon output in 100 tons FYM is similar to an output of 750 g / m^2 in native grassland (prairie) in Canada (De Jong et al. 1974). In beech wood in England, Phillipson et al. (1975), found an annual output of 128 g C / m^2, which however is somewhat low compared to 1073 g C / m^2 found by Edwards and Sollins (1973) in a second growth mesophytic forest stand in eastern Tennessee USA. In abandoned fields in Sweden, Persson and Lohm (1977), found an annual carbon output of 330 - 360 g C / m^2, making allowance for some accumulation to occur. In pine forests in Sweden and Finland, values around 220 g C / m^2 have been found by Persson et al. (1980) and Huhta and Koskenniemi (1975) respectively. This is of the same order of magnitude, 200 g C / m^2, as found in coarse sandy soil at Jyndevad, Denmark (Andersen et al. 1983).

SUMMARY

Earthworm populations in arable soil are influenced by a number of environmental factors, which here may be of more importance than in less exposed habitats as woodland and continuous grassland. In this thesis has been studied the influence of temperature and precipitation on the most common Danish arable soil species, from a continuous six years record. Especially different temperature regimes of the years, have been shown to excert a major influence on the development of earthworm populations, which has not been recognized before. Other investigations on respiration and growth rates, including a detailed investigation of seasonal dynamics under field conditions provide a better understanding of the function of these species in agro- ecosystems. Likewise the significance of mechanical treatments has been studied, including the effect of addition of organic matter, in form of animal manures or different catch crops. In this country there are old traditions with respect to earthworm research, e.g., Müller (1878-1879), who for the first time described the significance of the earthworms in mull formation in forest soil. This tradition was carried on by Bornebusch, during the 1920'ties (1930). No research on earthworm ecology in arable soil, however, has been made until recently, 1976, when the studies reported on in the present account were initiated. Hopefully an improved knowledge on the parameters affecting earthworms

in arable soil, as presented in this thesis, may help to provide a basis for management schemes being able to secure long term soil fertility.

INFLUENCE OF TEMPERATURE

The influence of temperature regimes under field conditions have not been studied previously, and here, in a system with constant mechanical treatment (ploughing) and organic matter input, 100 tons Farmyard manure / ha / year, it has been shown that good correlation exists between earthworm density and certain temperature regimes of the year. Thus it has been possible to establish a common temperature index, C_i, which shows a linear correlation with the density of the species, _Aporrectodea longa, A. rosea_ and _Lumbricus terrestris_ within the range of C_i values (-0.24 - 1.30) for the years 1976-1981. The species _Aporrectodea caliginosa_ and _Allolobophora chlorotica_ tended to have a population maximum between values of 0.4 - 0.6. It was also shown that reproduction responded more quickly to changing C_i values than total population. It was suspected that some interaction existed between temperature and precipitation also. From three-dimensional plots of these two parameters and total density, as well as the proportion of newly hatched (%) in October month of the different years, it was found that precipitation during summer, together with temperature (C_i), may define the most favourable conditions. This was done for _A.longa_ and _A.caliginosa_ respectively. The combined effect of temperature and precipitation was very pronounced in the case of newly hatched. There were no ill effects on A.longa of hot and dry conditions, but also greater amounts of precipitation were beneficial. This is consistent with the distribution of A.longa, occurring in not too cold maritime climates, as in Britain, or climates of more continental predominance, in the USSR etc. In Norway the summers seem to be too cool. Only from around Oslo, there are records of A.longa. A.caliginosa showed a temperature optimum somewhat below the middle of the recorded range of C_i values, at relatively high amounts of precipitation. This is also consistent with the distribution, circum - boreal - subtropical (Arctic circle - North Africa). It is characteristic, however, that at relatively low temperatures, a fast decrease in density is seen when the precipitation becomes less abundant. Another effect of temperature was found in A. longa (a species prefering relatively high quality food), namely that there was a decrease in density with increasing C_i values in 50 tons farmyard manure, compared with 100 tons. In fertilizer the decline was still faster. In A.caliginosa, probably not being that strict in food requirements, this effect was not observed.

RESPIRATION

Oxygen consumption was measured in the species, A.caliginosa, A.tuberculata and A.longa at 12 °C. The respiratory rate, μl O_2 $g^{-1}hour^{-1}$, varied with body weight in a linear manner -

thus no specific level of respiratory rate may be assigned to the different developmental stages, newly hatched, juveniles and adults. In A.caliginosa the respiratory rate ranged from 46 μl O_2 - 65 μl O_2 $g^{-1}hour^{-1}$ (adults - newly hatched). In A.tuberculata the range was 38 - 59 μl O_2 $g^{-1}hour^{-1}$. The lower figure for adult A.tuberculata is due to the higher weight of adults (1.0 - 1.6 g) in comparison with that for adult A.caliginosa (0.4 - 0.7). The respiratory rate of subadult A.longa was 29.5 μl O_2 $g^{-1}hour^{-1}$. The respiratory rate of A.longa fitted the same straight line as for A.tuberculata. It was shown that use of a burrowing medium of unsterilized sandy loam, which is the natural habitat of the above mentioned species, resulted in higher respiratory rates, than in a series without burrowing medium (A.caliginosa). Thus in a suitable burrowing medium, the measured O_2 consumption is probably close to what happens in the field. In comparison with other studies(Phillipson and Bolton 1976), it is shown here, that their use of an unsuitable burrowing medium (sandy material) for respiratory measurements of epigeic species (litter dwelling), may induce abnormal behaviour in terms of elevated respiratory rates of variable duration and abnormal high ingestion of the burrowing medium, offsetting the relevance of the results obtained, in calculations of energy budgets. Measurements were also made on aestivating, subadult A.tuberculata at 2.5 $^{\circ}$C. The respiratory rate under these conditions, 8.5 μl O_2 $g^{-1}h^{-1}$, was found to be 36 % lower than respiration during normal activity, corrected to the same temperature. Thus a physiological adaptation, seems to be coupled to the onset of aestivation. Respiration of earthworms was compared with that of other poikilotherms. The respiratory rates (including literature) were converted to total caloric output per hour and plotted against body weight on a double logarithmic scale. The slope of the resulting regression line, n = 0.854 was close to n = 0.751 for a standard poikilotherm line (Hemmingsen 1960). The level of earthworm metabolism was 1.9 times below the mean of all poikilotherms, being similar to that of other relatively sluggish animals (Hemmingsen 1960). The respiratory rate of A.caliginosa measured in water, without burrowing medium was about 1.22 times below active metabolism, and presumably close to standard conditions, because in water, A.caliginosa becomes relative motionless and flaccid. This may not apply to other species, e.g., E.fetida, which left alone in water tend to aggregate and form bundles, which is an energy consuming process. The factor 1.22, seems to stress the "K"- strategy of endogeic earthworms.

ECOLOGY OF *A.tuberculata*

The ecology of this species was studied for more than one year by weekly (biweekly) sampling. 0.5 m^2 quadrats were investigated to 0.60 (0.70) m depth by digging and handsorting of the soil strata (0-10, 10-30 and 30-60) cm. Thus it was possible to study (in more detail), the seasonal vertical migrations of individual size classes, as well as activity / aestivation patterns and general population development. There was a marked seasonality in activity, the worms going into aestivation during the end of October- beginning of November. Activity was gradually resumed during March - April. Adult worms tended to retreat deeper (60 cm) during aestivation than smaller worms, presumably because of better burrowing capabilities. Close to the onset of aestivation, a significant mortality was recorded, mainly among adults and larger juveniles, which is ascribed to senescence partly (adults), including parasites and pathogens. It was also possible to estimate the reproduction of A.tuberculata, and it was found that the reproductive rate was highest during August - October (2.7 cocoons / adult / month), and lowest during spring, March - May (0.5 cocoons / adult / month), being intermediate during summer (1.1). This trend in reproductive rates is consistent with the development of soil temperatures during the year, including vertical distribution of the worms.

FIELD RESPIRATION

The population data on A.tuberculata were used in a calculation of the annual oxygen consumption, which amounted to 25.5 l O_2 / m^2/ year. The oxygen consumption data used in the calculations were those of active and aestivating A.tuberculata, obtained during the respiratory measurements. It was found that 94.4 % of the annual oxygen consumption took place during activity, with 52 and 46 % of this part, being allocated to the 0-10 and 10-30 cm layers respectively. These results further enlighten the trend in reproductive rates mentioned above.

GROWTH OF EARTHWORMS

Growth of *A.longa*, *A.caliginosa* and *Octolasion cyaneum* was recorded for 45o-520 days, using crushed litter (*Tilia* - *Ulmus*) and ground barley straw as food. Growth of *A.tuberculata* was recorded for 150 days. Logistic growth curves were seen in all the species. The worms were held at 12 °C and constant darkness. In the two large sized species, *A.longa* and *O.cyaneum* clitellum developed after 320 and 200 days respectively. In a more dense culture of *O.cyaneum* (4 instead of 2), the time to maturity was 250 days. *A.longa* was kept single. Individuals of *A.caliginosa* kept single took about 120 - 200 days to reach maturity. A single individual kept on litter, reached a very large size, 1.9 g. This individual reached maturity after 200 days (see above). In another, kept on ground straw, the time was 135 days. In a third, kept on litter (in this culture the number of individuals were gradually reduced from 6 to one individual), the time was 120 days, but the maximum body weight reached in these two induviduals was only about 1 g. These experiments indicate that food availability may influence growth patterns in a complex manner, in terms of onset of maturity and maximum weight obtained, although the growth curves were not significantly different. From the original growth data, the relative specific growht rates (v') were calculated, and it was shown that v' tended to decline exponentially with increasing body weight, through a linear regression on log v' and body weight.($p < 0.001$ for all of the four species). The slopes of the regression lines were different in the four species, as well as initial v′ (y- intercept). The lowest slope was found in O.cyaneum (-0.35), as well as the lowest initial growth rate (log v′ = 1.28). This points towards O.cyaneum, being among the most typical K- strategists. At the other end of the spectrum among the endogeic, is A.tuberculata, with the highest initial growth rate, log v′ = 1.60. However, the slope of the regression line was rather steep, -0.61, which is about twice that of O.cyaneum. This sets the limit of maximum body weight obtainable, to a somewhat lower level, about 1.9 g, which is reached relatively fast, in approximately 300 days. A.tuberculata became clitellate after 120 days. Intermediate between these, were A.longa and A.caliginosa. Initial growth rate of A.caliginosa was as low as in O. cyaneum (log v′ = 1.28) also, whereas the slope of the regression line was steeper (-0.46). In A.longa, initial growth rate (log v′ = 1.36), was higher than in A.caliginosa, and the slope (-0.38) less steep. This seems to indicate that A.tuberculata and A.longa may require more high grade food than the other two species. Data on A.longa in this respect are more comprehensive, whereas data on A.tuberculata, apart from what has been presented in the present account, are missing. This is due to a general confusion between A.caliginosa and A.tuberculata by most workers, and secondly because practically no work on earthworm ecology has been performed between 1930 and 1976 in this country, which might have yielded collections, being able to provide a better idea of the distribution of the most common species in arable soil. It appears also that it has been the general habit to discard any earthworm material obtained during ecological investigations after preliminar identification. So here it may be appropriate to mention that all of the authors material has been sorted out, identified to species, labelled and is kept in the collections of the Zoological Department of the Royal Veterinary- and Agricultural University, Copenhagen, and is available for further research work. Now finally, in connection with the growth experiments, the respiration / production ratio for A.caliginosa was estimated. Production was estimated from the growth curve, and respiration was taken from the results previously mentioned. The R/P ratio was set in relation to body weight, and a linear relationship between log R/P and body weight was found until close to maximum body weight, when growth (P), rapidly approximates zero. Also the part of assimilation, which is converted into production was estimated, declining from 75 % in newly hatched to about 22 % at maximum weight. Thus although body weight becomes constant, some energy is converted into mucous secretion etc., including production of sperm and eggs.

AGRICULTURAL PRACTICE

Here different implements have been investigated, and it may be concluded that the less heavy impact, the more earthworms may be found. In this respect it appears that there is an interaction with soil type, i.e., the more heavy the soil, the less damage is caused by mechanical treatment. This general effect seems to account for the response of the endogeic species, A.caliginosa, A.tuberculata, A.rosea and Allolobophora chlorotica. The various implements may be arranged in order of increasing damage as follows: Spade-roller harrow, disc harrow, plough, rotavator and stubble cultivator. As to the effect on the deep burrowing species A.longa and L.terrestris, which possess more vertically arranged burrow systems, only data on L.terrestris are available. Here it appears that any kind of superficial soil treatment is beneficial, whereas ploughing is more detrimental. Various catch crops have been investigated in connection with the evaluation of the effects of mechanical treatment. All of the catch crops excerted a positive influence on the earthworm fauna, being able to counterbalance the negative influence of mechanical treatment. The catch crops were, white mustard (Sinapis alba), Italian ryegrass (Lolium multiflorum) and Medicago. In the experiments with ryegrass and Medicago, it was found that at low levels of fertilizer (0 N), there was a significantly better effect in comparison with ryegrass. At high levels of fertilizer (150 N), there was no difference, which may be due to the symbiotic nitrogen fixation of Medicago. Especially it was found that Medicago was beneficial for L.terrestris. This was found both in a coarse sandy soil (Jyndevad) and a clay soil (Tåstrup). In comparison with catch crops it was found that animal manures, farmyard manure or slurry, have a much better influence, However, FYM tend to favour the larger species, A.longa and L.terrestris, in comparison with slurry, which seemed to suppress these. In slurry, A.caliginosa became strongly dominant. The other two small sized species, A.rosea and A.chlorotica were less influenced. The experiments on animal manures (as to the earthworm fauna) were conducted from 1976 - 1981, and as mentioned earlier large differences between individual years were recorced, being caused by climatic effects. In good years (1980 - 1981), very high densities and biomasses were recorded (400 individuals / m^2 and 100 g / m^2). The greatest mean biomasses (1976 - 1981), were found at 100 tons manure / ha / year (32.8 g / m^2 in slurry and 50.0 g / m^2 in FYM). The difference may be due to the lack of the large sized species in slurry, but also to a lesser content of organic matter than in FYM. The effect of direct drilling on earthworms has not previously been studied in Denmark, whereas in Britain, research has been more comprehensive. In two preliminar studies, it was found that after one year of direct drilling, there was no difference between this treatment and ploughing, whereas after more than 8 years of direct drilling, the double biomass was found, i.e., 30 g / m^2 vs. 15 g / m^2. The number of individuals was approximately the same, 130 / m^2. This was due to a different species composition in the long term direct drilled fields (Heininge, south west Zealand). Here A.longa and A.tuberculata were abundant, both being of larger size than A.caliginosa, which was dominating at the other site (Ballum, western Jutland). Both study sites were clay soils, and the crop winter heat.

DANSK RESUME

UNDERSØGELSER AF REGNORMENES *(Lumbricidae)* ØKOLOGI I LANDBRUGSJORD

Regnormefaunaen i den dyrkede jord påvirkes af en række miljøfaktorer, som her måske er af større betydning end i mere beskyttede habitater, som løvskove, enge og overdrev. I denne afhandling er effekten af temperatur og nedbør på de mest almindelige arter i landbrugsjorden blevet undersøgt, ud fra materiale indsamlet gennem seks år (1976 - 1981). Det vises her, at især temperaturforskelle mellem de enkelte år er af stor betydning for regnormebestandenes udvikling, hvilket ikke tidligere har været erkendt. Desuden er der foretaget undersøgelser af respiration og vækst, samt detaljerede undersøgelser af en enkelt arts biologi under markforhold. Desuden er det undersøgt, hvorledes forskellige jordbehandlingsredskaber påvirker regnormene, og i sammenhæng hermed, hvorledes tilførsel af organisk stof (husdyrgødning eller efterafgrøde) påvirker regnormene. Her i landet er der gamle traditioner for regnormeforskning. Således påviste Müller (1878-1879), som en af de første, sammenhængen mellem dannelsen af muldjord og regnormenes aktivitet i skovjord. Dette arbejde videreførtes af Bornebusch i 1920'erne (1930). I forbindelse med landbrugsjorden, har der dog ikke været udført undersøgelser af regnormenes økologi før 1976, hvor de undersøgelser, der ligger til grund for denne afhandling blev påbegyndt. Forhåbentlig vil en bedre forståelse af de faktorer, der påvirker regnormene i landbrugsjorden, sådan som det her er beskrevet, kunne bidrage til en forbedret strategi for bevarelsen af landbrugsjordens frugtbarhed.

TEMPERATURFORHOLDENES BETYDNING

Hvorledes regnormene påvirkes af temperaturforskelle mellem de enkelte år er ikke før blevet undersøgt. Her vises det (i et system med samme jordbehandling år for år, pløjning, og tilførsel af samme mængde organisk stof, 100 tons fast staldgødning/ha/år), hvorledes, der er en sammenhæng mellem tætheden og forskelle i temperaturniveauet på forskellige årstider (vinter, forår og sommer) gennem årene. Der kan således udregnes en temperatur index, C_i , for hvert enkelt år, med hvilken, der for visse arter (_A_.longa, _L_.terrestris og _A_.rosea) er en lineær sammenhæng ($p < 0.001$ - $p < 0.05$). Fra 1976 - 1981 antog C_i værdier mellem -0.24 og 1.30, således at højere værdier af C_i påvirkede bestanden i positiv retning. Arterne _A_. caliginosa og _A_.chlorotica trivedes bedst mellem $C_i = 0.4$ og 0.6. Der er også vekselvirkninger mellem temperaturen (C_i) og nedbøren, når det gælder regnormebestandens størrelse. Dette blev vist gennem en tredimensional afbildning af C_i, nedbør og bestandens størrelse (total antal og % af nyklækkede).

Det vistes,at især nedbøren om sommeren, sammen med temperaturforløbet i denne periode, og vinteren, var af betydning for, hvor stor en bestand, der kunne registreres om efteråret (her findes normalt den største bestand). De undersøgte arter var her A.longa og A.caliginosa, repræsenterende en dybtgravende og overfladisk levende endogen art, hver især. Det vistes at A.longa var mere varmekrævende, samt tålte lavere nedbør end A.caliginosa. Dette synes også i overensstemmelse med de to arters udbredelsesmønster. A. longa findes i mildere maritimt klima, f.eks. i England, hvorimod det er for koldt i Norge. A.caliginosa går længere mod nord, op til polarcirklen i Norge; men også langt sydpå, til Nordafrika. Også A.longa findes i mere kontinentalt præget klima, i øst og sydøst Europa. At A.caliginosa krævede mere nedbør end A.longa viste sig især ved de lavere værdier af C_i. Ved den lavest fundne værdi af $C_i = -0.24$, faldt antallet af begge arter betydeligt. Hos en art som A.longa, der kræver en føde af relativ høj kvalitet, viste det sig, at de tilgængelige ressourcer udnyttes hurtigere når C_i stiger. Således konstateredes et fald i populationens størrelse ved 50 tons fast staldgødning, når C_i steg. Dette fald indtrådte ved en endnu lavere værdi i kunstgødning. I 100 tons staldgødning, var der en fortsat stigning i bestanden ved stigende C_i værdier. Tilsvarende effekter sås ikke hos de andre arter.

RESPIRATION

Iltoptagelsen måltes hos forskellige udviklingsstadier (nyklækkede, juvenile og adulte) af de tre arter, A.caliginosa, A.tuberculata og A.longa. Iltoptagelsen, µl O_2 /g/time hos A.caliginosa varierede med kropsvægten (adulte - nyklækkede) fra 46 - 65 µl O_2 /g/time. Hos A.tuberculata varierede iltoptagelsen fra 38 - 59 µl O_2 /g/time. Hos subadulte A.longa var iltoptagelsen 29.5 µl O_2 /g/time. Der var en lineær sammenhæng mellem iltoptagelse og kropsvægt ($p < 0.001$ - $p < 0.02$), og der er således ikke nogen specifik størrelsesorden af iltoptagelse knyttet til de forskellige udviklingsstadier. Iltoptagelsen hos A.longa lå på samme rette linie som for A.tuberculata. De ovennævnte værdier for iltoptagelse måltes i respirationskamre med ikke-steriliseret jord, for at gøre forholdene så naturlige som muligt.
I en serie målinger på A.caliginosa uden jord fandtes lavere værdier. Brug af et medium, der ikke stemmer overens med ormenes normale habitat, vil kunne medføre ukontrollerbare og uønskede effekter på den respiratoriske rate. F.eks. vil brug af et overvejende sandet materiale til epigene (førnlevende) arter kunne resultere i forøget respiration/aktivitet, samt indtag af uforholdsmæssig store mængder af mediet. Dette er her vist ved en analyse af Phillipson og Boltons (1976) resultater. Iltoptagelse hos subadulte A.tuberculata, som lå i dvale (aestivation) ved 2.5 °C, måltes til 8.5 µl O_2/g/time. Dette er 36 % mindre end aktiv iltoptagelse korrigeret til 2.5 °C. Der er således tale om en fysiologisk til-

pasning til dvaletilstand. Iltoptagelsen hos regnorme sammenlignedes med andre poikilothermers iltoptagelse. Den respiratoriske rate (µl O_2/g/time), konverteredes til calorier/individ / time og afsattes, dobbelt logaritmisk, mod den tilsvarende kropsvægt. En regressionsanalyse gav en line med hældningen, $n = 0.854$ ($p < 0.001$), hvilket ikke er meget forskelligt fra $n = 0.751$, for samtlige poikilothermer (invertebrater såvel som vertebrater; Hemmingsen 1960). Stofskiftets niveau lå 1.9 gange under gennemsnittet for samtlige poikilotherner (Hemmingsen 1960), hvilket er i god overensstemmelse med niveauet for andre invertebrater med relativt begrænset mobilitet. Niveauet for stofskiftet hos *A.caliginosa* målt uden jordmedie, var ca. 1.22 gange under niveauet med jordmedie, og er formodentligt tæt på standardstofskiftet, idet *A.caliginosa* (iltoptagelsen her målt med ormene i vand), under disse forhold var ret inaktiv og slap. Dette gælder dog ikke nødvendigvis for alle arter. Således vil *Eisenia* under disse betingelser klumpe sig sammen i et nøgle (hvis flere individer er tilstede), hvilket er energikrævende, og vil påvirke målingerne i modsat retning.

ØKOLOGI HOS *A.tuberculata*

Denne undersøgtes ved ugentlige - (14 dage) prøveudtagninger (håndsortering) af dybderne, 0-10, 10-30 og 30-60 cm (0.5 m^2 prøveflader). Den vertikale fordeling af ormene gennem året kunne således fastlægges ret nøje, såvel som aktivitetsmønstret. Efter vinteren genoptoges aktiviteten i løbet af marts.

Om efteråret begyndte ormene at vandre nedad og gå i dvale i slutningen af oktober - begyndelsen af november. Adulte orme overvintrede dybere end juvenile, ned til 0.70 m dybde. Om sommeren (1981) bestemtes den vertikale fordeling af nedbøren. Der konstateredes dog ingen inaktivitet om sommeren. Om efteråret konstateredes en stor mortalitet omkring tidspunktet for vinterdvalens indtræden, især blandt adulte. Årsagen hertil formodes at kunne henføres til en kombination af senilitet og parasiter / pathogener. Reproduktionsraten (antal kokoner / adult / måned), bestemtes til (minimum), o.5, 1.1 og 2.7, for henholdsvis forår, sommer og efterår. Denne tendens hænger godt sammen med ormenes vertikale fordeling og udviklingen i jordtemperaturer.

POPULATIONS RESPIRATION

O_2 optagelsen hos ovennævnte population af A.tuberculata, beregnedes til 25.5 l / m^2/ år. 94.4 % af iltoptagelsen repræsenteredes af aktive orme. Denne andel fordelte sig mellem 0-10 og 10-30 cm lagene med henholdsvis 52 og 46 %. Dog således, at fra forår til efterår, stiger 0-10 cm andelen jævnt. Dette stemmer også overens med de reproduktive data.

VÆKSTFORHOLD HOS REGNORME

Disse eksperimenter strakte sig over 450 - 520 dage (A.longa, A.caliginosa og Octolasion cyaneum). Som føde anvendtes knuste, visne linde og elme blade, samt formalet byghalm. Væksten hos *A.tuberculata* måltes i 150 dage. Hos alle arter fandtes logistiske vækstkurver. Væksten måltes i mørke ved 12 °C. Hos isolerede individer af *A.longa* (på elme og linde blade) udvikledes klitellum efter 320 dage. Hos *O.cyaneum* (2 individer sammen) efter 200 dage. Med 4 individer sammen, efter 250 dage. Isolerede individer af *A.caliginosa* udviklede klitellum i løbet af 120 - 200 dage. Det synes her, at lidt forskellige vækstbetingelser har nogen betydning. Et isoleret individ på blade, nåede en meget høj slutvægt, 1,9 g (klitellum efter 200 dage). Et andet på halm udviklede klitellum efter 135 dage. Et tredje, hvor antallet af individer gradvist reduceredes fra 6 til 1, udviklede klitellum efter 120 dage. Slutvægten for disse to var ca. 1,0 g. Imidlertid var der ikke nogen forskel på vækstraten. Der kan således forventes relativt komplicerede sammenhænge mellem fødemængde, føde kvalitet og tæthed for såvidt angår tidspunktet for udviklingen af klitellum og den maksimale vægt der vil kunne opnås inden for den samme art.

Der påvistes en lineær sammenhæng mellem log specifik vækstrate (mg / g / dag) dvs. log v′ og kropsvægten ($p < 0.001$). Den rette linies hældning var forskellig hos de forskellige arter. Den mindste hældning fandtes hos *O.cyaneum* (- 0,35), såvel som den laveste initiale vækstrate (log v′ = 1,28 ; skæring med y- aksen). Hos *A.tuberculata* fandtes den højeste initiale vækstrate (log v′ = 1.60), samt en stejl hældning (- 0,61). *A.longa* og *A-caliginosa* lå imellem disse to yderpunkter. Hos *A.caliginosa* var den initiale vækstrate den samme som hos *O.cyaneum*, medens hældningen var stejlere (- 0,46). Hos *A.longa* var den initiale vækstrate højere (log v′= 1.36) og hældningen knap så stejl (- 0.38). Det ses således, at kombinationen af hældning og initial vækstrate er bestemmende for den omtrentlige maksimalt opnåelige størrelse hos den enkelte art. Hos ingen af de undersøgte arter fandtes den samme kombination, hvilket formodentligt er med til at nedsætte den interspecifikke konkurrence. De to arter med den højeste initiale vækstrate (A.longa og A.tuberculata), kræver sandsynligvis føde af højere kvalitet end de to andre arter. Dette synes ihvertfald veldokumenteret for A.longa, hvorimod data i denne henseende, ikke har kunnet fremskaffes for A.tuberculata. Årsagen hertil er givetvis, at denne art jævnt hen forveksles med A.caliginosa. Der findes heller ikke samlinger, hidrørende fra andre økologiske undersøgelser (for så vidt angår regnorme), som ville kunne have bidraget til et større kendskab til denne art. Tilsyneladende har man ikke bevaret noget materiale efter en første identifikation og biomasse bestemmelse. Det må således her være på sin plads at bemærke, at al forfatterens materiale forefindes i sorteret og etiketteret tilstand (bestemt til art), og opbevares i Zoologisk Instituts samlinger, hvor det vil være tilgængeligt for yderligere undersøgelser. Endelig ansloges respirations / produktions forholdet for den mest almindelige art, A.caliginosa, ud fra vækstkurven og respirationsmålingerne. R/P forholdet vistes at forholde sig lineært (log R/P), til kropsvægten, indtil nær maximumsvægt. Det ansloges endvidere, at ca 75 % af assimilationen konverteres til produktion hos nyklækkede, faldende til ca. 20 % hos adulte (produktion af slim, kokoner, sæd og æg).

INDVIRKNING AF DYRKNINGS- PRAKSIS

Undersøgelser af forskellige jordbehandlingsredskaber viste, at jo mere skånsom behandling, desto flere regnorme kunne forventes. Denne effekt hænger sammen med jordtypen, således, at jo højere lerindhold, desto mindre effekt af det pågældende redskab. Denne generelle effekt ses typisk at gælde for de endogene arter, A.caliginosa, A.tuberculata, A.rosea og A.chlorotica. De forskellige jordbehandlingsredskaber kan ordnes efter stigende negativ effekt: Spaderulle harve, tallerken harve, plov, fræser og stubkultivator. På de dybtgravende arter, A.longa og L. terrestris, synes overfladisk arbejdende redskaber mest gunstige, hvorimod pløjning har en negativ indvirkning. I forbindelse med de forskellige jordbehandlingsredskaber, undersøgtes også indvirkningen af efterafgrøder. Der var en gunstig effekt af alle efterafgrøder (gul sennep, italiensk rajgræs og sneglebælg) på regnormene. I forsøgene med rajgræs og sneglebælg, var der en større effekt af sneglebælg ved lav tilførsel af handelsgødning (0 N), hvorimod der ingen forskel var ved 150 N. Dette skyldes sandsynligvis den symbiotiske N- binding hos sneglebælg ved 0 N. Effekten af sneglebælg var størst på L.terrestris, og sås både i sandjord (Jyndevad) og lerjord (Tåstrup). Effekten af organisk stof i form af husdyrgødning (fast staldgødning og gylle), er dog meget større end effekten af efterafgrøder. Fast staldgødning var fremmende for både A.longa og L.terrestris, hvorimod gylle synes at undertrykke disse to arter. Ved gylle tilførsel blev A.caliginosa stærkt dominerende. De mindre arter, A.rosea og A.chlorotica påvirkedes knapt så meget. Som tidligere nævnt var der store svingninger i bestandenes størrelse gennem årene 1976 - 1981. I gode år, 1980 - 1981, optrådte store bestande, indtil 400 individer / m^2 og 100 g / m^2. Gennemsnitsbiomassen (1976 - 1981), var højest ved tilførsel af 100 tons gødning / ha (32.8 g / m^2 ved gylle og 50.0 g / m^2 ved fast staldgødning). Virkningen af direkte såning har ikke før været undersøgt her i landet. Efter 1 års direkte såning, fandtes en biomasse på 15 g / m^2 (det samme ved pløjning). Efter mere end 8 års direkte såning fandtes en biomasse på 30 g / m^2. Antallet af individer var omtrent det samme i de to forsøg. På lokaliteten med 1 års direkte såning (Ballum, lerjord), dominerede A.caliginosa, hvorimod de to større arter, A.longa og A.tuberculata, dominerede på den anden lokalitet med 8 års direkte såning (Heininge, lerjord). Afgrøderne begge steder var vinterhvede.

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Institutter m.v. under Statens Planteavlsforsøg

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Planteværnsafdelingen på »Godthåb«, Låsbyvej 18, 8660 Skanderborg	06 52 08 77
Institut for Ukrudtsbekæmpelse, Flakkebjerg, 4200 Slagelse	03 58 63 00
Analyselaboratoriet for Pesticider, Flakkebjerg, 4200 Slagelse	03 58 63 00