

THE SOIL MEIOFAUNA OF THE
ACCRA PLAINS

BY

W. BELFIELD

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CONTENTSVolume I

	Page
1. Summary	2
2. Introduction	5
3. General Methods	8
4. Distribution throughout the year	14
a. Introduction	14
b. Methods	16
c. Results	17
d. Discussion	34
5. The effect of Overhead Watering during the dry season	41
a. Introduction	41
b. Methods	41
c. Results	43
d. Discussion	50
6. The effect of shade	54
a. Introduction	54
b. Methods	57
c. Results	58
d. Discussion	67
7. The effects of cultivation	79
a. Introduction	79
b. Methods	85
c. Results	87
d. Discussion	95

	Page
8. The population of contrasted types of soil	102
a. Introduction	102
b. Methods	110
c. Results	111
d. Discussion	123
9. General discussion	136
10. Acknowledgements	146
11. References	148

Volume II

Tables, Graphs and Figures.



Summary

Samples of soil have been taken from various situations at different times to illustrate the effects of season, water, shade, agriculture, disturbance and type of soil, on the soil meiofauna of the Accra Plains.

It is shown that there is a significant difference both in numbers and in vertical distribution of the animals in different seasons and in different soils. Water is thought to be the most important factor, as it is demonstrated that there is a direct correlation between size of population and the rainfall of the previous month, and that the vertical distribution can be correlated with the rainfall of the same month. Waterlogging however causes a reduction of population.

Shade produces a marked effect on both the numbers and the vertical distribution, the population, with the exception of the Acarina, being smaller and deeper in exposed than in shaded bare fallow soil. This is almost certainly caused by the desiccation conditions in the exposed soil.

Disturbance of the soil by agricultural practices causes a reduction of population, and this smaller population persists during crop growing, and after

harvest when the plot is allowed to return to grass. Disturbance causes a rapid drying out of the soil, the crop does not give enough cover, and harvesting causes impoverishment of the soil. Each of these conditions is shown to reduce the population.

Different kinds of soil are shown to be associated with a difference in size and distribution of population. In both dry and wet seasons, the population of latosol is greatest, clay lowest and sand intermediate. During the dry season the population of latosol is found deeper than in the other two soils. It is suggested that this is because there is more food and water at lower levels in the latosol. This enables the animals to avoid the desiccation conditions in the upper layers, and to form a reservoir for a large population increase under the improved conditions of the wet season.

INTRODUCTION

Much work has been carried out on the fauna of the soil in various parts of the world but the main proportion of it in Europe and America. A certain amount has been done in and around the West Indies (Dammerman 1925 and 1937, Strickland 1945 and 1947) and in Hawaii (Van Zwaluwenburg 1926 and 1931). The results of only one investigation has been published from tropical Africa, and that from East Africa (Salt 1952 and 1956).

No observations on West African soil arthropods have been published apart from those on the more obvious fauna, such as termites, ants and crickets. Nothing was known of the vertical, horizontal or seasonal distribution and variation of the smaller forms, such as for instance, Collembola and Acarina.

It was realised that the detailed study of one particular group is of the greatest value, but this can only be accomplished when, firstly, the systematics of the particular group have been worked out very carefully in the area under observation, and secondly, when it is known what group is, in fact, important in the area. Both these considera-

tions were taken into account when it was decided to collect all the fauna and examine it from a general point of view. This type of investigation would firstly show what groups could profitably be studied in more detail and secondly provide a great amount of material for systematic studies. All the specimens collected have been preserved and deposited with specialists (mainly at the British Museum of Natural History) and will be dealt with in due course.

This work is, therefore, an investigation into various aspects of the meiofauna of the soil on the Accra Plains under different conditions. The term "meiofauna" is used to describe that group of animals which live in existing soil pores and interstices, and usually cannot create additional living space through burrowing activity (Murphy 1953), and corresponds to the terminology used by Mare (1941-1943) in her classification of the bottom fauna of the sea. The animals which would fit this description in the soil are the smaller arthropods (size range of about 100 microns to 1 cm.), often referred to as micro-arthropods.

The work has three main ends in view.

1. To find the numbers and vertical distribution of arthropods in undisturbed pasture soil throughout the year, i.e., during the wet and dry seasons.
2. To investigate the effects of cultivation, comparing it with what was considered normal in undisturbed grassland.
3. To investigate the manner in which arthropods are distributed in different soils.

Experimental work was also carried out in an attempt to find the causes of some of the distributions found in the basic samplings outlined above. To this end the following were tested :-

1. The effect of watering during the dry season.
2. The effect of shade on bare soil.
3. The effect of disturbance on the soil by digging.

In addition, a considerable amount of collecting was carried out over the Accra Plains. This was done by actually looking for evidence of animal activity in the soil (holes etc.), and digging up the animals. The larger animals, not strictly members of the meiofauna, are not, however, included in this account.

GENERAL METHODS

As the water and electrical supply could not always be relied upon, it was necessary that any apparatus used for extracting the animals should not require a dependable supply of either of these services. It was also felt that any extraction method used for this type of work (where nothing at all was known about groups to be found), should be as little selective as possible. Flotation methods, depending for their action on a purely physical principle, are less selective than funnel arrangements, relying on the response of animals to their environment, for tropisms, of every kind are different for different species, and vary even amongst individuals of the same species. A further factor involved in the choice of extraction method was the type of soil to be examined. The fact that they are not organic on the Accra Plains favours the use of a flotation method. It was therefore decided to use Ladell's method of extraction (Ladell 1936). This is a flotation device using a 25% solution of magnesium sulphate,

which gives a specific gravity of 1.11. This solution floats the arthropods out of the soil, which is being stirred thoroughly. Air is bubbled through the soil at the same time to ensure that it is completely broken up. If necessary, this apparatus can be worked manually, and the air supply delivered from a car tyre pump.

Although Ladell's method has been shown to be less efficient in some respects than other methods, (Macfadyen 1953), it has the advantage, as shown above, that it does not require water at high pressure as would be necessary in Salt and Hollick's (1952) method, nor does it require a steady electrical supply as would be necessary in the use of funnel techniques. (Macfadyen's 1953 account of his paraffin burning development of the Tullgren-type funnel was not available when this work was first started).

Because of the necessity of separating the animals from the vegetable matter coming from the apparatus, a modification of Ladell's original method similar to the one used by Glasgow (1939) was introduced. The resulting animals floated out from the apparatus were

filtered off in a Buchner funnel. The filter paper with its contents were then transferred to a petri dish, more magnesium sulphate added, and examined by means of a binocular microscope. Each piece of vegetable matter was subjected to a detailed examination separately. The use of a microscope mechanical stage modified to fit a petri dish, ensured that the whole of the dish was examined.

Reclamation of the used magnesium sulphate proved to be a problem because of the large volumes of liquid involved. A filtration method for regeneration of magnesium sulphate was eventually devised however, and is shown in figure 1. The used, dirty liquid was poured into the aquarium tank. Therefore, with taps A1, B2, D2 and C2 closed, and taps B1 and D1 open, liquid is filtered from the aquarium tank, through the stones and into carboy I. At the same time, filtered liquid can be delivered from carboy II by opening taps C1 and A2. The opposite arrangement of the taps would, of course, filter to carboy II and deliver from carboy I. This method was found to maintain a steady supply of filtered magnesium sulphate to the Ladell's

apparatus effeciently and, because, being virtually a closed circuit, it avoids the mess usually resulting from the use of large volumes of liquid.

The samples of soil were removed by means of a soil corer (K.C. Productions Ltd., Model 110) of 4" diameter and 18" deep (Fig 2a). This instrument has many advantages for use in the soils of the Accra Plains, which are mainly either gravelly or of clay. These advantages include a removable cutting head, and a very heavy jarring link, which was especially useful, as it enabled the sampling tube to be driven in despite the iron concretions and gravel of the upland soils of the plains. The sampling tube was removed from the soil by means of a lorry raising jack in order that removal could be accomplished neatly and with as little disturbance of the surrounding soil as possible. The soil samples were removed from the tube by means of a piston arrangement worked by a hydraulic jack (Fig. 2b.)

The cores, which were 18" long, were cut

into sections, these sections being, the top 2", 2-6", 6-12" and 12-18". The top 6" was split into 2 and 4 inches fractions in order to ascertain the proportion of animals at or near the surface in the top 6". By adding these two top sections together the results could be compared with those of many other workers who have taken the top 6" without any division. Samples were taken to a depth of 18", because it was felt that the lower levels of the soil would assume importance during the dry season. It is admitted that there will be a loss of animals because of this handling. Each sample, however, was treated in exactly the same way, and the results will, therefore, be comparable.

Lack of records and the traditional shifting method of agriculture used by African farmers made the finding of areas which could be regarded as undisturbed land difficult. In the main, this difficulty was solved by taking samples at Agricultural establishments, where adequate records have been kept. When samples of different soils were examined, however, this was not possible and so

pains can, therefore, be confused with the "big" rains, with a resultant mistake of six months. National and political events can be a more reliable guide, but human memory is not infallible. The areas were chosen mainly, therefore, on the first two methods.

reliance had to be placed on three other methods.

1. Careful examination of the area to find any evidence of past agriculture such as boundary markings, furrowing, destroyed termite hills etc.

2. Examination of actual grass species in order to ascertain whether they were normal climax communities.

3. Questioning of local farmers and chiefs.

This third method, however, is difficult and not very reliable because years are not normally reckoned by calendar, but by seasons. The "small"

VERTICAL DISTRIBUTION THROUGHOUT THE YEAR

Introduction

Many authors have shown that soil populations vary at different times of the year, according to season (Ford 1935, MacFadyen 1952 et al).

It is felt that normal seasonal variations must be known before conclusions can be drawn from any other work. Theories accounting for seasonal distribution in temperate zones, such as the effects of freezing, cannot be applied to the tropics, because of the very different physical conditions found in the two regions. Little is known of seasonal distribution of soil fauna in the tropics, and it was decided, therefore, that the first stage of this work must be to investigate the seasonal fluctuations in the numbers and vertical distribution of the soil arthropods in normal undisturbed grassland.

The period of examination was from December 1953 to December 1954. The temperature and rainfall figures for this period may be found in Table 1. It can be seen from these figures that December 1953

and January 1954 are hot and very dry and that February, March, April and May are progressively wetter. July and August are dry, and September, October and November are progressively wetter. December 1954 and January 1955 are again dry. There are thus two rainy seasons and two dry seasons. The "big" rains and the "small" rains mentioned above are the March/June and the October/November periods respectively. The very high rainfall in November is abnormal. It may be seen roughly, that the higher the rainfall, the higher the relative humidity and the lower the temperature.

The soil is rather gravelly at lower levels, very slightly acid (pH 6.7) except in the top few inches (pH 7.6), and of low organic content. The top 6" is a grey-brown humic gritty gravel. The next 18" is a brown coarse loose sand with small amounts of quartz gravel and stones. Below this the soil contains many more iron concretions, quartz gravel and stones. Between 4½' and 6½' there is a clay gradually merging into decomposing biotite granite and pegmatite between 6' and 7'.

A profile description of the soil (from the report of the Soil and Land Use Survey) may be found in Figure 4. Unfortunately no mechanical

and chemical analyses were available for the actual field of survey, and the analysis found in Table ¹⁸13, is, therefore, for a nearby area of very similar soil.

A vegetation analysis may be found in Table ¹³14.

Methods

The cores were removed from the soil, split into sections and the soil arthropods extracted, as described on pp. 8-13. The samples were taken in an area of about 15 acres situated in the Agricultural Station, Pokoase. This field had been used intermittently for grazing over the past ten years. Six stations were established in this field and a sample taken from each station in such a way that each was within a yard of at least two other samples at the station. By this method of sampling, the numbers and vertical distribution of the soil fauna throughout the year could be determined.

In order to ensure that the techniques involved were completely standard throughout the year, samples were taken in October and November 1953 the population extracted and then discarded. The necessary operations were, therefore, learned thoroughly before the samples were taken in December 1953.

Results

Table 2a gives the total number of animals removed from all six samples during the observation period at the various depths. The totals of the samples from all six stations were used in order to give a clearer idea of the overall distribution and Table 3 shows that these totals can be used as a representation of the distribution of the soil fauna. Table 3a shows the monthly totals of all groups at each station expressed as a percentage of the monthly total for all stations. It can be seen that these percentages do not vary a great deal in the period of sampling. It may be seen also that the Standard Deviation is low at all stations. Tables 3b, c, d and e, are similar figures calculated for the main groups of animals found. Here again, although not so low as in Table 3a, the Standard Deviations are not high. It is felt that this shows that there is no marked deviation from the general pattern at any of the stations and, therefore, the totals from all stations can be compared on a monthly basis.

Isoptera and Formicidae are not included in the monthly totals of Table 2a, as they were considered to be aggregated animals. Samples were taken as far away as possible from the nests of these two orders. If, however, these animals were found in any quantity in a sample, it was then rejected, and another one taken. The main reasons for this rejection are that the available volume of soil for other animals would be very much reduced by their tunnels, there is often a specialised fauna

living in the nests, and the effect of the activities of these animals on the surrounding microhabitats is not certain.

Columns 3, 4 and 5 of Table 2 are adjustments of the figures obtained from the top 6". Column 3 is obtained by adding the top 2" and the 3" - 6" figures, giving therefore, the total animals in the top 6". This top 6" total will, unfortunately, be slightly less because of being divided than if it had been taken all in one piece. Column 4 is obtained by multiplying the top 2" figure by three, thus making them comparable to the numbers extracted from 6" of core. Column 5 is obtained by multiplying the 2" - 6" figures by 1.5 which again makes the figures comparable to the figures obtainable from 6" of the core.

The most striking result obtained from these figures is the continual rise of the total number of animals (Column 8) from December to May, corresponding to the increased rainfall (Graph 1). Some measure of this increase may be realised when it is seen that the total numbers in May are more than treble the numbers in December. This period of continual rise is followed by a drop in June. This June sample, which perforce had to be taken during a period of leave was subsequently found to be inadequately extracted and check analyses showed that the numbers of animals present was approximately double that recorded. If this correction is applied to the June figures it will be found to show a slight increase on May and to fit into the histogram much better (unshaded extension in Graph 1), than the original estimation. The rise is maintained in August, but is followed by a marked fall in September and October (a sample was not taken in September because of illness). After the low numbers of August and October there is a very sharp rise in November and December.

The population in December 1954 is found, therefore, to be about five times as great as

in December 1953, which would appear at first sight to be anomalous. The rainfall preceding the two periods is, however, quite different, November 1953 - 1.10", December 1953 - 0.01", but November 1954 - 10.44", and December 1954 - 1.22". The very high population of December 1954, therefore, follows upon the abnormal rainfall of November 1954. In fact, throughout the year, the population does not correspond to the rainfall in the same month, but to the rainfall of the previous month.

Using only the figures for the three sections of the cores 0-6", 6-12" and 12-18" (Columns 3, 6 and 7, Table 2a). It may seem that the greatest density of animals in December was found between the depth of 6" and 12". In January the maximum, though not so marked, was still at the same depth. From February to July the maximum density was markedly in the top 6". August and October show a reduced density in the top 6" though the maximum density is still in this upper level. November and December show a return to the May distribution, with the maximum density in the top 6". The lowest section (12"-18") was the lowest density through the period of observation.

Graph 2 is a representation of the figures from columns 4, 5, 6 and 7. It may be seen from this that when the numbers for the top 2" are adjusted to compare with 6" of the core, the greatest density of animals is in the top 2" throughout the observation period. This density increases as the season becomes wetter and decreases during dry periods. The density of the animals in the 2" - 6" section also increased and decreased in a similar fashion during the same periods. Statistical support for the above conclusions may be found in Table 22 .

The results obtained from the individual groups of animals extracted are found in the rest of Table 2 and will be discussed separately.

Diplura - Table 2b.

It may be seen that there is a general increase in numbers until April, a decrease from May till August and then an increase in October until December. Analysis of so few animals is hazardous, but it would seem that there is no marked preference for any particular depth, although there is a possible preference for the upper layers. Further information however, can be gained from a perusal of the two sets of

figures in Table 2b. The first figure is the number of japygids found, the second campodeids. It may be seen immediately that there are many more japygids than campodeids. The japygids prefer the top 12", but still occur with moderate frequency in the 12-18" section. Although the figures are not good, there seem to be possible rises in population corresponding very roughly to the rises of the general population. The campodeids are in such low numbers that no conclusions can be reached about their distribution except that there may possibly be two species present, one favouring the top 2" and the other the lowest layer.

Collembola - Table 2c Graph 3

There is an increase in numbers of this order until May, a steady decrease until October (June total excluded for the reasons given on page 19) and then an increase in November and December. This corresponds to changes in rainfall, i.e., a high population corresponding to a high rainfall of the previous month. The vertical distribution also changes. The lowest density was the lowest section of the core throughout the period. The highest density

in December and January is in the sections 2 - 6" and 6 - 12". From February onwards however, the highest density is in the top 6". This is mainly due (excepting December 1954) to the great increase in density in the top 2". In December 1954 the density of the top 2" is very similar to that of the 2 - 6" section. Graph 3 illustrates these changes in density. Statistical evidence supporting the above conclusions may be found in table 22b.

Psocoptera - Table 2d

The numbers are rather low in this order. It does seem, however, that they show a preference for the upper layers of the soil, especially the top 2". There seems also to be a drop in numbers from April onwards, contrary to the general trend of the rest of the fauna.

Hemiptera - Table 2e

Because of the small numbers captured, little can be said about this order except that they were very few in number in December 1953 and January 1954, and the highest numbers were in February, March, April and December 1954. Some of these insects have been kindly identified by Dr. J.D. Williams of the Commonwealth Institute of Entomology.

Unfortunately, he reports that a large proportion of the collection are nymphs and first-stage larvae, and in most cases there is no satisfactory method of determining these. He was, however, able to link some of these larvae with adults. The following check list is of the hemiptera so far identified.

Cydnidae

Cydnus sp. nr. lepedus. (Stal).

Aphidae

Tetraneura hirsuta (Baker)

Geocis sp.

Geocis lucifuga (Zehnt)

Coccidae

Geococcus coffae Green

Dimargarodes sp.n.

Radicoccus sp. nr. incrassatus James

Radicoccus sp. (different from species above)

Ferrisia virgata (Ckll)

Pseudococcus sp.

It may be noted that the species of Dimargarodes is new and will ultimately be described by Dr. A.W. Jakubski, who is at present working on this group. The normal distribution of these ground-pearls is just

under the surface of the soil. Only four specimens were found, but two of these (from different samples) were in the 6 - 12" section of the core.

The identification of the two species of Radicoccus is uncertain at the moment, but will be incorporated in due course in a paper on the mealybugs by Dr. Williams. So few specimens have been captured that little can be said of the vertical distribution of the different species except in the case of Geococcus coffeae Green which was the common species occurring. This shows a definite preference for the lower layers i.e., 2"- 6" 2, 6"- 12" 6, and 12"- 18" 14.

Hymenoptera - Table 2f

The two families found were Mymaridae and Formicidae. The Formicidae were disregarded for the reasons stated above (page 18). Mymaridae, although not common, formed a more or less constant part of the population, and also showed a seasonal fluctuation of population, i.e., they were completely absent from June to October. The numbers captured are too low to show conclusively, any vertical distribution. It does seem possible, however, that they are rather more prevalent in

the top 6".

Diptera.

Very few specimens (31) of this order were captured. A number of these have, however, been identified by Dr. P. Freeman of the British Museum of Natural History. Most of these are not known to be associated with soil, and were probably merely using cracks in the soil as refuges. One is known to have a soil habitat: Bradysia sp. (Sciaridae) is known to have species which are litter feeding, and breeding in the soil.

Arachnida

Chelonethi - Table 2g

There are no marked fluctuations in total population recognisable except perhaps that March, November and December, are high, and January and February are low. The vertical distribution however, is quite definite. In only three months (February, August and November) were any found in the top 2". They were found in the 2 - 6" section in every sampling (except June), but not in any quantity. In fact, there were more found between 12" and 18" than in the top 6". Except for the odd case of February, when the maximum was in the

top 2", the maximum density of this order is quite obviously in the 6" - 12" section throughout the year.

Palpiaradi - Table 2h

There is an increase in numbers corresponding to increased rainfall throughout the year. There is, despite the low numbers found, a very clear vertical distribution. None was found in the top 6" at all. Their maximum density is markedly in the 12" - 18" section; the numbers found in this section are almost three times as many as between 6" and 12". It is possible from this to suggest that they may even be found below 18" in quantity.

Acarina - Table 2i, Graph 4

Fluctuations of total population again correspond to increase or decrease of rainfall. As in the case of the Collembola, these fluctuations are largely accounted for in the top 2". There is a marked preference for the top 2" and the lowest density is found in the lowest section throughout the period. Statistical evidence for these conclusions may be found in table 22..

The acarines were roughly sorted into two groups, armoured and non-armoured. On more detailed examination the armoured types were found to be all Oribatidae, the non-armoured mainly larval stages of various kinds. The results of this sorting are shown in Tables 2i and 2j. It may be seen from these tables that they form only a small proportion of the total acarine population (about 10%). The Oribatid total roughly follows the general trend, i.e., high in April, May and November. In every month except one (April) these Oribatids show a marked preference for the top 2". In April the maximum density was in the 2" - 6" section. The general preference for the upper layers has been shown by many authors in Europe, and has also been demonstrated in Trinidad by Strickland (1945, 1947), though he was working in forest, whereas these samples are from grassland. Some of the Oribatids, have to a certain extent, been identified with the aid of Dr. G.O. Evans of the British Museum of Natural History, and have been found to belong to the families Belbidae, Calumnidae, Lohmanniidae, Epilohmanniidae, Oppiidae, Ceratozetidae, Oribatulidae, Fremaiidae

and Oribotridae. It is thought by Dr. Evans that they are mostly new species. One hundred and forty-four specimens have been examined with the results as tabulated in Table 2k. Although only part of the collection has been examined, it would seem that the Oppiidae are the most important family, and the Lohmanniidae and Oribatulidae also significant. As the Oppiidae show a discontinuous vertical distribution, i.e., the densities of the top 6" and 12" - 18" are about equal, but there are very few in the 6" - 12" section. It would appear that there are at least two species involved, one inhabiting the upper regions of the soil, the other occupying the lower layers. All the rest of the families, where the numbers are large enough to be analysed, show a marked preference for the upper layer. This does not, of course, rule out the possibility of their being more than one species in each family.

Myriapoda

Pauroboda - Table 2(1)Graph 5. Table 22.

The fluctuations of population are not very definite. There does appear, however, to be a rise from December to July, a fall in August and

October, and then a very great increase in November and December. The maximum vertical distribution varies. In December, January and February, the maximum density is between 6" and 18", though the maximum in February is not so definite. In March there is a large increase in numbers in the top 2" and to a lesser extent between 2" and 6". In March and April the maximum density is in the top 2", but in May is in the top 6". Except for the month of October, the maximum density remains in the top 2" for the rest of the year. The overall conclusion is that the higher levels are preferred by this group of animals and that their density becomes less as lower levels are attained.

Symphyla - Table 2m, Graph 6. Table 22.

The seasonal distribution of this order is not perfectly clear. December and January are the lowest totals. February shows a considerable increase, March to June, however, are progressively smaller. In July there is a sudden increase to more than twice the June total.

Except for October, there is a steady increase from July to December. Vertical distribution is also rather complex. The maximum density in December is quite definitely between the depth of 6" and 12". In January the densities in the 6" - 12" and 12" - 18" sections are almost equal, and both much greater than the two upper sections. In February the densities within the 2" - 6" and 6" - 12" sections are almost equal and are each greater than the top 2" section and the bottom 6". In March the densities of the 6" - 12" and top 2" layers are almost equal and are each greater than the other two sections. In April and May the greatest density is in the 2" - 6" section. There is a drop in the density of the top 2" and bottom 6", although the 6" - 12" section still remained quite high. In June and July, though the maximum is still in the top 2" - 6" section there is a considerable rise in the top 2". In August, however, the maximum has gone to the deeper layer of 6" - 12" as in the early months of the year, but in September and November the maximum has risen to the 2" - 6" layer once again.

In December the density of the top 2" section is very much higher than in November, in fact, the highest of the year.

The maximum density is, therefore, not fixed at the same depth throughout the year, but moves up and down. It is never in the top 2" or the bottom 6", and its position in the two middle sections is not very clearly determined. It does seem possible though, that the maximum density is in a higher section in response to higher rainfall and wetting of the upper layers.

Because of the small numbers captured, little can be concluded about the following groups: Isopoda (1), Protura (16), Thysanoptera (6), Coleoptera (12), Orthoptera (2), Araneida (9), Phalangidae (1), Diplopoda (18), and Chilopoda (35).

Table 4 shows the percentage of the total of each group of arthropods. Similar figures are included from East Africa and a pasture in England, for comparison (Salt 1952 and Salt et.al. 1948). It is felt that although a slightly different method was used in this work, the figures can be compared as both methods use a flotation principle and would not show the great differences which would be expected if one technique involved the use of a funnel

principle. It may be seen from the first three columns of this table that in all areas, the Acarina and Collembola account for a very high proportion of the population. i.e. England 88%, East Africa 86% and West Africa 77%. There is, however, a difference in the proportions of the two groups. The figures for Collembola are similar in England and in West Africa, but lower in East Africa, but in the case of the Acarina the figures for East Africa and England are similar, and low in West Africa.

The main differences to be noted from this table are that the Paurepoda and Symphyla are very obviously higher in West Africa than in either England or East Africa. Other differences are a higher proportion of Pseceptera in West Africa than in the other two areas, and lower proportions in West Africa in the cases of the Thysanoptera, Hemiptera and Coleoptera.

Within the West African samples there is a marked difference between the fauna of the top 6" and that of the lower samples. In the lower layers

the Collembola and Acarina are very much fewer, the Symphyla, Palpigradi and Chelonethi, very much more numerous. The reason for this is to be found in the vertical distribution of these groups (pp 26 - 31). It is interesting to note that the Diplura show similar proportions at this lower depth to the proportions found in the top 6" in England and East Africa. This seems to indicate that the distribution of this group is at a lower level in West Africa than in the other two areas.

On the whole however, this table does show a remarkable similarity in the proportions of the groups to the total fauna in these three widely separated areas.

Discussion

This method of sampling appears to be successful in showing the vertical distribution of the soil fauna over a period of time. It has shown many points of value.

The increase in numbers as the wet season progresses from December to May could be expected from the appearance of the soil. In December and

January at the beginning of the sampling period, the top few inches of the soil were hard-baked and completely dry. Indeed it seems surprising that any arthropods manage to survive in it at all. These top few inches are, however, transformed by moisture into the richest layer of the fauna. When these upper layers are dry the arthropod population will be exposed to desiccation.

Etching of the wax layer by the soil most probably increases the susceptibility of arthropods to desiccation and this in turn influences them in their avoidance of dry conditions.

Except in soils covered with heavy litter, (i.e., in forest,) humus is practically non-existent in the tropics, and the layer of food bearing soil (excluding roots) is extremely thin compared with the soils of more temperate regions. This may be seen from the soil analysis in Table 18. Animal populations will, therefore, be more concentrated, as is shown by the much greater overall density in the top 2".

The vertical distribution of the orders Collembola and Acarina, was similar to that of

the whole population. The Acarina were, with very few exceptions, free-living mites, and presumably, with a few possible exceptions, vegetable feeders. The occurrence of these two vegetarian groups in large numbers in the upper layers would seem to support the view put forward above, namely, that plant food is present in the top few inches, but desiccation is the deterrent to large animal populations at this level during the dry season.

Two groups of the Arachnida, the Palpigradi and the Chelonethi, were found in the main in the lower layers, and seem to be completely soil living. This is particularly obvious in the case of the Palpigradi, none of which were found in the top 6". If these orders are carnivorous they are obviously not in the optimum zone for food, at least in the wet season. Their distribution must, therefore, be controlled by some factor other than food. As the orders in general are retiring in habit, these particular ones are not behaving in any unusual fashion by staying in the lower layers of the soil. It seems possible, therefore, that the desiccation in the higher layers of the soil

is again the inhibiting factor. Temperature could also play a large part in determining this distribution. From Table 5 and Graph 26 it may be seen that the temperatures are lower and more stable in the lower layers of the soil, (Meteorological Service, Accra). This is consistent with what is known of soil temperatures from other parts of the world. It would appear that the distribution of these two orders is controlled by either desiccation or temperature, or the two factors in conjunction.

The Paupoda are reported to have a diet of humus and decaying plant and animal matter (Starling 1944). This agrees with their distribution, i.e., the greatest concentration in the upper layers. Their rather indeterminate seasonal distribution could possibly be explained if more were known about seasonal fungal populations. The Symphyla, however, are in their greatest concentration in the lower layers (between 2" and 12"). Whether they are carnivorous or herbivorous, like the Palpigradi and Chelonethi, they are not in the optimum depth for food. It is possible, therefore, that again desiccation or temperature, or both, are the controlling factors. Over the sampling period the

the population was from 499,000 to 6,985,000 per acre, at the least populated station, and from 3,992,000 to 48,399,000 per acre, at the highest populated station. These figures are of the same order as the population figures given by other authors, (Williams 1931, Michelbacher 1939 and Williams 1955). They do, however, show a wider range and are higher at the most densely populated station at the best part of the season and lower in the lowest populated station at the worst part of the season, than the figures quoted by the authors mentioned above. These comparisons are made with samples taken outdoors and not with samples obtained in glasshouses where very high populations are found under certain circumstances. It is felt that, because of the similarity of the extraction techniques used, these comparisons are valid. It has been reported that Symphyla are more numerous in soils with an open structure and good organic matter content, (Edwards 1929). The soil at all the stations in this study are free-draining with a good open structure. It appears therefore, that there may be differences in the organic content of

the soil at the various stations.

Comparison of the numbers of animals found in this area with the numbers found in East African pasture (Salt 1952) shows that the density of animals is less in the Gold Coast than in East Africa. This could be the result of many factors.

The methods used for the extraction of the arthropods are different. In East Africa, the Salt and Hollick method was used, in the Gold Coast, Ladell's. There is, therefore, the possibility that the two methods obtain different numbers of arthropods from the soil, the Salt and Hollick method being more efficient.

Another important factor which is different in the two studies, is rainfall. In the East African work, the rainfalls, with the exception of the samples taken in the Arusha Chini district, were higher in every case, than the rainfall in the Gold Coast. If the argument, that rainfall controls the size of population is correct, then this could be very important in producing the higher arthropod populations in East Africa.

The amount of cover given by vegetation is important also and must be taken into consideration. The denser the cover, the less water will be

evaporated from the soil below it, and therefore, the more effective will be the rainfall in moistening the soil. This is particularly so in the higher levels. It is significant that the lowest density found by Salt in East Africa, was from bare ground in an area of low rainfall.

In an attempt to support some of the conclusions of this section, the following experiment was carried out.

THE EFFECT OF OVERHEAD WATERING DURING THE DRY SEASON

Once it had been concluded that water played a great part in controlling the numbers and the distribution of the arthropods, it was decided to test this conclusion experimentally. It was realised that experimental ecological analysis is very difficult because of the almost impossible task of varying one factor only in conjunction with a standardisation of all other conditions. It was thought nevertheless, that in this case, the advantages to be gained by examination of the animals in situ outweighed the advantages of working in the laboratory with all its attendant difficulties of maintaining the animals in as natural an environment as possible.

Method

Two stations were chosen in a field near the place where the yearly fluctuation samples were taken. Each of these stations consisted of four circular areas each of one yard diameter. The centres of these circles formed a square with sides of one yard length. Two samples were taken from each of two of the four areas in January before any treatment was given. During the next five weeks, one of the remaining two areas was watered, two gallons being delivered from a watering can every

other day at 17 30 hrs., at Station A and only twice a week at Station B. Mr. H.O. Walker, Chief Meteorologist of the Gold Coast, calculated that this treatment would give approximately the same amount of water as 7 inches of rain per month at Station A, and 2 inches at Station B. After this treatment, two samples were taken from the watered area and two from the remaining "dry" area. The first samples at Station A were taken on the 24th January 1955, and the second on the 28th February 1955. At Station B, the first samples were taken on the 31st January 1955, and the second on the 7th March 1955. Relevant rainfalls for the period are, December 1.22 ins., January 2.03 inches, and February 0.51 inches.

By this method of sampling, it was hoped that the first samples (before treatment) would show that the same population was sampled in the two areas at each Station. The second sampling, after treatment, should show what effect the watering was having on the arthropod population as compared with the untreated area. Station A should show a greater response than Station B.

The cores were extracted as before (pp.8 - 12) and the results may be found in Tables 6a to q and 7a to p. Graphs 7 - 11 are graphical representations of Tables 6a, d, m, n and q, and Tables 7a, d, l, m and p.

Results.

Considering Station A only, it may be seen that, except for one sample, the total population shows a very similar distribution (Graph 7, Table 6a). There is, however, a great difference in the "wet" and "dry" areas after watering. These conclusions are supported by statistical evidence (Table 23a). An analysis of variance shows that there is no significant difference between either duplicate samples or between the total populations of the two plots ($P > 5\%$). The possible significance of changes in distribution of animals by depth was assessed by comparing the two plots before and after treatment, by chi-squared tests. These two tests show that there was no significant difference between the plots before treatment ($P > 5\%$), but there was a significant difference between them after treatment ($P < 1\%$). The vertical distribution in the wet area is still similar to that found before watering, i.e. the maximum density in the top 2". The dry area on the other hand shows a difference, the maximum density being in the 2-6" section. Chi-squared tests show that there is no significant difference ($P > 5\%$) between the vertical distribution of the population of the "wet" area before and after watering, but a significant difference between the vertical distribution of the first and second sampling in the "dry" area. ($P < 1\%$).

It is interesting to note that there is no drop in total numbers in the dry area. The difference between the two areas therefore is a movement of maximum density only and not a change of numbers.

Examination of the various orders separately reveals a number of interesting points.

Protura.

The numbers captured are too small for analysis (Table 6b). It would seem, however, that they are possibly deeper seated in the soil in the second sampling in both wet and dry areas, as none were found in the top 6".

Diplura.

There is apparently no change in the distribution of this order (Table 6c). A great change in their composition is apparent however. Campodeiidae, although forming about half of the total Diplura found in the first sampling, are completely absent in the second. The Japygidae in the other hand roughly maintain the same numbers and distribution in all of the samples.

Collembola

This order follows the same changes of distribution as those found in the totals, i.e. the maximum density in the top 2" in the wet area and in the 2-6" section in the dry area in the second set of samples, though the maximum density had been in the top 2" in both areas in the samples

taken before treatment. (Graph 8, Table 6d.) There is no difference in total numbers between the wet and dry areas and, therefore, as in the total population, the change brought about by watering is of vertical distribution, and not numbers. These conclusions are supported by statistical analyses similar to those used for the total populations on p.43 (Table 23a, b & c).

Palpigradi.

The numbers of this order captured are too small to analyse (Table 6k.) It is worthy of note, however, that all the specimens found were in the 12-18" section of the core.

Chelonethi.

There appears to be no difference in distribution between the wet and dry plots in this order (Table 6l). Before watering, the maximum density is somewhere in the top 6", possibly in the 2-6" section. After watering, however, the maximum density is in the 6-12" section in both wet and dry plots. Again there is no difference in total numbers between the wet and the dry areas. It would seem therefore, that watering has produced no difference in either the numbers or distribution of this order.

Acarina

The same pattern of changed vertical distribution

in the dry area, shown by the Collembola, is repeated by this order (Graph 9, Table 6m). This conclusion is again supported by statistical analyses similar to those used for the total population on p. 43 (Table 23a, b & c).

Pauropoda.

The distribution of this group was not very clear in the first sampling and it is therefore difficult to arrive at any definite conclusion about their distribution after treatment (Graph 10 Table 6n). It is perhaps significant however, that although Pauropoda were quite abundant in the dry area at the second sampling, none were found in the top 2".

Symphyla.

Although there is variation in the numbers of this group extracted in the four cores taken in the first set of samples, there is little doubt that their maximum density is in the 2-3" section. (Graph 11 Table 6q). This position of maximum density is maintained in both the wet and dry areas in the second set of samples. It is perhaps significant however, that as in the case of the Pauropoda, they are entirely absent from the top 2" in the dry area.

Because of the small numbers captured, little can be concluded about the following groups: ^{Symphyla} ~~Collembola~~ Gerrodontia (Table 6e), Hemiptera (Table 6f), Coleoptera (Table 6g)

Mymaridae (Table 6h), Araneida (Table 6i), Opiliones (Table 6j), Chilopoda (Table 6o) and Diplopoda (Table 6p).

The results obtained from Station B are different in many respects from those obtained at Station A. After watering, the total population of the wet and dry areas show a similar vertical distribution, i.e. the maximum density in the 2-6" section (Table 7a, Graph 7), but as at Station A, there is no difference in total numbers. These conclusions are supported by statistical evidence, (Table 23a). An analysis of variance shows that there is no significant difference between either the duplicate samples or between the total populations of the two plots ($P > 5\%$). Comparison of the two plots before and after treatment by the chi-squared test, showed that there was no significant difference between them in the depth distribution of the animals either before or after treatment ($P > 5\%$). Chi-squared tests show that there is a significant difference between the vertical distributions of the wet area before and after watering and also in the dry area between the first and second samplings ($P < 1\%$). The vertical distribution has therefore changed in both areas in the second series of samples.

Individual groups illustrate still further, the differences at the two stations.

Diplura.

The distribution of this order is not as clear at this station as at Station A (Table 7c). One point is perhaps worthy of mention. Two Campodeidae were found in the dry area of the second sampling (one in the top 2" and one in the 12-18" section). This is contrary to the expected result (see pp. 44 and 59), that Campodeidae are absent from dry soil.

Collembola

This order shows a similar distribution to Station A, the maximum density being in the top 2" in the first samples and in the top 2" in the wet area after watering, but in the 2-6" section in the dry area. (Graph 8, Table 7d) These conclusions are supported by statistical analyses similar to those used for the total populations of Station A on p. 43 (Table 23a,b & c) This distribution, however, is not nearly so pronounced as at Station A, i.e. the difference between the density of the top 2" and the 2-6" section appears to be very small at Station B.

Palpigradi.

The numbers obtained in this order are too small to reach any definite conclusions about their distribution. (Table 7j). They do, however, show the normal vertical distribution, none being in the top 6" and the maximum

density in the 12-18" section (25 in the 12-18" section and 4 in the 6-12" section).

Chelonethi.

It would seem that no change took place in the distribution of this order. (Table 7k).

Acarina.

This order shows a similar distribution to the total population, i.e. no differences between wet and dry areas in the second sampling, the maximum density being in the 2-6" section (Graph 9, Table 7i). These conclusions are supported by statistical analyses similar to those used for the total populations of this station on p. 47 (Table 20a, b and c).

Paurozoa.

As at Station A, the distribution in the first sampling is not clear and it is therefore difficult to arrive at any definite conclusion about their distribution after treatment. (Graph 10 Table 7m). It may be noted that one sample in the dry area is unusual in having its maximum density in the top 2" in the second sampling.

Symphyla.

The maximum density of this group is (except for one sample) in the 2-6" section in the first sampling (Graph 11, Table 7p). In the second sampling, however,

it is in the 6-12" section in every sample, with apparently no differences between the wet and dry plots.

Because of the small numbers captured, little can be concluded about the following groups: Protura (Table 7b) Orthoptera (Table 7e), Psocoptera (Table 7f), Thysanoptera (Table 7g), Hemiptera (Table 7h), Hymenoptera (Table 7i), Chilopoda (Table 7n) and Diplopoda (Table 7o).

Discussion.

It would seem from analysis of the results obtained that the experiment has been successful in showing that water does play a part in the distribution of soil arthropods. The results would have been more conclusive if more samples had been taken. The short length of the dry season unfortunately prevented this.

There is no evidence from these results to show that the watering affected the numbers of the population. In most cases the populations remained about the same throughout the experimental period.

An insignificant amount of rain fell during the period of observation, i.e. 0.01 inches in February, and the artificial rain was therefore the only water received. It has been shown, however, that the number of animals

responds to the rainfall of the previous month (see p. 19). The population total is therefore in response to the 2.03 inches of rain in January and was not affected by the watering or dry conditions of February.

The hot dry conditions of February would result in the majority of the population being at a lower level in the soil, and this was found to be so in the dry plots of Station A and all the plots of Station B at the second sampling. In the wet plot of Station A, however, the maximum density was maintained at a higher position in the soil. As the watering was the only primary difference between the two areas, it is thought that the upper layers of the watered area at Station A, being wet, allow the population to stay in the top 2". It would appear therefore, that although the preferred position of the majority of the fauna is in the uppermost layers, dryness of the soil forces it to adopt a lower position. The watering at Station B seems to cause very little difference in distribution. Apparently, therefore, 2 inches of rain per month does not moisten the soil sufficiently to allow the majority of the soil fauna to stay in the top 2".

Temperature may play some part in this experiment as the vegetation in the wet area of Station A was noticeably thicker and less shrivelled after the watering, than the dry area and all the areas at Station B. It is possible therefore, that the soil of the wet area of

Station A was kept slightly cooler because of the deeper shade afforded by the thicker vegetation. It is also possible that the evaporation of water from the soil is greater in the wet area of Station A. This would have the effect of cooling the surface layers. These two factors namely slightly increased shade and evaporation from the surface layers, could therefore have the effect of reducing the temperature of the surface layers. Temperature has been shown to be an important factor in the vertical distribution of many soil arthropods (Dowdy 1944) and funnel methods have been known for many years, using the principle of arthropod migration from higher to lower temperatures (Berlese 1905). Temperature could, therefore, be playing some part in the different distributions of the wet and dry areas.

Food may also be a factor in the experiment, as the watering may increase the micro-biological population and so provide more food for the meiofauna. This, however, would increase the total meiofauna, but not alter the distribution, unless the distribution of the micro-biological population was being governed by the watering in much the same way as the meiofauna appears to be

governed. Water is still therefore, the primary factor.

It would seem, therefore, that the conclusion is correct that the preferred depth for the majority of the arthropods is in the top 2" (possibly because of food). Desiccation during the dry season however, is the deterrent to the adoption of this area permanently. Also, although there has been shown to be a direct correlation between the rainfall of the previous month and the number of soil arthropods, the rainfall of the same month can be correlated with the vertical distribution of the soil arthropods.

THE EFFECT OF SHADE ON THE ARTHROPOD POPULATION

Dowdy (1944) has shown that in America, temperature is the main stimulus behind the movements of soil invertebrates deeper into the soil during the Autumn and Winter, and closer to the surface in the following Spring. In the previous section, it has been shown that water content of the soil is a very important factor in the vertical distribution of soil arthropods in the soils of the Accra Plains. As the two factors, water and temperature, are linked inseparably in natural conditions, it was thought that the amount of shade over the soil would prove to be an important factor. Another consideration also prompted this attempt to find the effects of shade on the arthropod population of the soil below.

Fluctuations of nitrate level in the soil have been the study of many agriculturalists in all parts of the world. In the tropics particularly, results have been obtained which do not fit in with normally accepted ideas, i.e., in Nigeria (Diamond 1937), in Trinidad (Hardy 1946) and in Uganda (Griffith 1951). More recently, work has been carried out in the Gold Coast, (Greenland 1956).

A typical nitrate fluctuation graph is reproduced from Greenland's work in Graph 12. A few figures for soil arthropod populations were obtained from grassland in the same area (in the course of the sampling to find the effects of cultivation), during the same period when Greenland was obtaining the nitrate figures, and these are superimposed (broken line). It will be seen from this that there is a possible correlation, between the arthropod population and nitrate level in the soil. This correlation is not understood as yet. Salt (1956) has put forward an extremely interesting suggestion from his work in East Africa, that the nitrate increase at the start of the rainy season is due to the breakdown of arthropod moults by bacterial action, which have been lying undamaged in the soil during the dry season. Support for this theory may be found in the fact that bacteria of the genera Achromobacter, Flavobacterium, Bacillus, Cytophaga and Pseudomonas, Actinomycetes of the genera Streptomyces, Micromonospora and Nocardia and Aspergillus spp. and Mortierella sp. are known to break

down arthropod cuticle, (Veldkamp, 1955). Much more work has to be done however before the full nitrogen cycle is understood in the tropics.

One of Greenland's experiments was to sample soil for nitrate in two adjacent plots of 1/40 acre each situated at the University College of the Gold Coast Experimental Farm at Nungua on the Accra Plains. Both plots had all vegetation removed from them, but one was shaded by woven palm leaves supported at a height of about three feet, while the other plot was left completely unshaded. The plots were surrounded by a stout barbed wire fence. Interference by man or cattle was therefore eliminated.

The soil of these plots is a pale coloured sand over 2 ft thick. This lies over a variable thickness of quartz stones and gravel in a grey or brown, often mottled, sandy matrix which becomes more clayey with depth. The underlying rock consists of moderately weathered, clayey, acidic Archaean gneiss or schist containing numerous quartz veins. This soil readily absorbs water and may become waterlogged in the lower horizons following prolonged heavy rainfall. Moisture is probably retained satisfactorily at depth during the dry seasons, but the sandy upper layers quickly become parched. The sandy upper layer accumulates

very little organic matter and is almost barren of nutrients. The clayey lower layer is moderately strongly leached but appears to satisfactorily retain, amounts of mineral nutrients. The whole soil however, is conspicuously deficient in phosphorous. The upper layer shows a tendency to "pack" on exposure.

A profile diagram, and mechanical and chemical analysis may be found in Figure 5 and Table 21.

A higher nitrate level was found in the shaded plot than in the unshaded (Greenland 1957). It was decided, therefore, to take samples in these two plots in the hopes that information would be obtained, firstly on the effect of shade on the arthropod population (all other factors being equal), and secondly to find any possible correlation between the arthropod population and the nitrate content of the soil, the nitrate content being a measure of bacterial activity.

Methods.

Each sampling consisted of two samples taken in the shaded plot and two in the unshaded. Each sample of a pair was taken well away from the other so that any great difference in the two samples would indicate a local aggregation. The cores were split and extracted in the usual way. (p.8-12). The results appear in Table 8.

Results.

It may be seen from table 8a, that over the whole period, there were almost twice as many animals in the shaded as in the unshaded plot. On comparing the numbers found at the different depths, the differential is seen to diminish as greater depths are attained. The ratios of shaded to unshaded are approximately as follows :-

	Shaded	Unshaded
Top 2"	3.2	1
2" - 6"	1.9	1
6" - 12"	1.3	1
12" - 18"	1.0	1
Totals	1.9	1

This is roughly the condition at every sampling and it may be concluded that the main differences in population can be accounted for in the top 6", though there is also a certain amount of difference in the 6" - 12" section (Graph 13). There is no difference in the lowest section.

Statistical evidence supporting these conclusions may be found in Table 8a and b.

The results obtained in respect of the various groups of animals are shown in Table 8 and are here discussed separately.

Diplura

Only 5 specimens were found in the 24 samples taken. These were all Japygidae, all in the shaded plot, and none were below 6", (Table 8b).

Collembola

There is a very marked difference in the populations of the two plots in total numbers captured. This difference was confined almost entirely to the top 6" i.e., the ratios of the numbers found in the two plots were :-

	Shaded	Unshaded
Top 2"	7.3	1
2" - 6"	2.3	1
6" - 12"	1	1.1
12" - 18"	1.1	1
Totals	2.7	1

When the top 2" and 2" - 6" figures are adjusted to compare with 6" of core by multiplying

by 3 and 1.5 respectively, the densities of the upper sections of the shaded plot are found to be quite different from the densities in the unshaded plot (Table 8c). Graph 14 is a diagrammatic illustration of Table 8c. This graph shows that in the shaded plot, the density of the top 2" is the highest and the densities of the other three sections become lower as the depth increases, as in the normal "wet season" distribution of April and May in the regular sampling at Pokoase (Graph 3). In the unshaded plot however, the overall picture is one in which the 2" - 6" section is of the highest density, the top 2" of the next highest, and the two lowest sections with similar densities to those of the shade plot. This is not true at every sampling, but is true in seven out of the twelve samples taken. In one case the two upper sections had no Collembola at all, and in only four cases was the highest density in the top 2". This is what could be termed "dry season" distribution, as in the December 1953 and January 1954 samples at Pokoase.

Despite the variations in the unshaded plot results, there can be no doubt that there is not only a greater density in the shaded plot, but there is also a different vertical distribution in the two plots, the animals in the unshaded plot being at a greater depth than in the shaded. Statistical evidence supporting these conclusions may be found in Table 24a and b.

Psocoptera

Only a few specimens (12) were found, but these were mainly in the top 2" of the shaded plot, only one specimen being found in the unshaded (Table 8d).

Because of the small numbers captured, little can be concluded about the following groups :- Hemiptera (4), Mymaridae (6) and Coleoptera (1).

Acarina

There is apparently little or no difference in the populations of the two plots, i.e., taking the ratios of the totals at the various depths as before, the results are as follows :-

	Shaded	Unshaded
Top 2"	1.2	1.0
2" - 6"	1.1	1.0
6" - 12"	1.2	1.0
12" - 18"	1.0	1.5
Totals	1.1	1.0

Graph 15 is a diagrammatic representation of the results obtained by adjusting the figures from the top 2" and 2" - 6" sections to correspond to 6" of the core (Table 8h). There seems to be little difference in the vertical distribution under the two conditions. In the shaded plot nine out of twelve samples show the maximum density in the top 2", two samples have equal densities in the two upper sections and in only one sample is the maximum in the 2" - 6" section. In the unshaded plot ten samples show the maximum density in the top 2", one sample has equal densities in the two upper sections, and in one, the maximum density is in the 2" - 6" section.

Differences may be found in the species present when specific determinations are made, but until this happens, little can be recorded beyond the important fact that shade has apparently no effect

on the population density of the Acarina. Statistical evidence supporting these conclusions may be found in Table 24a and b.

Chelonethi and Palpigradi.

It is worthy of note that no specimens of either of these two orders were found in any of the samples.

Pauropoda

Although the numbers captured are low, the distribution of this group follows much the same pattern as the Collembola, i.e., much higher numbers in the shaded plot than in the unshaded, with the animals in the unshaded plot being situated deeper in the soil than in the shaded (Table 81, Graph 16). The results, however, are not quite so conclusive, as in two cases (17.10.55 and 29.11.55) the numbers were equal in the two plots in the top two inches. Similar cases may be found in other samples at other depths. This is possibly because the low numbers involved in these particular cases are not really significant.

On analysis of the results from individual samples it may be seen that in the shaded plot, the maximum density of six samples, was in the top 2", and in the 2" - 6" section in four samples, and in the 6" - 12" section in two samples. In the unshaded plot, the position is rather the reverse, the maximum density in six samples is in the 2" - 6" section, in the top 2" in four samples and in the 6" - 12" section in one sample (Pauropoda were completely absent from one sample). A more significant fact, however, is that in the unshaded plot, Pauropoda were absent from the top 2" in eight samples, whilst in the shaded plot, this was only the case in three. Statistical evidence supporting these conclusions may be found in Table 24a and b.

It is believed, therefore, that the overall distribution is as stated above.

Chilopoda

Only two specimens were found (Table 8j). This is possibly significant in view of the absence of litter and stones from the surface.

Symphyla

This order again shows a greater density of population in the shaded than the unshaded plot (Table 8k). The vertical distribution is, however, rather different from the other groups. Their overall maximum density is in the 2" - 6" section in the shaded plot (as at Pokoase during the wetter months) and in the 6" - 12" section in the unshaded (as at Pokoase during the drier months).

It may be seen from Graph 17, that, as in the case of the pauropoda, there is variation in

the individual samples. In the main, however, individual samples follow the same pattern of distribution as the totals. In the shaded plot the maximum density is in the 2" - 6" section in eight samples, in the 6" - 12" section in three and in the top 2" in one. In the unshaded plot however, only three samples had the maximum density in the 2" - 6" section, while in six, the maximum density was in the 6" - 12" section. In one the maximum density was in the 12" - 18" section and two were completely negative. As would be expected, therefore, the greatest difference in the instance of this group is in the 2" - 6" section.

Again there is very little, or no difference, in the lowest section of the two plots.

Statistical evidence supporting these conclusions may be found in Table 24a and b.

Discussion

The conditions affected by shade are primarily physical. Vegetation is not a factor to be taken into consideration in this experiment as the plots were kept free of any plants by hand weeding. The soil was the same in both plots, and they both received the same rainfall. They were, therefore, as identical as possible in everything except the one factor, shade. Shade will affect the soil physically in two ways, firstly the soil will dry out much more slowly after wetting and secondly, temperatures during the day will be much less. Light will also be less intense under the shade, but as this can only affect the first few millimetres of the soil, it will not be taken into account. Physical conditions in the shade plot will thus be much less variable than in the unshaded plot. Any changes, therefore, in the population of the two plots will be due to one primary cause, shade.

From the results obtained, shade has a marked effect on the arthropod population. Not only is the total population reduced by exposure, but also adopts a different vertical distribution. This is due to the Collembola, Pauropoda and Symphyla,

which he studied, Onychiurus armatus Tulib., and Tuliberella krausbaueri Börner, both showed a positive correlation with soil moisture and temperature. Onychiurus ambulans Nic., however was independent of temperature, and Tuliberella quadrispina Börner was not significantly correlated with either moisture or temperature (Glasgow 1939). The succession of species of Sphagnum in a Sphagnum bog is well established (Osveald 1923, 1925 and 1949). D.H. Murphy (1955) has shown that there is a correlation of

which are all found lower in number and deeper in the soil in the unshaded plot. The Acarina seem not to be affected by exposure.

The generally accepted opinion, is that Collembola are much affected by desiccation and therefore, need to live in an atmosphere of high humidity, that they are less influenced by temperature than moisture, and that higher temperatures are detrimental, particularly if the rise is rapid. The relations of Collembola to moisture and temperature are, however, not so simple when individual species are examined. Glasgow (1939) showed that of the Collembola

species of Collembola with the succession of Sphagnum species in the characteristic hummock of a Sphagnum bog. In a hummock, there is a gradation from free water to xerophitic conditions. He suggests that the underlying factor or factors that are responsible for this distribution are not known with certainty, although from the known ecology of many of the sphagna and Collembola present it is evident that water relations must play a large part. It would seem, therefore, that Collembola are, on the whole, sensitive to the amount of water in their environment, though in varying degrees according to species.

As already pointed out, in the samples taken from shaded and unshaded plots, moisture and temperature are the only important environmental differences. Unfortunately it is not possible to separate the effect of these two factors. In the unshaded plot temperatures in the upper regions are very high and the rise during the day is rapid (Table 5, Graph 28) Therefore, except in the lower layers, where temperatures are similar in both plots, it is not possible to conclude whether

70.

high temperature or drying out of the soil is the operative factor. Further, this higher temperature will have the effect of raising the saturation deficiency (which is the operative factor in the desiccation of arthropods), in the soil interstices. It is possible, therefore, that the distribution of Collembola is a combination of any one, or all of these factors, as Collembola have been shown to respond to them all.

A further factor to be taken into consideration

in view of recent investigations is the tendency of this soil to "pack" on exposure. Kühnelt (1950) suggested that there is a relation between the average size of soil interstices and the meiofauna inhabiting them. Haarløv (1955) as a result of direct observations of soil sections has found that there is a correlation between the size and shape of the cavities available in the soil, and the vertical distribution of the various sizes of Collembola and Acarina. This is not a simple correlation between available "living space" and the microfauna, as many other factors such as

food and humidity must be taken into consideration. Food is most definitely a factor involved, as, from Haarlov's figures, it would seem that very little of the available space in the soil is actually occupied. If one animal of a particular species can live in the particular conditions of a cavity, then others of the same species could also live there if there was enough food. Humidity is also an important factor, for as Murphy (1955) has pointed out, the larger the cavity, the quicker it will dry out.

From the foregoing considerations it will be seen that the sandy soil of this experiment has two properties which are opposed to each other. On the one hand, being sandy, they have large pore space which would make them dry out easily, on the other, the tendency to "pack" on exposure reduces pore space with a consequent reduction in their susceptibility to dry out. Both these factors, however, will have an effect on the soil fauna. Firstly, by reducing the humidity of the pore space, and secondly by reducing the size of the animal which can live in it. The argument may be put

forward, therefore, that when the plot was first cleared of vegetation, the first movement of Collembola downwards, was away from high temperature and low humidity, but later as the soil packed, pore space must be taken into account especially when considering the species present.

It has been found that both Pauropoda and Symphyla need a moist atmosphere in which to live. Little is known of the life history and feeding habits of the Pauropoda, though they are reported to feed on fungus (Starling 1944). Because of their more obvious economic importance, more is known of the Symphyla. They are reported to have varying feeding habits, species of Scutigereella frequently attack growing plants possessing a succulent root system, but are able to live saprozoically on fungi and bacteria. Symphylella species, however, are exclusively saprozoic (Edwards 1955).

Similar arguments to the ones used above for the Collembola, may be applied here to explain the distribution of these myriapods. There is possibly a reasonable explanation also of their greater density under shade when their food supply is taken into consideration. There is almost certainly better fungal growth in the moister

and cooler shade plot. If this is so, then there will be a greater food supply for these predominantly saprozoic groups, in the shaded plot, than in the unshaded.

The Acarina show no significant difference in numbers in the two plots. From the findings of many workers it seems very probable, however, that species differences will be found. It has been demonstrated that the Oribatidae show quite different susceptibilities to desiccation in different species. The ability of different species to withstand desiccation has even been graded by measuring the time of survival of different species after they had been placed over calcium chloride (Riha 1951). As already pointed out, Haarløv found a correlation between pore size and distribution of Acarina.

It would seem, from the above, therefore, that there are almost certain to be differences in species composition in the two plots, the species of the unshaded being smaller in size (because of packing) and more resistant to desiccation than in the shaded.

It is interesting to note that there is a

marked drop of oribatid population in these samples when compared with the normal grassland from Pokoase,

viz,	Pokoase	Nungua
% Oribatidae of total Acarina population	11.2	2.1
% Oribatidae of Acarina of top 2"	11.7	0.5

Only twelve specimens were found in all twenty-four samples. Their vertical distribution was :-

Top 2"	-	1
2" - 6"	-	6
6" -12"	-	4
12" -18"	-	1.

This small population, was therefore, not in the surface layers. It would seem, therefore, that the Oribatidae which were found were not litter feeders and that the low population was related to the absence of litter feeding forms.

Salt (1952) working on two similar plots in East Africa, found no significant difference between two samples in shaded and two samples in unshaded conditions. The plots in East Africa however, were not completely stripped of vegetation, and the shade was supported at a height of 6ft. Unfortunately Salt did not have sufficient time to

take more samples or to split them into different depths, and so vertical differences in density will not be shown by his results. The size of the plots is not recorded, but as one was covered by a shade, it is assumed that they were small. As the matting shade was supported at a height of about 6 ft., a large proportion of this plot would be exposed to the sun for quite long periods of the day. The tropical sun is not directly overhead all day, but can be very strong many hours before and after its overhead position. It is thought, therefore, that the shade at a height of 3 ft., in these experiments in West Africa will be having a greater effect than in the East African experiments with the shade at 6 ft.

Effects on Nitrate level

As in the yearly fluctuation of nitrate level, there is a correlation between the arthropod population and nitrate level. Greenland (1957) found a higher level in the soil of the shade plot, and these samples have

shown that there is a correspondingly higher arthropod population. The link between nitrate level and arthropod population is not simple. Veldkamp (1955) reports that the breakdown of cuticle by bacteria and fungi (see p.55) is a very slow process. Beetle elytra were buried in the soil and dug up six months later. Although they had actinomycetes growing on them, they were still all in one piece. Miss Meiklejohn of Rothamsted Experimental Station, points out (in a private communication) that, although nothing is known about chitin-decomposing bacteria in tropical soils, they must obviously be there, because remains of insects disappear from the soil. Also, the breakdown of cuticles may well be quicker in tropical heat, especially in the wet tropics.

The application of van t'Hoff's rule will give a rough idea of the possible difference in speed of break-down between Holland and West Africa. If it is taken that there is approximately 20°C difference in

average temperature, and six months is the time taken to break down a cuticle in Holland, then break-down should occur in six weeks in the Gold Coast. This would seem to be too long a period to fit in with the sudden flush of nitrate at the beginning of the rains, although breakdown of cuticle may account for some of the later nitrate release.

Another possibility of a link between the arthropod population and nitrate, is through excreta which is a much more readily available nitrogenous material. This could also explain the sudden flush of nitrate at the beginning of the rains, i.e., excreta lying untouched by bacteria during the dry season and then being broken down rapidly as the bacterial population rises with the onset of the rains. The higher the arthropod population, the more excreted material there would be in the soil, as in the shade plot. A higher population, of course, would also produce more moults.

Until more precise knowledge is obtained, it seems that although arthropods are concerned in some way in the nitrate fluctuations in

tropical soils, their actual role remains obscure. It would appear, however, that soil meiofaunas can be used as indicators of micro-biological activity, i.e., the greater the density of the arthropod fauna, the greater must be the micro-biological population, for two reasons. Firstly, conditions which are beneficial to soil meiofaunas are almost certain to be beneficial to bacteria and fungi, and secondly, the food chains of most of the meiofaunas depend ultimately on micro-biological populations.

THE EFFECTS OF CULTIVATION ON SOIL FAUNA

Introduction

The effect of agricultural practices on soil fauna has interested many workers. Unfortunately much of this work is of little value because the fauna of the cultivated soil was not compared with that of the surrounding undisturbed soil, and techniques have varied enormously. As Murphy (1955) has pointed out, the small populations of arable land may be a reflection of technique, although there is a general impression that soil disturbance causes major reductions. It would be unwise to attach too much importance to these data since there is not sufficient information to provide a comprehensive picture of population densities, but they are the best available.

Buckle (1921) came to the conclusion that the distribution and numbers of the soil fauna are more stable on grass than on arable land, that there is a corresponding increase in the fauna on both arable and grassland as vegetative growth increases and that there was no characteristic fauna of arable. Morris (1922 and 1927) working mainly on the effects of manuring, came

to the conclusion that artificial manures have little or no effect on the soil fauna, while the effect of dung in increasing numbers and the number of species of the fauna is considerable. Edwards (1929) comparing cultivated land with a pasture of a similar soil type in the same area came to the conclusion that, in the cultivated land, although there was an increase in Symphyla, Diplopoda and some Collembola (Tullbergia sp.), there was a reduction of other Collembola, Acarina, Coleoptera, Diptera and Oligochaeta. Franz (1949 and 1953) working on similar lines to Morris confirms this view. The latest work on the effects of cultivation by Tischler (1955), shows that soil populations are influenced by the time of ploughing and that deeper working ploughs (after one year's investigation) were rather more favourable (to the fauna) than surface scraping types. The results of his experiments carried out on the effects of manuring, also agree with those of Morris quoted above, that organic manure was found to increase the fauna. Tischler, however, found that inorganic manure increased the fauna indirectly by increasing the vegetation cover and plant refuse.

It is interesting to note that all the investigations of true soil dwellers in the tropics have included attempts to discover the effects of cultivation on soil faunas (Van Zwaluwenburg, 1926 and 1931; Strickland 1945 and 1947; Salt, 1952 and 1956). Agriculturalists in the tropics, facing the difficulty of very rapid soil degeneration after cultivation are keenly interested in gaining any information which may lead to a solution of this ever-present problem. Van Zwaluwenburg (1926 and 1931) working in Hawaii found that there was a larger arthropod population in the soil under sugar-cane than in fallow ground after the cultivation of the crop. Strickland (1945) in the West Indies, took samples in untouched forest and cacao estates and found that both the soil and litter arthropod populations were much smaller under the cacao than the forest. He concluded that this was a result of regular trampling and cutting of weeds in the cacao estates. Comparing savannah grassland and cacao however, he found that although the population totals were very similar in both areas, their generic composition was

quite different (Strickland 1947) In East Africa, Salt, after taking samples from savannah and crops of coffee and cassava, came to the conclusion that the arthropod population of cultivated soils was much less than that of adjacent pasture land, (Salt 1952) It would seem, therefore, that the nature of the crop is a factor in determining the size and perhaps the species composition of the population beneath it. This agrees with the findings of workers in Europe, i.e., Tischler (1955) states that if one takes the biomass of a winter cereal on heavy soil as being equal to 100%, then the biomass on potato fields on the same type of soil equals 50%.

In view of the above, it was thought that it would be of value to investigate the effects of cultivation in West Africa, and extend them by attempting to discover the recovery rate of the population after the crop was lifted. The two areas compared, therefore, were undisturbed grassland savannah, and a plot of twelve months old cassava. Cassava was chosen as the cultivation to be studied because, firstly, it is the basic staple crop grown on the Accra

Plains and secondly, the results could be compared with those obtained in a different area of the tropics under different conditions, (Salt 1952). Cassava forms very little litter, as few leaves are shed. The surface of the ground, therefore, is almost bare of any cover, which is accentuated by the fact that cassava, even fully grown, forms a very open canopy. This is because only the leaves at the top of the stem are left growing, and these, although broad, are not dense.

The soil was sand-clay complex (Simpa-Agawtaw Complex of the Gold Coast Soil and Land Use Survey). The surface layer of about 12" consists of a grey-brown, porous, fine to medium sandy loam, firm and porous in the profile, but crumbling loose when disturbed. Humus staining is slight and confined to the topmost 2". There is a distinct break between this horizon and the subsoil, which consists of up to 18" of dark grey-brown, often mottled, very compact, sandy clay, cracking into six-sided columns on drying. This grades downwards to pale grey or pale brown, cloddy, sandy clay, with lime and often manganese concretions. The base of the profile, usually at 3 - 4ft., is characteristically marked by a thin line of small ironstone

concretions and/or quartz gravel overlying moderately to highly weathered gneiss or schist which often contains lime nodules. A profile diagram of this soil may be found in Figure 6.

The topsoils are capable of absorbing water to a certain extent, but the subsoil is highly impervious, and a considerable amount of rain water is lost by surface run-off. The topsoils rapidly become dried out during the dry season, moisture retained in lower horizons is probably not easily available to plants and animals, and in fact, the lower part of the profile often appears permanently dry.

They accumulate very little organic matter, and are moderately leached in the upper part of the profile. Nitrogen and especially phosphorous are deficient, but the potash content is moderate and calcium and magnesium are plentifully supplied in the lower horizons.

An analysis of the grassland flora may be found in Table 14, and relevant meteorological data in Table 11.

Further information on the effects of agricultural practice was also gained. Two small adjacent plots (3 yards by 1 yard), of

sandy soil were kept completely free of vegetation by weeding. One of the plots, however was turned over by spade to a depth of one foot every week for three weeks. Unfortunately, it was not possible to arrange this experiment on the same soil as the cultivation/grassland plots, and was, therefore, carried out at a Government Agricultural Station in Accra, a few miles away. It was hoped by this treatment to show the effects of disturbance on the soil meiofauna.

Methods

Buckle (1921) was probably the first to put forward the view that in studying the effect of cultivation upon the soil fauna, a comparison of grass and arable land in similar areas will be of value, since it may be taken that grassland is the initial condition and that differences demonstrated on arable land are due to environmental conditions induced by cultural operations. This view has been taken by a number of soil zoologists since that date. The ideal method, however, is probably to sample the area and its surrounds before cultivation, in order to ascertain the normal

population, and whether the surrounding population is comparable with that which is in the area to be cultivated. Regular sampling should then be carried out in the cultivated plot and in the surrounding soil. Unfortunately it is very rarely possible to find undisturbed soil which is about to be cultivated, and most workers have, therefore, sampled only in the cultivated and surrounding soil, without the initial survey. The initial survey had to be omitted in this survey also. Sampling was, however, carried on for six months after the crop had been lifted, and the area allowed to return to grass. It was hoped to continue this sampling for at least twelve months. This was not possible, however, as the original plans for the plot were changed, and another crop was planted.

Two samples were taken in the cassava and two in the adjacent grassland at each sampling. The cores were split and extracted as before. Each sample in the grass was taken approximately 12 yards from a sample in the cassava. It is thought that the samples of any one set taken on the same days are, therefore, comparable.

Results

Comparing the total arthropods in the grassland and the cultivated plot, it may be seen that the two populations are not greatly different in size (Table 9a). The population of the grass, is, however, larger than the cultivated. On the other hand, after the crop had been lifted there was a much bigger difference in the two areas, the population of the grass being very much the larger. Reference to Graph 18 which is a representation of the total population of each pair of samples in the two areas, shows that the population in the cultivated plot was below that in the grassland throughout the observation period. The fluctuations of the total numbers of the two areas, in fact, were remarkably similar, except for one sampling (7.11.55.)

The vertical distribution of the meiofauna in the two areas shows a very important difference (Graph 19). The grassland fauna shows a very similar distribution both while the crop was growing, and after it had been lifted, the maximum density being in the top 2", the 2" - 6", 6" - 12" and 12" - 18" sections having successively lower densities. In the cultivated plot, however, the

distribution while the crop was growing, was quite different from that shown when the soil was reverting to grass after the crop was lifted. During cultivation the maximum density was in the 2" - 6" section, the 6" - 12", top 2" and 12" - 18" sections having successively lower densities. After the crop had been lifted, however, the overall picture is one in which the maximum density is in the top 2", and the 2" - 6", 6" - 12" and 12" - 18" sections having successively lower densities as in the grassland.

It will be seen from Graph 18, that there are two very low populations, one in July and the other in November. These are the result of the populations of the Collembola and Acarina decreasing, and will be discussed later.

Graph 19 illustrates that the results from individual samples mirror the general pattern of distribution given above with the notable exception of September, which showed a typical "dry season" distribution in both the grassland and cassava, i.e., the maximum density not in the top 2", but somewhere between 2" and 12". This is the expected distribution when it is noted that practically no rainfall fell in August, and September up to the time of taking the samples.

In general, therefore, it would seem that whilst actually under cultivation, the total fauna showed only a slight decrease in numbers, but a very definite difference in vertical distribution, the majority of the fauna being at a lower level than normal, (i.e. in the grassland.) After the crop had been lifted, however, there appeared to be a rather larger reduction of population, but a more normal vertical distribution. Statistical evidence supporting the above conclusions may be found in Table 25a and b.

Differences may also be noted in the individual groups of arthropods.

Collembola

The numbers obtained of this order are rather variable. It would seem, however, that the population was higher in the cultivated plot than the grassland, whilst the crop was still growing, but smaller after its removal (Table 9c, Graph 20). There was a very great difference, however, in the vertical distribution of the population whilst the crop was growing. The maximum density in the grassland was in the top 2", the 2" - 6", 6" - 12" and 12" - 18" sections having successively lower

densities. On the other hand the maximum density in the cultivated plot was in the 2" - 6" section, the 6" - 12", top 2" and 12" - 18" sections having progressively lower densities. After harvesting the crop the vertical distribution in both areas are the same. During cultivation, therefore, the population occupied a deeper position in the soil. Statistical evidence for these conclusions may be found in Tables 25a and b.

The grassland shows two very low populations in July and November. This is rather interesting, as it contradicts the general theory put forward earlier (pp. 19 & 20) that the population is the result of the rainfall of the previous month. In this case, however, the rainfalls of the previous months of June and October were exceptionally high. Examination of the soil when the July and November samples were taken showed them to be waterlogged below the top few inches which was the result of 21.56 inches of rain falling in June, and 5.06 inches falling on the 27th October. Almost all the specimens found in the July and November samplings were in the top 6", (Graph 21), i.e.

	Percentage of Total	
	Top 2"	Top 6"
Grassland July	69.2	84.6
Grassland November	51.0	87.8

It is thought, therefore, that the low population, mainly occupying the uppermost layers, is the result of waterlogging of the lower layers of the soil, i.e., the animals either being killed or forced to the drier uppermost layers to escape. Similar figures for the cultivated area show that the population is not nearly so concentrated in the upper layers, i.e.,

	Percentage of Total	
	Top 2"	Top 6"
Cassava July	18.2	45.4
Cassava November	11.7	73.4

It was observed when taking samples from the cultivated plot that the soil was only waterlogged in the bottom few inches.

Hemiptera

There is a very definite reduction of this order in the cultivated plot, i.e., 63 specimens from the grassland and only 2 from the cassava (Table 9f). Almost all the specimens collected from the grass were Geococcus coffeae Green. It

is thought, therefore, that this species is associated with grass roots. Some confirmation of this may be found in the fact that, although the species is best known for its association with the roots of the coffee plant, it has been found quite frequently on monocotyledons, i.e., Canna Lily.

Acarina

Table 9(1) and Graph 22 illustrate that the population of the cultivated plot is lower than the grassland throughout the whole period. In fact, there is an almost perfect correlation of the fluctuations of population in the two areas. There is a great amount of difference, however, in the vertical distributions in the two areas while the crop was still growing (Graph 23). The maximum density in the grassland during this period was quite definitely in the top 2", the 2" - 6", 6" - 12" and 12" - 18" sections being successively smaller. In the cassava however, the maximum density is definitely lower in position in the 2" - 6" section, the 6" - 12", top 2" and 12" - 18" sections being successively lower. After the crop was lifted, however, the distribution in the old cultivated area was the same (with lower numbers) as that of the grassland. Cultivation, therefore,

resulted in a smaller and deeper positioned population of this order.

Statistical evidence supporting these conclusions may be found in tables 25a and b.

As in the case of the Collembola, there was a low population in July. In November, however, although the Collembola again showed a great decrease of population, the Acarina maintained their September total.

Pauropoda

The total population of this order shows a very marked change after lifting of the crop (Graph 24, Table 9m). In the first set of samples, while the crop was still standing, only 10 specimens were obtained from all the six samples taken in the cassava, whilst in the corresponding period in the grassland 99 specimens were obtained. After the crop had been harvested, however, there was a great increase in population until in the November samplings, the cassava population was slightly higher than the grassland. In both areas at all times, the maximum density was below 2" (Table 9m).

The effects of disturbance

The possible effects of disturbance are shown by the results tabulated in Table 10. It was intended to take many more samples, but unfortunately the plot was required for other purposes and the experiment had to be abandoned. The results, however, do agree with the findings of other workers, but are only included in this work as confirmatory evidence.

From Table 10a it may be seen that the totals from the undisturbed plot are nearly twice as great as in the turned-over plot, and that this increase is due entirely to the larger population of the top 6".

The Collembola do not show a great difference in size of population, but are rather deeper seated in the turned-over plot (Table 10b). The Acarina, Pauropoda and Symphyla on the other hand, show a great reduction of population in the turned-over plot. (Tables 10e, f and h respectively).

The general impression left by this experiment is, therefore, that mechanical disturbance by digging, is detrimental to the meiofauna of the soil.

Discussion

From the effects of disturbance experiment, it seems possible that there may be considerable reduction of the population during ploughing and planting of the crop. When this disturbance is finished, and the soil allowed to settle down and adopt a more permanent structure, however, it appears, from the results of the cassava sampling, that the population rises until, under the well-established crop, only a small reduction of the total population occurs. After lifting of the crop, the difference in the two populations is rather more evident. This is possibly again the result of disturbance to the soil caused by the digging-up of the root crop. On the other hand, the population was still smaller than the grassland sixmonths later, when the soil of the plot was settled down and more or less covered by grass. It is thought, therefore, that this is not the result of disturbance, but of the so-called "hunger years" starting. Tischler (1955) has pointed out that a reduction in the number of animals follows each measure which is taken to cultivate the soil; the number of animals, however, can very rapidly become adjusted again as a result of the better

conditions caused by cultivation and, therefore, this is not always harmful. Only when one wishes to reconvert a tilled field to grassland does one abandon the impoverished soil to itself. The low population six months after the lifting of the crop is thought, therefore, to be the result of impoverishment of the soil by the crop.

The large drop in population in both the cultivated and grassland areas in July, appears to result from waterlogging of the soil after the unusually high rainfall of June. Murphy (1955) has shown that water may become an active competitor with the meiofauna for living space. It is thought, therefore, that in this case, water has filled the available pore space with a resultant reduction in soil arthropod population. In November, however, the high rainfall occurring a short time before sampling, results in reduction of population in the grassland, but not in the cultivated plot. This lends support to the above arguments, as it was found that the soil of the grassland was visibly waterlogged while that of the cultivated plot was merely damp. The reason for this, is that as a result of cultivation, the drainage is better than in the undisturbed grassland.

Individual groups of arthropods although all following the general trend of reduced numbers in the cultivated plot, showed rather important differences in distribution.

The Collembola seemed to benefit by cultivation in that the population was higher in the cassava than in the grassland. Waterlogging however, reduced the population to that of the grassland (15.7.55). Waterlogging also reduced the population in November in the grassland but in the cultivated plot, the numbers remained approximately the same. It may be stated, therefore, that in general, cultivation, probably as a result of improved aeration and drainage is apparently not harmful to Collembola. This is supported by the results of the disturbance experiment, which showed practically no reduction in total population of this order.

The Acarina, on the other hand, were definitely reduced in numbers throughout the whole period in the cultivated plot. Waterlogging affected both areas in July, but not in November. It has been shown that small pore space can result in a scarcity of Collembola and an increase of the smaller species of Acarina (Murphy 1953). If

the arguments put forward above, are correct, then the acarine population not being reduced in either area in November is explainable. The extremely waterlogged conditions of July result in a reduction of population of the Collembola and Acarina in both areas. In November, however, the grassland was waterlogged, but the cultivated area was not, and this resulted in a reduction of Collembola in the grassland but not in the cultivated area. On the other hand, the Acarina were not reduced in numbers in either area, possibly because the soil of the grassland though not as waterlogged as in July, contained enough water to reduce the Collembola population. The smaller sized Acarina, however, were able to survive in the limited pore space.

The Pauropoda were very definitely reduced during cultivation, but showed an interesting increase in numbers after the crop was lifted. It was observed, by digging where the cassava had been growing, that fragments of the tuber were left in the soil and were degenerating rapidly through the action of insects and fungi, which could be seen with the naked eye. It is thought

therefore, that the increase of the Pauropoda population in the cultivated area after the harvest, is a result of increased food supply in the form of fungi. From the effects of disturbance experiment it would seem that this group is considerably affected by disturbance.

The vertical distributions of the Collembola and Acarina were quite definitely affected by cultivation, i.e., they were situated at a lower level in the soil. This is certainly the result of the lack of protective covering. As already pointed out, cassava forms a very open canopy, and the soil beneath is quite bare of litter and exposed. Physical conditions are, therefore, rather similar to those found in the exposed plot of the experiment on the effects of shade, where it was shown that exposure of the soil decreased the population and forced it to adopt a lower position in the soil (p. 67). Exposure, therefore, with consequent drying out and high temperature is almost certainly the initial factor involved in the lower level adopted by the majority of the Collembola and Acarina in the cultivated plot.

This is, however, not in complete agreement with the results obtained in the experiment on the effect of shade, where the Acarina were found to be not affected by exposure of the soil. Some other factor, therefore, has been introduced in this case. It is feasible that this may be that disturbance by cultivation caused the soil to dry out more than in the shade experiment, and that this extra dryness forced the Acarina to adopt a lower position.

Exposure of the soil/^{was} probably the primary factor in the smaller population found before the crop was lifted. Its influence, however, would become less as grass established itself after harvesting.

It has been shown, therefore, that disturbance by cultivation methods reduces the population. Once the soil has settled, however, and the crop established, the reduction is not so evident, but there is an adoption of a deeper position in the soil by the majority of the arthropods present. There is a larger reduction of population, however, after the crop has been

harvested and the soil left fallow. Exposure of the soil is thought to be the primary factor involved in the deeper position, and lower numbers of the arthropods in the cultivated plot.

Harvesting of the plot probably reduces the numbers because of the disturbance caused in lifting the tubers. Exposure will be of decreasing influence as grass is established on the fallow ground, and in this period, impoverishment of the soil after the crop is probably the main factor in the reduction of the population.

THE POPULATION OF CONTRASTED TYPES OF SOIL

It has been known for a long time that there is a correlation between certain soil animals and soil type. Almost eighty years ago, it was noted that earthworms were absent for a "mor" type of soil and present in a "mull" type (Muller 1879 and 1884). More recently earthworm distribution has been correlated with the sandiness of the soil (Guild 1948), and acidity and calcium deficiency (Satchell 1955). Carabid species of the genus Harpalus have been shown to avoid coarsely granulated soil (Lindroth, 1949). Various authors have shown that certain species show a preference for certain moisture conditions (Marchand 1953, and Heydemann 1953). Tischler (1955) comparing the fauna in two fields found that although the majority of the Chilopoda and Diplopoda were less prevalent in sandy soils, certain species actually preferred them. Blower (1955) points out that most millipedes are influenced to a certain extent by calcium in the soil, but this may be due to the fact that calcium ions in the soil water may exert a beneficial effect by limiting the permeability of the epidermis

and thus restricting any water intake by endosmosis. Tischler (1955) working on the influence of soil types found that most species of Collembola appeared to show no preference for sandy or loamy soils. Kenylla maritima Tullb. and Hypogastura viatica Tullb., however, preferred the lighter soil. Among the mites, Gamasids were found predominant on the loamy soils but on the sandy soils Trombidids predominated. Mites and Collembola were found at greater depths in the sandy soils;

In discussion at the University of Nottingham 2nd. Easter School in Agricultural Science 1955, Professor Kühnelt stated that it is very difficult to correlate soil fauna and soil groups in general, as the same soils may occur in different parts of the world where different faunas occur (Kühnelt 1955a). Dr. P. W. Murphy pointed out, however, that there are many animal groups which have been very little studied and until they are, the possibility of particular species being confined to certain soil types cannot be dismissed, (Murphy 1955a).

In previous sections, the soil has been taken as a "constant", i.e., experiments have been

carried out on a site chosen for the homogeneity of its soil, and other factors such as water, shade and mechanical disturbance have been varied. While it is obviously impractical to experimentally vary soil types, it is comparatively easy to choose different types. In this section an account is given of the population in different types of soil, which are typified in fact, by the profile and other data provided by the Soil and Land Use Survey of the Gold Coast. The soil, however, cannot be considered as a single variable in the same way as water or shade. It is clear from the literature however, that the soil type might often be a result rather than a cause of the fauna (Kubiens 1955). As in most ecological problems, however, cause and effect are very difficult to distinguish.

Three main types of soil occur on the Accra Plains, Latosol (commonly misnamed "laterite"), Black Clay and Sand. These are all found in a natural undisturbed state within two miles of each other near Nungua where a Meteorological Station is established. They had all been analysed by the Soil and Land Use Survey of the Gold Coast, and all supported sparse grass. An analysis of the different plant communities may be found

in Tables 15, 16 and 17 and Met. Records for the period in Table 11.

Colour is the first difference to be seen between these soils, the latosol being a brownish red, the clay, black, and the sand a light yellow. The large hills of Macrotermes sp. are prevalent on the latosol but absent from the other two areas (possibly another example of a particular species being associated with a particular soil type). Nasutitermes sp. which build very much smaller hills are on all the soils. Thicket clumps develop on the broken-down hills of Macrotermes on the latosol and it is because of the presence of this species that thicket is very much more prevalent on this soil than the other soils. Samples were not taken from the thicket, however, but from the grassland between. Photographs of the three areas may be found in Figures 3a, b and c.

An interesting point arises from a study of the black clay. A certain amount of thicket is found on this soil, apparently on broken-down mounds. These mounds appear to have been quite large. Macrotermes however, has never been found on this soil except once, and that on the piled soil from a ditch. This is not merely a superficial

observation, but the result of a detailed search covering many scores of miles. It appears that these mounds are the result of successive Nasutitermes mounds built on each other, or Macrotermes has been present in the soil at some time. As each clump of thicket on the clay, however, usually contains at least six mounds formed by Nasutitermes, it is thought that the first theory is correct.

A description of the different soils from the Soil and Land Use Survey is as follows.

Latosol (Nyigbenya Series)

The topsoil, about 5" thick consists of brown or dark reddish-brown, loose or friable sandy loam. Below this is about 2 ft of friable red, sandy, light clay containing abundant iron-stone concretions. In some areas (but not in the area investigated in this work) variable amounts of quartz gravel occur within one foot of the surface. The concretionary horizon usually extends below 3 ft. Where rock has been encountered it has been thoroughly decomposed to a red, rather mottled and usually gritty clay. Generally the complex is underlain by Archaean crystalline rocks.

The soil is well-drained and absorbs water freely during the heaviest rainfall. The topsoils dry out thoroughly during dry periods, but the clay subsoils appear to retain moisture more satisfactorily. They are poorly provided with plant nutrients, and these are concentrated in accumulated organic matter. Phosphorous seems to be particularly deficient. Lime accumulates very locally (but not in these samples) in and below old termite mounds.

Soil profile description and mechanical and chemical analysis may be found in Figure 7 and Table 19. Floral analysis may be found in Table 15.

Black clay (Akuse series)

The surface 4 - 6 inches consists of black or dark grey clay, heavy and plastic when moist, but compact and nutty to small cloddy when dry, with wide vertical cracks. This horizon grades downwards into 1 - 3 feet of dark grey, heavy cloddy clay, cracking widely into large columnar blocks continuous from the ground surface. Below this is a mid-grey, cloddy plastic clay containing abundant small, hard lime concretions. This clay

overlies a number of different rocks.

On wetting, the soils quickly absorb water, which causes the clay to swell rapidly and close up all the cracks. During rainfall, therefore, they are impervious, and shed water by surface run-off. The surface relief generally ensures good external drainage, but internal drainage is impeded. On drying, wide vertical cracks develop, but the interior of the structure units remains moist, although little of this moisture is likely to be available to living organisms.

The soil has a satisfactory lime-status but is rather poorly provided with nitrogen, potash and especially phosphorous.

Profile description, chemical and mechanical analysis may be found in Figure 8 and Table 20 respectively. Floral analysis may be found in Table 16.

Sand (Simpa Series)

This soil is a pale coloured sand over 2 ft., thick. This lies over a variable thickness of quartz stones and gravel in a grey or brown, often mottled, sandy matrix which becomes more clayey with depth. The underlying rock consists of moderately weathered clayey, acidic Archaean

gneiss or schist containing numerous quartz veins.

This soil readily absorbs water and may become waterlogged in the lower horizons following prolonged heavy rainfall. Moisture is probably retained satisfactorily at depth during the dry seasons, but the sandy upper layers quickly become parched. The sandy upper layer accumulates very little organic matter and is almost barren of nutrients. The clayey lower layer is moderately leached but appears to satisfactorily retain amounts of mineral nutrients. The whole soil however, is conspicuously deficient in phosphorus.

Profile description, mechanical and chemical analysis may be found in Figure 5 and Table 21 respectively. Floral analysis may be found in Table 17.

It may be seen from the above, that the black clay is very different in character from the latosol and sand as an animal habitat. The sand and latosol are, however, quite similar. They both dry out considerably during the dry season in the upper layers but the latosol is more clay than the sand and retains water at lower levels better than the sand. Neither the latosol nor

110.

the sand show a proper crumb structure, though this can be formed in latosol under the elephant grass, Pennisetum purpureum, (Martin 1944 and 1946).

It was decided to take samples in these three contrasted soils, occurring in the same area under the same climatic conditions, and under about the same vegetative cover. By taking samples in the dry and wet seasons it was hoped that the effects of the different soils on the arthropod distribution could be demonstrated.

Methods

Four samples were taken at random in each of the soils in January 1956 and May 1956, i.e., during the dry and wet seasons respectively. The cores were extracted and split in the usual way and the results appear in Table 12 and Graphs 25, 26 and 27. The clay samples, however, received a slightly different treatment, by being placed in a refrigerator and frozen for 24 hours before extraction of the animals was carried out. This treatment is necessary in clay soils in order to break down their structure.

Results

It may be seen from Table 12a and Graph 25a that the latosol supports the highest population, the clay the lowest, and the sand intermediate in size between the two (2944, 1381 and 2381 from all eight samples respectively). All the soils have a greater population in the wet than in the dry season (Graph 25a). This agrees with the findings during the year's sampling at Pokoase (p.19).

Comparison of the populations at the different depths, however, show that the animals are not at the same depths in all the soils. Graph 25b illustrates that in the dry season in the top 2" and 2" - 6" sections, the sand supports the greatest population and the clay the lowest. In the lower sections, however, (6" - 12" and 12" - 18"), the greatest population is in the latosol and the clay and sand are about equal, the clay being perhaps slightly greater than the sand. In the wet season on the other hand, the position is slightly different. In the top 2", the latosol and sand are about equal, and in the 2" - 6" section the sand probably greatest and the clay the lowest. In the 6" - 12" and 12" - 18" sections the latosol is the greatest and the clay the lowest.

Graphs 25c, d and e illustrate the differences in the vertical distribution in the three soils. In the latosol, the maximum density is in the 6" - 12" section, although the density is quite high in the top 2". In the clay, the maximum density is in the top 2". In the sand, however, it appears to be somewhere in the top 6", i.e., three samples show a maximum density in the 2" - 6" section and one in the top 2", but the totals of all four cores show the maximum density in the top 2", because of the high number in that section in the first sample. In the wet season on the other hand, the maximum is quite definitely in the top 2" in all the soils. In the latosol and sand, therefore, there is a move upwards of the maximum density in the wet season, which again is in keeping with the results obtained in the yearly sampling at Pokoase. The maximum density in the clay although in the top 2" in both sets of samples, shows a much larger maximum in the wet season compared to the other three sections, i.e., the ratios of the density of the top 2" and 2" - 6" are 1.2:1 in the dry season and 2.5 : 1 in the wet season. It appears, therefore, that although there is no movement of the position of maximum density in

the clay, there is a change in the density of animals found in the top 2".

Statistical evidence supporting the above conclusions may be found in Table 26.

There are differences, therefore, between the numbers of arthropods in the three soils and in their vertical distribution during the dry season. Comparison of the different groups illustrate these differences still further.

Protura

This order was found in all three soils but in very low numbers (latosol 2; clay 5; sand 1), and all were found in the wet season. (Table 12b). It appears, therefore that Protura cannot exist in dry conditions in any of the soils and that clay is possibly preferable to sand, as the numbers, though low, do show a positive correlation to the clay content of soils.

Diplura

Again, very few specimens were collected, but in this, some were found during the dry season. (Table 12c). It is interesting to note that the numbers found correspond exactly to the Protura, i.e., latosol 2: clay 5: and sand 1. It is possible, therefore, that the same arguments may

be applied to this group as to the Protura. It must be emphasised, however, that because of the very low numbers found in both these orders, any suggestion about their distribution must be very tentative indeed.

Collembola

The sand is the richest in Collembola, the clay poorest, i.e., sand 699; latosol 375 and clay 231 (Table 12d. Graph 26a) Rather surprisingly there appears to be a reduction of population in the wet season in the latosol, though there is an increase in the other two soils as expected. Comparison of the densities at the different levels is interesting, (Graph 26b). In the dry season the densities are roughly similar in all the soils in the top 2", but in the 2" - 6" section the sand is by far the greatest, and the clay the lowest. In the 6" - 12" and 12" - 18" section however, the latosol is greatest. In the 6" - 12" section, the clay and sand are roughly equal, but in the 12" - 18" section the clay is greater than the sand. In the wet season, on the other hand, the sand shows the highest density in all sections of

the core, and except for the bottom two sections where the latosol and clay are roughly equal, the latosol is the lowest in density.

The vertical distribution of Collembola in the three soils is not absolutely clear. In the latosol of the dry season, the maximum density is, apparently, somewhere between 6 and 18 inches, probably in the 12" - 18" section, (Graph 26c), but in the wet season it is in the top 2" (although in one sample it is in the 2" - 6" section). In the clay (Graph 26d) the maximum density is in the 6" - 12" section in the dry season, whilst in the wet season it is in the top 2" (although in one sample it is in the 2" - 6" section). The sand (Graph 26e) has a very clear distribution in the dry season, only one specimen being found in the top 2" of all the samples, and the maximum density in the 2" - 6" section. In the wet season there is a definite move upwards of the Collembolan population to the top 2", but the maximum density is still in the 2" - 6" section. The actual position is not absolutely clear, however, as two samples have a maximum in the top 2" and two in the 2" - 6" section.

It appears, therefore, that there are differences in both the distribution and numbers of this order in the different soils. The richest population is in the sand and the poorest in the clay and the greatest density in both seasons at all depths is in the sand 2" - 6" section. There is, however, an important high density at the lower levels in the latosol of the dry season. All the soils show the same upward movement of maximum density in the wet season.

Statistical evidence in support of the above conclusions may be found in Table 26.

Hemiptera

The numbers captured of this order are low, (Table 12g). It seems certain, however, that the greatest numbers are in the latosol and the lowest in the sand (latosol 69; clay 36 and sand 17). This difference in numbers, however, is only during the dry season. In the wet season the total numbers are about equal from all soils. The sand has roughly the same population in both seasons, but the latosol and clay have a very great drop in numbers in the wet season. Nothing can be concluded about their vertical distribution during the wet season as the numbers are too low

In the dry season, however, it would seem that the maximum density is in the top 2" in the latosol and somewhere between 2 and 18 inches in the clay. The sand numbers were too low for analysis.

Chelonethi

Rather unexpectedly, no specimens were found of this order in either the latosol or the sand (Table 12m). They were found, however, in the clay in two out of the four samples in both the dry and wet seasons.

Palpigradi

No specimens were found in the clay and sand. Only one was found in the latosol and this was at its usual depth of 12" - 18" (Table 12n).

Acarina

By far the greatest number of mites were found in the latosol, i.e., latosol 2237; clay 986 and sand 1507, (Graph 27a, Table 12o). The totals in all soils rose in the wet season.

In the top 6" in the dry season the greatest density was in the sand, the latosol being only slightly greater than the clay (Graph 27b).

Below the top 6" the latosol had a greater density than the other two soils. In the wet season on the other hand, the greatest density at all depths was in the latosol. In the top 2" the clay had the lowest density, but in all other sections, it was higher, or equal to the sand.

Regarding the soils individually, it may be seen that in the latosol during the dry season, the maximum density was in the 6" - 12" section, though there was a high density in the top 2" (Graph 27c). In the wet season, however, the maximum is quite clearly in the top 2". In the clay the maximum density is in the top 2" in both the wet and dry season, but as in the case of the totals, there is a proportionately a much higher maximum density in the wet than the dry season (Graph 27d). This type of distribution is also found in the sand (Graph 27e).

Too few Oribatidae were collected to make any definite observations. It is interesting, however, to note that their distribution in the various soils was as follows, latosol 1; clay 22; sand 10. Only five of all these specimens were found in the top 2" and it is thought, therefore, that the rest of the specimens were not litter feeding forms. This would agree with the observations that in this

very dry area, litter is practically non-existent. If these Oribatidae are not litter forms, it would perhaps account for the low numbers collected as compared with the rather wetter area sampled at Pokoase which, although having a very small amount of litter, does have a little more than Nungua, i.e., the reduction in numbers is mainly because of the absence of litter-eating Oribatidae.

It may be concluded from the foregoing, therefore, that the greatest population of Acarina is to be found in the latosol, the smallest in the clay. There is a movement upwards of the population in the wet season in all the soils. There are also differences in vertical distribution, the sand having the greatest density in the upper layers and the latosol being greatest in the lower layers during the dry season. The latosol, however, has the greatest density at all depths in the wet season.

Statistical evidence supporting these conclusions may be found in table 26.

Pauropoda

The numbers of this order collected are rather small for definite analysis, (Table 12p). It would seem, however, that the population is possibly largest in the latosol, i.e., latosol 128;

clay 74; sand 69. The population in all the soils shows a decrease in the rainy season.

In the dry season, none of the areas have the maximum density in the top 6", the latosol being in the 6" - 12" section, the clay in the 2" - 12" section and in the sand the 6" - 18" section. The Pauropoda, therefore, seem possibly to be at a rather higher level in the clay than in the other two soils. The position in the wet season, however, is slightly different. The maximum in the latosol is in the 12" - 18" section, in the clay, in the 0" - 6" sections, and in the sand in the top 2". There has, therefore, been a movement of population maximum upwards in the sand and clay, but apparently downwards in the latosol.

As already pointed out, the figures are rather low to give definite conclusions, but it seems certain that the numbers are greater in the dry than the wet season, and that the maximum density is in the lower layers in the dry season in all soils but (with the exception of the latosol) moves to the upper layers in the wet season.

Symphyla

It would seem that the latosol supports the highest population of this group, latosol 111; clay 31; sand 80. (Table 12s). In the latosol and sand the population rises in the wet season. The clay on the other hand does not appear to alter.

The position of the maximum density is roughly the same in all soils during the dry season, i.e., latosol 12" - 18", clay 6" - 12" and sand 2" - 18". No specimens were found in the top 2" in any of the soils. In the wet season, however, quite a number of the specimens appeared in the top 6", but the majority of the population remained in the lower layers in all the soils, i.e., latosol maximum density 6" - 12", clay maximum density 2" - 18" and sand maximum density 2" - 12".

Unfortunately, the small numbers obtained do not permit a more exact analysis. It seems certain, however, that the population is definitely greater and moves to a higher level in the wet season in the latosol and sand.

Because of the small numbers captured little can be concluded about the following groups, Psocoptera (Table 12e), Thysanoptera (Table 12f)

Lepidoptera (Table 12h), Coleoptera (Table 12i),
Mymaridae (Table 12j), Diptera (Table 12k),
Araneida (Table 12 l), Chilopoda (Table 12q),
and Diplopoda (Table 12r).

Discussion

It can be assumed that the vegetation is almost certainly not a factor influencing the arthropod population in these soils, as, although the species composition of the flora was different in the three soils, the percentage cover was practically the same. Also, to all intents and purposes, no litter was formed by the vegetation. Dead leaves in this area dry very quickly on the surface, break up and are blown away by the strong prevailing W.S.W. winds (Beaufort Force average 2 - 3). The soils, therefore, are all sparsely covered by grass, under which the soil is in an almost exposed condition. Unless the different species of grass (possible by their root systems) affect the arthropods, then it is thought that in this particular set of samples, any differences between the populations are the result of different properties of the soils.

It has been shown that quite definite differences occur both in the sizes of the populations and their vertical distributions. There are, however, many similarities. In general there was an increase in numbers in the wet season in all groups in all soils. As already pointed this could be for many reasons, such as

eggs which have been lying in the soil during the dry season hatching out at the beginning of the rains, less mortality from desiccation, and increased food supply at the microbiological level. Another general trend in all soils is the moving upwards of the position of the maximum density in the wet season. Again the reasons for this have been discussed (pp. 35, 36), i.e., the food concentration of the upper layers not being available to the majority of animals during the dry season because of the danger of desiccation, but becoming available when this danger is not present during the rainy season. These two general trends agree with the results obtained from the yearly fluctuation samples already taken.

There are differences of these general trends, however, between the soils, and it is thought that these are the results of the different qualities found in the soils.

The clay supports by far the lowest population. Pore space is thought to be an important factor. It may be seen from tables 19, 20 and 21, that the clay soil has the highest silt/clay and, therefore, the pore space is the lowest of the

three soils. Less "living" space is, therefore, available. A further result of the small pore space is that the soil will be poorly aerated. Haarlov (1955) has shown from his studies of the humus layer, that very little of the pore space available is actually used by the meiofauna. Elton (1933) however, has pointed out that the optimum density of animals in a habitat is not necessarily the maximum density. It is possible, therefore, that it is merely a matter of the space available which restricts the size of the population in the clay. Other factors, however, must be taken into consideration. A great deal of mechanical disturbance takes place in this soil during its contraction in the dry season and expansion during the wet season. Disturbance of the soil is generally held to be harmful to soil fauna and the reason for the small populations found in cultivated soil.

It may be pointed out, however, that the animals survive the severe buffeting in the Ladell's apparatus with remarkably little damage, except to hairs and fragile protruberances. Many survive the treatment alive, and moreover, remain alive for a number of days after extraction. It

would seem, therefore, that loss of fauna through cultivation is for two reasons. Firstly that drying out of the soil after disturbance would cause desiccation conditions, and secondly, that animals would be directly exposed to the open atmosphere by having the soil structure broken and, therefore, probably die from desiccation. In the case of the clay, however, it seems possible that animals may be damaged more severely by the grinding action of the very fine particles moving during expansion and contraction in very small pore spaces.

If this is so, then the disturbance caused by the contraction and expansion in the clay could be a very important reason for the low population found. The water relations in the clay are, on the whole, rather favourable for animals. During the dry season, the clay does not dry out in the upper layers as much as the other two soils. (Moisture content air-dry soils, Tables 19, 20 and 21). During the wet season, most of the rain runs off the surface when once it is fully expanded and so the clay does not become waterlogged except during heavy and prolonged rain. Its colour, on the other hand, is a slight disadvantage, as, being black, reflection will not be as great and

the surface soil temperatures, therefore, a little higher than, for instance, the sand. This difference will be so small, however, that it need not be taken into account. A further point of great significance, is that the organic content of the clay is higher than the latosol or the sand, and it may be assumed, therefore, that there is a higher food content.

As it does not appear to be food or water content of the soil which causes the low population in the clay, it is thought that small pore space, lack of aeration, and mechanical disturbance are the important factors influencing their arthropod distribution.

In the latosol and sand however, (because of the lower silt/clay content), pore space is very much higher and mechanical disturbance very much less. The latosol supports a higher population than the sand and it is, therefore, possible that food supply and water must be taken into account in explaining this difference. It is significant that during the dry season, the latosol maintains the majority of its population below 6", whereas the sand supports most of its population above 6". In both soils there is a huge increase in size of population during the wet season in the top 2".

It is thought, therefore, that during the dry season, water is available in the lower layers of the latosol, and because of this a high population can be maintained at the lower levels. This view is supported by the fact that the latosol retains a much greater amount of water in the lower layers when air dried (Tables 19, 20 and 21). The sand on the other hand, has no water at these lower levels and the soil arthropods are under water deficient conditions at all depths. Organic material in the sand is very localised in the upper layers. (Percentage Organic matter, Table 21). The animals are, therefore, concentrated in the top 2" as there is probably insufficient food in the lower layers. It seems possible, therefore, that the species existing in the sand are desiccation resistant and are able to live in this food bearing, but dry, layer. In the latosol on the other hand, more food is available in the lower levels. (Percentage Organic matter Table 19). The soil arthropods, therefore, need not necessarily be species which are resistant to desiccation as there is also water at the lower levels. For these reasons the latosol is able to support a larger population at lower levels than the sand. This "reservoir" of animals

in the lower levels of the latosol possibly forms a foundation for the higher populations of the wet season in the upper layers.

Sand appears to be the most favourable soil for the Collembola. In fact the numbers show a positive correlation with the sand content of the three soils. Pore space, therefore, is possibly a factor influencing their distribution. In none of the soils are Collembola found in great numbers in the top 2" during the dry season and it is thought, therefore, that the dryness of this upper layer is the operative factor, especially when it is noted that there is a great increase of population in all the soils in the top 2" during the rainy season. It is perhaps significant that in the wet season, although there is an increase in population in the top 2" the maximum density remains in the 2" - 6" section of the sand, whilst in the clay and latosol, the maximum is in the top 2". It would seem, therefore, that even in the wet season, because of the greater drainage and drying out of the larger pore space, (see p.71), the amount of water is still insufficient in the top 2" of the sand for the majority of the Collembola.

During the dry season, the maximum density is

at a lower level in the latosol than in the sand. It is possible, therefore, that the same remarks may be applied to this group as to the totals. In the latosol, more organic material and water are found at the lower layers than in the sand. Species living in the latosol are, therefore, able to avoid the dryness of the upper layers. In the sand, however, where the organic material is more concentrated in the upper layers, and dry conditions exist at all depths, the population tends to concentrate in a higher position, possibly through the presence of desiccation-resistant species. It is significant that the population is higher in the latosol than in the sand during the dry season. No explanation can be put forward for the decrease of population in the latosol during the wet season, as it is contrary to all the results obtained.

It appears, therefore, that the primary factors in the distribution of this order are water, pore space and food, each of which assumes primary importance in different circumstances.

It is perhaps worthy of note, that Chelonethi are absent from the sand and latosol. It is rather unexpected in the case of the latosol, as a moderately high population was found in the similar soil of pokoase, (Distribution throughout the year).

Vegetation should not be a factor in the distribution of this carnivorous animal. Low water content of the soil is possibly the cause of their absence, as they were present in the clay (which does not dry out so much), and also the rainfall is lower at Nungua than at Pokoase. Food supply is not significant, as the clay in which these carnivorous arthropods are present has the lowest population of the other arthropods. Only one Palpigradi was found in the latosol and none in the other two soils. Many reasons could be put forward to explain, firstly, their paucity of numbers, and secondly, their apparent absence from the clay and the sand, but it is felt that the presence of just one specimen does not warrant speculation.

The latosol has by far the richest population of Acarina. Following the general trend, there is an increase of population in all the soils during the wet season.

As in the case of the Collembola, there is a very much lower population in the top 6" of the latosol than in the sand during the dry season. On the other hand, the population in the sand is

very much smaller than in the latosol below 6".

The Acarina in the latosol are, therefore, greater in numbers, but at a lower level than in the sand during the dry season. In the wet season, on the other hand, the latosol population was higher at all levels, the sand and clay being about the same below 6", as in the dry season.

Possibly, therefore, the arguments put forward to explain the distribution of the Collembola, also apply to this group of arthropods. The only difference between the two groups is that the Acarina of the latosol increased in numbers in the wet season, whereas the Collembola unaccountably reduced during the same period.

The latosol appears to be the best soil for the Pauropods. Sand and clay, though showing slightly different vertical distributions, seem to support about the same size of population. It would be expected that the Pauropoda, if fungus eating (Starling 1944), would increase in numbers during the wet season as more fungus should be growing under wet conditions than dry. It appears, however, that there is almost certainly a reduction of numbers in wetter conditions in all soils. It is

perhaps, significant that the greatest drop in population occurs in the clay and it is, therefore, possible that the drop is a result of too much water, i.e., the sand and latosol not having such a large drop because they are better drained.

The Symphyla also prefer the latosol, though the sand also supports a comparatively high population. The clay, however, has a very low number present. This agrees with the work of Edwards (1929) who found that Symphyla were most numerous in soils with an open structure and good organic content. The sand and latosol do not have a good

organic content, but they do have a good open structure. The population is rather less than that expected from European soils (Thompson 1921 and Michelbacher 1939) and this is probably the result of the lower organic content in these soils, especially when it is noted that the sand, with lower organic content has a lower population than the latosol. The low population found in the clay however, is almost certainly in response to the fact that the clay does not have an open structure. Both latosol and sand show an increased density in the upper layers during the wet season. This would seem to indicate

that the Symphyla are seeking the moister and cooler lower regions during the dry season but able to move higher in the wet season. This may be in response to the purely physical conditions of water content or temperature, but could also be in response to their main food supply of fungi and bacteria, which would also be more prevalent in moist conditions.

In general it would seem that the latosol is, on the whole, a better soil for meiofauna than the two extreme soils, sand and clay. This is because of many factors. The latosol is well-drained, but retains water in the lower layers during the dry season. This second factor is thought to be of great importance, as it allows a high population to remain in the soil during the long dry period encountered in this area. There is also a reasonable distribution of organic material at lower levels. The sand, on the other hand, although free-draining, does not retain water at the lower depths as much as the latosol, and so arthropods living in this soil cannot retain as high a population during the dry season. Another disadvantage of the sand is its low organic content concentrated in the upper layers. The clay, however, seems to be the least suitable soil as an arthropod habitat, and it is thought that

this is mainly because of its low pore space, bad aeration and the great amount of mechanical disturbance taking place.

It has been shown, therefore, that these three contrasting soils display different distributions of arthropod population, in response to their pedological characters. Whether species differences will be found is not yet known, but from the results of the general distribution of the various groups, it would seem that this is almost certain.

GENERAL DISCUSSION

Although this work falls naturally into separate sections each dealing with the meiofaunal distribution in different habitats, certain common factors appear throughout.

Water is of great importance in all habitats, but in a dry region it constitutes a significant limiting factor. The Accra Plains are no exception in this respect, as water has been shown in this study to be a constantly recurring factor limiting not only the size of the soil population, but influencing its vertical distribution.

Results reveal that the size of the population can be correlated directly with rainfall. This is particularly evident in the data assembled from the seasonal distribution samples, where a direct correlation with the rainfall of the previous month is apparent. The results of the artificial rainfall experiment indicate that the vertical distribution of the fauna could probably be related to the rainfall of the same month. Although two inches of rain was not sufficient to effect a difference in vertical distribution, seven inches caused a marked change.

Direct correlation between size of population and rainfall was also observed in different kinds of soil. It would seem, therefore, that the quantity of water in the soil is a factor limiting the size of the population in at least three of the different soils of the Accra Plains.

Too much water on the other hand, caused a reduction in the population. It is feasible to assume that the reason for this is that the water occupies almost all the available pore space in the soil leaving very little living space for soil animals.

Shade has an important effect on the meiofauna. It must be appreciated, however, that two physical factors are affected by shade, temperature and water content of the soil. Both these factors are known to exercise an effect on the distribution of soil arthropods. It has been shown in the present investigation, that whichever is the operative factor, exposure of the soil reduces the arthropod population. Vertical distribution was also altered, with the exception of Acarina the animals in general, being found at a higher level in the shaded soil than in the exposed soil.

It is possible that shade may be a significant factor in the experiments involving artificial rainfall, and the effects of cultivation experiment. In the case of the former experiment, the vegetation of the watered plot was thicker and the soil below, therefore, more shaded, and the animals generally occurred at a higher level in the soil. In the latter experiment, the population was smaller in the rather exposed cultivated plots, than in the adjacent undisturbed grassland. Further, the fauna in general was situated at a lower level in the exposed ground.

Disturbance of the soil causes a reduction in its population of meiofauna. Again two physical factors are involved, being in this case water content and mechanical movement of the soil. Soils dry out to a marked degree when disturbed and the lower populations following disturbance could well be due to lowering the amount of available water. Animals actually exposed on the surface of the soil during cultivation would undoubtedly die under tropical conditions from desiccation and too high temperatures. It is thought unlikely that an appreciable proportion of the meiofauna would be

killed by direct mechanical damage to the body in view of the fact that although hairs and small protruberances may be knocked off the body, animals survive, apart from an occasional individual, the extreme buffeting during extraction by Ladell's method with remarkably little damage.

Cultivation of the land also leads to an impoverishment of the soil and this remains apparent after removal of the crop. In the present studies, the arthropod population stayed small after harvest, even when the whole of the cultivated area was completely covered by grass.

Contrasted types of soil have been shown to have not only different vertical distributions, but different sizes of meiofaunal population. It is believed that this is attributable to differences in both the physical and chemical conditions of the soils. Water, clay, sand and organic content are all important factors. It has already been shown that water content is important, but when comparing the fauna of different soils, the water holding ability of the soil, was seen to be a considerable factor influencing the size and distribution of the population, especially during the dry season. Clay content, besides affecting

the pore space of the soil, may be important on account of its expansion and contraction in wet and dry seasons, possibly resulting in purely mechanical damage to the fauna. Sand content is important, in that the higher its proportion in relation to other soil constituents, the larger the pore space and the quicker the soil dries out. A high sand content also results in quicker drainage and less retention of water.

Organic content is an operative factor, providing that other conditions are satisfactorily fulfilled, as although clay had the highest organic content, it had the smallest population, i.e., drainage, pore space, and mechanical disturbance were thought to be the operative factors in this soil.

Individual groups of animals show characteristic distributions. Acarina and Collembola, as in other parts of the world, were by far the greatest in numbers. Biomass figures were not calculated. These, however, could be estimated since the range and size was similar to that found by Salt, Hollick, Raw and Brian (1948). In the present work, the same type of population, that is, small arthropods, has been compared under different

conditions. Biomass figures would not, therefore, affect conclusions drawn.

The greatest density of Acarina and Collembola occurred generally in the top 2" of soil, and the lowest density in the 12" - 18" section. This normal type of distribution of these two groups, altered when the top 2" was dry and exposed. Under such conditions the density in the top 2" became greatly reduced, sometimes even below the density occurring in the 2" - 6" or even the 6" - 12" layers. This latter type of distribution was encountered in the dry season, for example, in the seasonal distribution experiment, the dry area in the watering experiment, the unshaded area in the shade experiment and in the dry season in the contrasted soils experiment. In all these cases, however, the Acarina were not nearly so greatly affected as the Collembola. It would seem from these results that the Acarina are more able to maintain populations under dry conditions than the Collembola. Acarina populations were also less affected by waterlogging than Collembola, as shown in the cultivation experiment. This may be due to the fact that Acarina are generally smaller in size than Collembola and that they

are, in consequence, able to live in more restricted spaces when water becomes an active competitor for pore space.

It would appear that there is a direct correlation between size of Collembola populations and sandiness of the soil. This may be due to a variety of reasons, such as, larger pore space, better aeration, and better drainage.

Symphyla frequently occurred in all the habitats included in this investigation. They followed the general pattern of distribution observed by other workers on meiofauna, in having their maximum density below the surface layers. It was also found in the present studies that the maximum density of this group occurred at a greater depth when the upper layers were hot and dry, as exemplified for instance, in the case of the seasonal distribution experiment. Soil differences also had an effect on the Symphyla population. Latosol was the most beneficial, and clay the least, while sand proved intermediate. This phenomenon again agrees with that found by workers elsewhere, that is, Symphyla prefer a soil with a good open structure and a high organic content.

143.

In general pauropoda displayed a preference for the upper layers of the soil except during hot dry conditions when they moved to a deeper level.

Other groups are noteworthy even though very small in numbers.

Proctura occurred, but only during the rainy season, and then mainly in the lower layers.

Diplura were encountered quite frequently. The highest proportion were Japygidae, with Campodeidae of moderate prevalence.

Psocoptera seemed to show a preference for the upper layers of the soil.

Hemiptera were mainly represented by the commonly occurring species Geococcus coffeae Green which showed a preference for the lower layers of the soil. It is interesting to note that this species, known from other parts of the world for its association with Monocotyledons has a similar association in West Africa. It was absent in the bare fallow of the shade experiment, and also virtually absent in the caséve plot of the cultivation experiment, but present in practically every sample taken in grassland.

Chelonethi and *Palpigradi* were found in the lower layers of the soil, the former preferring the 6-12" section, and the latter the 12-18" section.

144.

Many other interesting features come to light in the present studies. Populations of the meiofauna are generally smaller, at least on the Accra plains, than in Europe. It must be appreciated, however, that the soil samples in this present investigation were taken in a semi-arid area and on land in a rather poor state of fertility and with a poor vegetative cover. As a habitat for any animal it could never be considered good. It is not surprising, in the circumstances, that the soil fauna was represented by small populations.

An interesting aspect was revealed in the course of carrying out the shade experiment. There seems to be little doubt that there is a correlation between the soil fauna and nitrate level but it is felt, at this stage, that it requires further investigation for two reasons. First, nitrogenous excretion forms a readily available source of nitrate. Cuticles, though not so readily available, are also a source of nitrate. Secondly, populations of soil meiofauna may be used as an indication of bacterial population, on the basis that conditions which are good for one living organism are also good for others. Bacteria are concerned in some manner or another in practically all the food chains of soil animals.

Most of the conclusions reached in this work are

145.

rather general and tentative as only the main groups of animals have been investigated. More specific work will be carried out later when all the various animals collected, and now deposited in the appropriate sections of the British Museum of Natural History, London, have been identified. Although much has been discovered in this relatively unknown field the results hitherto obtained must be regarded as a basis for further research on more specific lines with a view to solving the multitudinous problems still awaiting elucidation.

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