Ecology of Soil Fungi

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Preface

This book has grown out of courses of lectures on the ecology of soil fungi given to final-year undergraduates in Agricultural Science at the University of Sydney, Australia, and, in 1969, to graduate students in Plant Pathology, Soil Science and related disciplines at Washington State University, Pullman, U.S.A. This background delimits the readers for whom this book is primarily intended – senior undergraduates and graduate students in the earlier years of their research. It is hoped that more experienced workers may also find some matter of interest within these pages.

In writing, I have deliberately retained the rather personal approach to the subject which is perhaps more characteristic of the lecture than the scientific article. Such an approach is congenial to me and is underpinned by a conviction that it is unbecoming to speak *ex cathedra* on a subject so vast and so fast developing as soil ecology.

The reader will perceive a progressive change in the nature of successive portions of the book. The first chapters are very general, others in the first part of the book only a little less so. The intention is there to provide a critical introduction to the background facts and concepts in the ecology of soil fungi and to provide an entry to the literature by means of a relatively small number of references. often to review articles. With this foundation laid, I have proceeded in Part 2 to treat a portion of the subject, physical ecology, in greater detail and with such rigour as is presently possible. More references will be found in this section, often to articles outside the normal literature of soil microbiology but relevant to the physical aspects of that subject. If the core can be at the end, Part 2 is the core and *raison d'être* of the book.

I should like to acknowledge my indebtedness to a number of my teachers and colleagues. From Professor E. J. H. Corner, F.R.S., I learnt as an undergraduate to respect the unconventional approach in things biological and to appreciate the importance of careful observation. Dr S. D. Garrett, F.R.S., introduced me to

the whole topic of the ecology of fungi and has been a constant guide and friend. Where I have reached conclusions somewhat different to his, as expressed in his book *Pathogenic Root-Infecting Fungi*, I trust that he will consider a certain rebelliousness on the part of a student to be only right and proper in this day and age. Professor N. Collis-George and Dr D. E. Smiles of the Department of Soil Science, University of Sydney, have been my mentors in soil physics and much of my research has been greatly influenced by them.

This book was largely written, and nearly all my research work discussed in it was carried out, while I was a member of the Department of Agricultural Botany, University of Sydney. My indebtedness to the research students within that Department will be most obvious to them, for many of the ideas stated and positions adopted were formed in the light of their work and from discussion with them. Finally, but by no means least, I must thank my colleagues Professor N. H. White and Dr C. D. Blake for providing an atmosphere in which research was made easier. I am also grateful to Dr Blake for reading and criticizing the manuscript of this book.

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Contents

PART ONE General Ecology of Soil Fungi

1 Introduction

Ecology is the 'study of the relations of animals and plants, particularly of animal and plant communities, to their surroundings, animate and inanimate' (Abercrombie, Hickman and Johnson, 1954). Here lies both the challenge and the danger of the subject. The challenge lies in the inherent complexity of all stages in the study. The first stage is the adequate description in factual terms of the biological and physico-chemical components of the system and of their changes in space and time. An informed consideration of this description suggests to the investigator the causal relationships between various components of the system and leads to controlled experiments, usually with simplified systems. Finally, the results of the various experiments and the hypotheses derived from them are integrated to form an explanation of the system revealed in the original description. The processes of ecological research are thus basically similar to those of all scientific research but in ecology the system studied is at its most complex and the integration is, ideally, the integration of a large component of all biological knowledge. Such a recital of the challenge of ecology immediately reveals the correlated dangers, for it is singularly easy to fall into error through a failure to describe accurately the various parts of the system and to appreciate their possible significance. An error at this stage may lead to the development of inapposite experimental techniques, so that the final synthesis must inevitably fail. A constant temptation besetting the ecologist is that of loose thinking to enable him to gloss over intracticable parts of his study.

The topic of this book is primarily the ecology of soil fungi. This branch of ecology presents both special difficulties and exceptional possibilities. There are two difficulties. The first derives from the unusually complex physical and chemical environment provided by the soil. Secondly, fungi are microorganisms (if one neglects the large sexual stages of certain species) so that the spatial scale is microscopic. A small volume of soil contains a vast assemblage of minute organisms of diverse form and physiology. Their small size, however, precludes the morphological complexity attained by higher plants and animals so that their reactions to each other and to their environment should be more easily attributable to basic physiological processes than is usually the case. The smallest and least differentiated free-living biological entities are the bacteria, but the ecology of these is hindered by the difficulties attending the first stage of investigation – description of the system. The lack of easily utilized specific criteria makes the accurate identification of bacteria and the precise description of their distributional patterns difficult to achieve. With the recent development of selective media for defined groups, this impediment may soon be less serious.

In fungi, the vegetative hypha approaches the simplicity and uniformity of structure of the bacterial cell but identification is more readily made by virtue of their differentiated reproductive stages. The bacterium, unicellular, small and with a large surface to volume ratio, is well-suited for the absorption of nutrients from a solution in which the cell is immersed. The hyphae of fungi and actinomycetes, however, permit the penetration of solid nutrient substrates by physical force and the extension of the mycelium from one substrate to another over nutritionally uncongenial areas. It is of interest that those fungi that resemble the bacteria in their morphological simplicity, notably the yeasts, are those that predominantly grow in situations where the nutrients are in the dissolved, rather than in the solid, form.

The ecology of soil fungi, therefore, has many attractive features: that many have found it so is shown by the size of the literature. Many who write on the topic would not consider themselves to be soil ecologists, but rather plant pathologists, for an ecological approach is a necessity when considering soil-borne diseases of plants. In this book, I have attempted to reduce to a minimum the degree of overlap with Dr J. L. Harley's *The Biology of Mycorrhiza* (1969) and Dr S. D. Garrett's *Pathogenic Root-Infecting Fungi* (1970) and the reader should refer to these books for recent treatments of topics that form a part of soil ecology in the wide sense. There is similarly a growing literature concerning the ecology in soil of fungal pathogens of man and animals and of those fungi which degrade materials as diverse as aviation kerosene and tents. The ecology of soil fungi is thus no ivory-tower pursuit but one with many applications to the ultimate welfare of mankind.

This book is unashamedly a personal view of fungal ecology. Such an approach I believe to be not only valid but necessary. The concepts and techniques associated with the ecology of soil microorganisms are now so complex and varied that no one person is competent to write authoritatively on them all. More than ever before, the soil biologist must have some precise knowledge of soil itself, for it is now clear that the activity of microorganisms and their interactions are profoundly affected by the physical and chemical framework afforded by the soil. The soil can no longer be looked upon as a vague background to biological activity: the two are intimately interconnected. In the past two or three decades, soil physicists have provided an understanding of the physical nature of soil which is adequate for the purposes of most biologists and in this area there is now the possibility of rapid advance.

1.1. **The soil**

We shall consider the soil to be the surface layer of the land, consisting of an intricate mixture of inorganic and organic components physically and chemically distinct from the underlying material. Most roots and soil organisms are located in this upper zone, the thickness of which is measured in inches rather than feet. Although it is convenient to consider the inorganic and organic components separately, it is fallacious to imply, as some workers have recently done, that the mineral soil is the 'true' soil and the organic matter (particularly in its identifiable form) an intrusion.

1.1.1. *Soil profile*

If a vertical section through soil is produced by digging a trench the soil profile is exposed. The top layers, largely organic in content, will be discussed later. The highest horizon that is predominantly mineral is designated *A* and is eluvial (leached). It is frequently divided into two subhorizons. The A_1 horizon is distinguished by a relatively high organic matter content and usually dark colour. Beneath, the A_2 horizon has lost clay minerals, iron or aluminium, or even all three, so that there is a concentration of the more resistant minerals. Organic matter content is usually rather low. Cultivation destroys the top of the profile and a mixed horizon, sometimes designated A_p, results. Proceeding down the profile, the *B* horizon is characteristically illuvial in that there is an accumulation of clay, iron, aluminium and/or organic matter.

Although roots and organisms penetrate into the A_2 and B horizons, maximum biological activity is in the A_1 horizon.

In humid areas, leaching is intense and a marked A horizon develops, frequently acid in reaction. In drier climates, however, leaching is reduced and the A horizon may be shallow and near-neutral to alkaline. The B horizons usually contain an accumulation of calcium carbonate and/or calcium sulphate, even though the parent rock may not be calcareous. The depth at which these calcium salts accumulate becomes shallower as the climate becomes more arid, and the depth of penetration of water is reduced.

Gilgais are areas of microrelief consisting of small basins, knolls or ridges in an otherwise level area and occur extensively on heavy soils in semi-arid areas. They are produced by alternate expansion and contraction of swelling clays during wet and dry seasons. This action lifts material from the B horizon into the elevated portion of the gilgai and soil properties vary over small horizontal distances. Frost heaving is another mechanism whereby the soil profile is greatly disturbed.

1.1.2. *Inorganic matter*

The inorganic particles are derived, directly or indirectly, from parent rocks and their composition, especially that of the larger particles, reveals this derivation. Many of the rock minerals, however, are changed by the physical and chemical processes of weathering and most of the smaller particles are secondary in nature. A soil is thus a complex product of parent material, topography, climate, time and biological activity. Conspicuous among the secondary minerals are the colloidal clays, many of which are highly reactive and tend to dominate the chemical properties of the soil. The major mineral particle that occurs in its primary form in soil is quartz and most of the larger particle fractions consist of this unreactive silica.

Mechanical analysis of a soil is the procedure of breaking the soil aggregates down into the individual component particles and then determining the frequency of distribution of particles among various size fractions. This separation is performed by sieving (for the larger particles) and by sedimentation in a column of water (for the smaller particles). The velocity of sedimentation, by Stokes' equation, is proportional to the square of the diameter of spherical particles. The expressed results of both sieving and sedimentation thus assume that the soil particles are spherical and it needs to be borne in mind that the given diameters are equivalent diameters only. If the particles in reality have a plate-like form, the discrepancy can be considerable.

The sizes of soil particles have a continuous distribution: to divide them into fractions is arbitrary. This situation is reflected in the development of a number of different systems, although only two are in common use in the relevant literature. The more important fractions of these, the International and American systems, are given in Table 1.1.

Table 1.1. *Names and sizes of main soil fractions according to the International and American Systems*

Name of fraction	Equivalent diameter of particles (mm) International	American
Sand	2·0–0·02	2·0–0·05
Silt	0·02–0·002	0·05–0·002
Clay	< 0·002	< 0·002

Once obtained, the mechanical analysis of a soil can be shown as a single point in a triangular representation. The surface of such a triangle is conventionally divided into areas characteristic of the soil textural classes, but two triangles are then necessary because of the different dimensional definitions of the fractions in the American and International systems: that for the American system is shown as Fig. 1.1. In the sense just described, the texture of a soil is thus a simplified description of the particle size distribution or mechanical analysis.

The term texture is also used in a different sense to express the field assessment of shear strength, that is the force necessary to move adjacent planes of soil over each other. The soil is worked between the fingers, to destroy its aggregates, at a water content such that the soil just sticks to the fingers. The force that must be exerted by the fingers to work the soil in this structureless state is noted: if it is great, the soil is a clay, if small, a sand. Soils of intermediary shear strength are loams. The terms 'clay', 'loam' and 'sand' are thus arbitrary divisions of a continuous scale of shear strength. Qualifications of these terms are applied if a particular fraction is apparent to the fingers: hence 'sandy loam', 'silty clay' (silt has a characteristic buttery feel). Additional guides to the textural classes are afforded by the fact that the cast formed by squeezing a moist sand is exceedingly fragile; that of a loam may be quite freely handled without breaking; and clay may even be rolled into a ribbon.

Clearly, the term 'texture' and the names of the textural classes

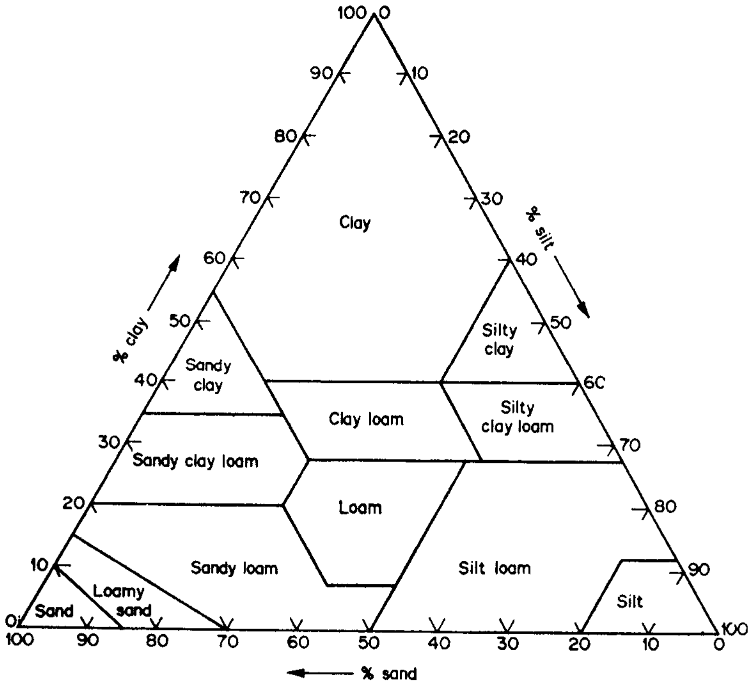

Fig. 1.1. *The composition of the textural classes of soils, as used by the United States Soil Survey*

are being used in two different ways. Usually the textural class obtained in one way will agree with that obtained in the other. Thus a soil determined as a 'sandy clay loam' in the field by its sandy feel and rather high shear strength will be shown to be a sandy clay loam by mechanical analysis. Occasionally, however, discrepancies occur so that the means of assessing texture should, strictly, be stated.

1.1.3. *Organic matter*

Above the A_1 horizon may be found organic horizons, the A_{00} and A_0. In the biological rather than soil literature, this organic layer is frequently divided into three, the *L*, *F* and *H* layers. In the majority of soils, the surface layer consists of a relatively unaltered mass of identifiable plant remains. This is the *L* (litter) layer or A_{00} horizon. In a 'mor' soil the F_1 (fermentation) layer lies underneath the *L* and consists of plant remains in the process of decomposition. The lowest organic layer is the *H* (humus) layer in which the organic material is amorphous and no longer identifiable. The *F* and *H* layers together form the A_0 horizon. In a 'mull' soil the *F* and *H* layers are usually scarcely discernible because the activity of soil animals, particularly but not exclusively earthworms, leads to a rapid intermixing of the decomposing organic material with the surface mineral layer of the soil. In a 'mull' soil, the *L* layer thus rests virtually directly on the A_1 horizon. Intermediate conditions between 'mull' and 'mor' are frequent and are sometimes referred to as 'moder'.

A characteristic feature of 'mor' is the slow rate of decomposition, a fact of considerable biological interest. It has been suggested that phenolic materials in the plant tissues tan the proteins and also form protective coatings over cellulose fibrils, thus rendering them relatively unavailable to microorganisms and the meiofauna. Such soils are also characterized by low base status so that they tend to be very acid.

Within the *A* and *B* horizons, organic matter can be divided into two components, that formed *in situ* and that derived from the *L*, *F* and *H* layers. Organic material formed *in situ* consists of the cadavers of soil animals, large or small, and the walls and cellular contents of bacteria, fungi and other microorganisms, but principally of the roots and other underground organs of plants. When dead, roots are clearly a part of the soil but they are not normally considered so when alive. A little reflection, however, will reveal the distinction to be tenuous because roots, by their excretions, greatly influence microbial activity within the rhizosphere. The rhizoplane flora, also, is largely saprophytic. The ecology of the rhizoplane and rhizosphere should thus be considered in any comprehensive treatment of soil ecology. I have chosen not to do so because these topics have been recently reviewed in a number of