Presidential Address delivered at the Eleventh Annual General Meeting.

SOME ASPECTS OF SOIL ECOLOGY

K. E. LEE

Soil Bureau, D.S.I.R., Lower Hutt.

It is well known that in most soils vast numbers and great variety of living organisms may be found. They range in complexity from the simplest of single-celled animals plants and bacteria, through to burrowing mammals and higher plants, and include representatives of almost every major group of organisms. Photosynthesis by the green plants that grow on the soil surface is the source of energy upon which the whole population ultimately depends, and most of the organisms are decomposers of plant tissue.

Macfadyen (in press) has recently constructed a balance sheet for the total annual flow of energy through a meadow exploited by means of grazing cattle. Of the total energy captured by plant photosynthesis, less than one seventh is respired by the plants, about two sevenths are consumed by herbivores, and about four sevenths are exploited by organisms engaged in the decomposition of plant material after it is dead. Macfadyen has further developed this line of investigation and has analysed the proportion of the total energy handled by the soil animals engaged in what he calls the "decomposer industry" into four components, due respectively to the herbivores, carnivores (predators), large decomposers (those which have a mechanical effect on the soil) and small decomposers.

Some of the material exploited by the decomposers is returned to the soil in a form that can be used again by higher plants, and this is the basis of organic cycles, which are a fundamental concern of soil science. However, from the point of view of the farmer and agriculturist, it is most important that, discounting the one seventh of energy respired by pasture plants, two thirds of the energy available from grass growth is lost to the "decomposer industry" and never becomes available to the grazing animal. Study of the ecology of individual species and groups of soil organisms, especially of their distribution, numbers, population dynamics, food preferences and energy consumption, acquires a special importance for the effective use of soils and economic plants. Earlier ideas of a trophic pyramid, with herbivores feeding on grass and themselves being fed on by carnivores are oversimplified. Most of the energy available in the system is actually falling to the unseen decomposers beneath the soil surface.

Apart from a few large animals, such as earthworms, which are able to make burrows, soil organisms live in the naturally occurring spaces between soil aggregates, and to a large extent on the surfaces of the aggregates. The feeding roots of higher plants share these ecological niches with the microfauna and microflora, and the environment that prevails in these minute spaces is of fundamental importance not only to plant growth, but as a reflection of the general physical, chemical and biological conditions in the soil that are the basic concern of soil scientists. If we, for instance, plot the numbers of dominant groups of soil animals in a series of soils, we find peak populations of one group or another at different stages in the series. If we continue this process further, say to individual species of mites, or Collembola, we find peak populations under particular plant species, in soils with certain textures or structure, moisture characteristics, and so on. If we knew enough about the ecological preferences of some common soil animals, their food requirements, limiting temperatures and moisture, reaction to acidity, pattern of nitrogen excretion, we could predict much of importance to the soil scientist, and also to the growth of plants, from a study of population figures. This may sound rather impracticable, but Ghilarov (1956a) has successfully used what he calls "soil invertebrate complexes" as diagnostic criteria for Russian soils whose affinities were in dispute. In New Zealand, profile characteristics due to soil animals, especially earthworms, may be used to distinguish yellow-grey earths from brown-grey earths, and may prove to be the most useful character for field recognition of some yellow-grey earths.

I should like now to discuss some trends in the study of soil organisms that have developed during the last few years and their implications both in the furtherance of the study of ecology and the better understanding of the properties of soils and soil forming processes.

In New Zealand, soil biology as a continuing study began with the formation of a biology section in the Soil Bureau, in 1946. It arose initially as an offshoot of soil surveys. Pedologists in the field felt the need to get some better understanding of the influence of living organisms on profile development and the processes of soil formation. The first studies were largely qualitative, and were aimed at finding out what kinds of organisms were present, how the species composition varied from one soil to another, and whether differences could be correlated in some logical manner with soil maps, vegetation, climate and various soil properties such as moisture content, texture, structure and chemical information. The lack of basic information concerning the constitution of soil populations is so great that this qualitative approach has continued right through to the present, and will need to continue for many years to come. In New Zealand soils there are many groups, particularly of animals, of which we know virtually nothing, and there is an open field for taxonomic and ecological work. So far, we have accumulated information on some bacteria, yeasts, fungi, algae, protozoa, and earthworms, and on a number of minor groups in the fauna, and have had some success in relating their distribution to pedological information.

Comparative studies have been made of soil organisms under particular vegetation types in various parts of New Zealand, e.g., a comprehensive study of soils under grazed pastures and native tussock, and of changes induced by the destruction of native vegetation and its replacement by pasture.

Qualitative studies have given soil biologists a background against which detailed quantitative and physiological studies can be planned and interpreted, and in the last few years an increasing proportion of the Soil Bureau's biological work has been quantitative and physiological.

Dr Stout has worked on the ecology of the animal and microbial populations of the litter layer of a soil under beech forest, relating numbers to physical features of the environment. Using measurements of the respiratory rate of litter decomposing organisms, made at monthly intervals for a year, he has attempted to work out a balance sheet of the carbon cycle, with encouraging results. He intends now to study the colonisation of dead leaves by soil organisms, and relate population changes to the rate and process of decay, and make a study of the contribution of individual groups of organisms to the processes of decomposition. This is an example of the kind of work that is occupying an increasingly important place in soil biology work in New Zealand. We are trying to get down to quantitative assessment of the contribution of individual species and groups of organisms to the turnover of organic material in the soil, and hence to their contribution to the processes that control soil formation and fertility.

Mycological work has recently been concentrated on the fungi that live in close proximity to grass roots. Among these fungi are some, known as endophytic mycorrhizae, which grow partly within plant roots and also have hyphal systems ramifying through the surrounding soil. The pathways by which minerals become available to plants are not well understood. This is particularly true, for instance, of the transference of nitrogen, originally fixed by nodule bacteria of legumes, through the soil to become available to grasses. It may well be that endophytic mycorrhizae provide the pathway, and a study of these fungi may prove most rewarding.

On the other hand, it is known that about half the nitrogen excreted by earthworms is excreted in the form of ammonia. It has been calculated by Satchell (pers. comm.) in England that a population of earthworms, *Lumbricus terrestris*, in a woodland soil, turns over approximately 100 kg/ha. of nitrogen per year. This figure is approximately equal to the amount of nitrogen available from the litter fall. Since earthworms in New Zealand pastures feed mainly on dead roots of pasture plants (Waters 1955), it is possible that they are major contributors to the mineralisation of nitrogen and its cycling through the soil. An attempt to assess the amount of nitrogen cycled by earthworms is being planned.

A great deal of work in soil ecology is at present in progress in Britain and Europe. At Liverpool, Prof. Burges and his school have made a detailed study of microbial ecology in an iron-humus podzol under pines. They have used direct microscopic examination of plastic impregnated sections of soil and litter horizons to measure the quantity of fungal hyphae and the species involved in successive stages of decomposition of plant debris; and have extended their studies to measurements of oxygen uptake by soil and litter samples, and the use of this data as a measure of microbial activity. Their work has contributed much to an understanding of the processes and rate of breakdown of soil organic matter, and at the same time it is important for its illustration of succession in microbial communities and relationships between the fauna and microflora of the soil.

Direct examination of soil sections as a method of studying the ecology of soil organisms is a relatively new technique, and one capable of providing much information, especially concerning micro-organisms. The preparation of satisfactory sections requires the spaces in the soil to be impregnated with a matrix that will bind the soil particles together without causing significant shrinkage of organic material, and without excessive damage to soil organisms in the soil spaces. Impregnation techniques have been developed largely in England and Europe. Haarlov in Denmark used agar and Minderman in Holland used gelatine, but these materials are suitable mainly for peats and soils with high organic matter content. Kubiena, in Germany, has developed a technique using plastic resins for impregnation, and this technique, combined with freeze drying of samples to minimise shrinkage, has been developed in Europe and England to become a most useful tool in soil ecology and also in the study of soil structure.

Much of the work on soil animals done in England and Europe has consisted of detailed studies of populations at specific sites, rather than the broad coverage of a range of soils that has been characteristic of New Zealand soil biology. Soil animals are very numerous. Up to 2.3 million arthropods per square metre have been found in forests in Sweden (Forsslund 1948), up to 20 million nematodes per square metre in the top few centimetres of Danish pasture soils (Overgaard Nielsen 1949), up to about 200,000 Enchytraeidae (Oligochaeta) per square metre (Overgaard Nielsen 1955) and about 1250 lumbricid earthworms per square metre (Waters 1955). Most soil animals exhibit violent fluctuations in numbers, both seasonally and in response to small changes in physical and chemical characteristics of the soil evironment. A wide variety of techniques for the extraction of animals from soil samples has been developed. Many have evolved from the classical Berlese funnel, which has been refined to a high degree of efficiency. Notable in the development of extraction methods have been Murphy and Macfadyen in Britain. A recently published volume on research methods in soil zoology (Murphy 1963) discusses extraction methods in detail. Now that efficient methods of extraction are available, soil animals are a fruitful and readily accessible field for students of animal populations, and for establishing basic principles in the study of mechanisms of competition between species, reaction to environmental change, control of animal populations, and many other fundamental aspects of animal ecology.

For measuring oxygen uptake and carbon dioxide production, much use has been made of the Warburg apparatus. Respiratory measurements done in the Soil Bureau have been carried out with a Warburg apparatus. This records reduction in pressure in a sealed chamber as oxygen is used up and carbon dioxide is produced and absorbed. Its usefulness is limited by the small volume of air contained in the system, and consequently the relatively short period for which experiments can be continued. Macfadyen has developed an ingenious and very accurate respirometer which can be run continuously for long periods, and which automatically records the amount of oxygen used and the rate at which it is used. The apparatus was designed originally for use with small soil arthropods, but undoubtedly has a much wider application in physiological and ecological research.

Ghilarov (1949, 1956 a & b, 1958) has put forward the hypothesis that terrestrial invertebrates evolved from aquatic ancestors by way of the soil as an intermediate habitat. He points out that in the spaces between soil particles there is an environment in which many invertebrate groups of aquatic origin could live and obtain oxygen without danger of desiccation. The fact that the soil fauna does include a wide variety of invertebrates, ranging from most delicate aquatic animals, such as protozoa, ostracods and copepods, through intermediate forms, to thoroughly waterproofed and highly successful terrestrial animals such as spiders and some insects, gives some credibility to his hypothesis. Whether his theory is accepted or not, a close study of the physiology, ecology and morphology of soil-inhabiting animals could provide much animals might have adapted themselves to life in a terrestrial environment.

I have not mentioned a wide range of work that is in progress in the fields of physiology, feeding behaviour, pest control, biochemical studies of humus formation and decomposition, and many other aspects of soil biology. I hope I have left with you the impression that the study of the ecology of soil organisms is an expanding and vigorous branch of biology. It is only a short time since soil science was the exclusive province of geologists, chemists and physicists. Biologists have now been accepted as essential contributors to soil studies and I believe that especially those with an ecological outlook and a willingness to use a variety of techniques and to collaborate with physicists, chemists and pedologists, can make a major contribution to soil science, and at the same time add much to the understanding of fundamental biological problems.

REFERENCES

FORSSLUND, K. H., 1958. Nagot om insamlingsmetodiken vid marksfaunaundersökninger. *Medd. Skogsforskn. Inst. Stockh.*, 37 (7): 1–22.

GHILAROV, M. S., 1949. *The peculiarities of the soil as an environment and its significance in the evolution of insects.* Moscow & Leningrad, (in Russian).

GHILAROV, M. S., 1956(a). Significance of the soil fauna studies for the soil diagnostics. *Proc. 6th Cong. Int. Soc. Soil Sci., Paris*, 3: 23.

GHILAROV, M. S., 1956(b). Soil as the environment of the invertebrate transition from the aquatic to the terrestrial life. *Proc. 6th Cong. Int. Soc. Soil Sci., Paris*, 3: 307–13.

GHILAROV, M. S., 1958. *Proc. 15th Int. Cong. Zool., London*, 354–7.

MACFADYEN, A. (in press). *Energy flow in ecosystems and its exploitation by grazing* in *Symposium on Grazing* ed. Crisp, D. J. British Ecological Soc. Oxford.

MURPHY, P. W. (Ed.), 1963. *Progress in soil zoology.* Butterworths Scientific Publications, London.

OVERGAARD, NIELSON, *C.*, 1949. Studies on the soil microfauna. II. *Nat. Jutland.* 2: 1–131.

OVERGAARD, NIELSON, C., 1955. In *Soil Zoology* ed. D. K. McE. Kevan, Butterworths Scientific Publications, London.

WATERS, R. A. S., 1955. Numbers and weights of earthworms under a highly productive pasture. *N.Z. J. Sci. Tech.* *A*36: 516–25.