Ecology of saprotrophic fungi

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Preface

The present state of fungal ecology in many ways resembles that of inorganic chemistry before the advent of the periodic table in that although a wealth of descriptive information exists there is no strong, coherent framework within which it can be ordered. The need to construct such a framework has more than a merely philosophical importance. Detailed floristics of the kind traditionally sought by fungal ecologists for specific habitats, although valuable, often indicate little of the nature of fungal activity in those habitats. Indeed, on its own such information may convey scant meaning except to the specialist who is familiar with particular habitats and their attendant species. Moreover, although it is increasingly being recognized that there is an urgent requirement for a more modern, conceptual approach related to other ecological fields, real progress in that direction is being hindered, in our view, by peculiarly mycological problems. These relate principally to an inadequate understanding of fundamental fungal attributes and, in particular, of the behaviour of mycelial thalli.

This lack of understanding, or the neglect of what is known of fundamental attributes, has promoted serious problems of methodology and data interpretation which, in turn, have retarded the emergence of clear ecological principles. We believe that by careful appraisal of fungal attributes in relation to available descriptive information on habitats some useful general concepts and principles can be promoted, and we feel that this book provides justification for, and is justified by, this belief. We hope that by offering such ideas for evaluation and debate, progress towards a more predictive approach to fungal ecology will be stimulated. Our first aim has been to establish those concepts and principles that we consider to be most important, and we have then gone on to examine natural fungal habitats within these contexts. It will quickly become apparent that we have viewed some areas from new directions and re-appraised some long-standing ecological tenets. While doing so we have tried to remain sensible of 'traditional' views but have also attempted to synthesize these with information on fungal morphogenesis, physiology and genetics.

We have concerned ourselves for the most part with obligate saprotrophs, mainly because more ecological information relates to these fungi, but where appropriate we have also viewed species with other nutritional modes. The propensity of many biotrophs and necrotrophs to switch from one nutritional mode to another during development, and the key role which temporary saprotrophy often plays in their survival, emphasize the dangers inherent in making strict distinctions between fungi on nutritional grounds. In addition, we feel that the ecological principles established here for obligate saprotrophs can be applied equally to obligate biotrophs and obligate necrotrophs.

There has been, inevitably, the need for selection and some specialists in certain areas, for example soil and aquatic habitats, may disapprove of our brief treatment of their particular fields. It should, however, be stressed that this brevity does not imply that these fields are unimportant. Rather it has been occasioned by lack of real ecological data, largely due to inappropriate methodology coupled with the difficulties that attach to reliable identification of the active fungal components of some ecosystems. Selection is also manifest at the end of the book where we have given some consideration to fungal biotechnology but have ignored fungal biodeterioration. This is because we have chosen to emphasize positive rather than negative aspects of applied fungal ecology and to outline the many benefits which might come from full exploitation of the physiological versatility of fungi. Furthermore, an account of biodeterioration within an ecological context would amount to little more than an annotated list of species, substrates and substrata, and would not add anything significant in terms of concepts. However, we do believe that many of the principles we discuss are readily applicable to biodeterioration studies, and hope that they will aid advancement of research and understanding in this field.

Finally, we would draw attention to our present inability adequately to discuss ecosystem processes. An understanding of these requires a degree of knowledge of the vital components which has not yet been obtained. We hope, therefore, that the essentially autecological approach adopted here will help to provide this knowledge, from which the ultimate integration of 'component' and 'black-box' approaches to microbial ecology into a viable, workable system can be made.

December, 1982

Rod Cooke, *Sheffield*
Alan Rayner, *Bath*

Note on nomenclature

The classification followed is that set out in the *Dictionary of the Fungi* (6th edn, 1971), edited by G. C. Ainsworth, P. W. James and D. L. Hawksworth, published by the Commonwealth Mycological Institute. However, when referring to Deuteromycotina (Fungi Imperfecti) we have elected to indicate their probable affinity by using 'imperfect Ascomycotina' or 'imperfect Basidiomycotina' as appropriate. In cases where fungi have both a perfect and imperfect species name, the most familiar binomial is usually used: that is the name occurring most frequently in current literature. On first mention the alternative, and less familiar binomial, is given in brackets. There are, however, a few cases where, in order to avoid confusion, the name of the perfect state is preferred even though it might be unfamiliar.

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Contents

PART ONE

Determinants of life-styles

Heterotrophy and its consequences

The most important factor affecting the distribution and life-styles of fungi is their heterotrophy, so that although they have some capacity to fix atmospheric carbon dioxide, virtually all their growth needs must be met by previously elaborated organic compounds which they absorb from their immediate environment. Fungi are thus confined, when active, to habitats in which a suitable supply of such compounds is available. Furthermore, although as a group they can probably exploit nearly all the sources of organic carbon available in the natural world, different fungi (often, but not necessarily, different species) vary widely in their ability to gain access to and utilize carbon compounds which differ in type and location. This variation is obviously ecologically important since the types of organic compound which a fungus can use will inevitably affect many aspects of its behaviour, including its pattern of establishment in natural nutrient sources, its interrelationships with other organisms, its contribution to ecosystem processes and, not least, the types of material which it can occupy. This begins to explain why particular kinds of material support only certain fungi, and has been used in attempts to find suitable bases for classifying fungi into ecological, as opposed to taxonomic, categories.

Ecological classification introduces the need for strict usage of such terms as habitat, substratum and substrate, which are often interchanged indiscriminately in the literature. Here, habitat is used to describe the place where a fungus lives, and so has some connotations as to the physicochemical environment within which development takes place. Substratum refers to the medium within the habitat which physically supports the fungus during development, and substrate to a specific biochemical constituent of the substratum. Fungal species living in a single habitat often occupy distinctly different ecological niches, that is they exploit different facets of the substrata on which they are growing. For example, in the habitat provided by leaf litter, cellulose breakdown may be effected by a certain assemblage of fungi, and lignin degradation is achieved by an overlapping, but nonetheless different, spectrum of others. In different kinds of leaf litter, or in litter decomposing under different environmental conditions, similar niches may be occupied by quite distinct species spectra. The concept of ecological niche, while taking account of habitat, also describes functional role, that is the contribution of a fungus or group of fungi to ecosystem processes. The genetic properties of a fungus determine its niche; substratum composition and the occurrence of other micro-organisms control its activity within that niche. Another useful concept in this context is that of resource, which can be applied as a general term to materials, be they either potential or actual substrates or substrata, from which fungi may or do obtain nutrients.

Substrates

The ecological relevance of substrate-specificity will be explored more deeply in subsequent chapters, but an important first step towards understanding fungal ecology is to delineate the nature of substrate relationships. This has been the object of numerous, mainly laboratory-based studies that have resulted in a large body of information which, although inevitably incomplete, can be used here to establish certain general principles.

Fungi may absorb substrates either directly from their substrata, if the molecules are capable of passing through the cell wall and membrane, or they may first break them down into more assimilable units by means of extracellular enzymes. A selection of common substrates available to fungi as major carbon sources is listed in Table 1.1 together with information on origins, assimilability and persistence, and an indication as to what kinds of fungi can utilize them.

It can be seen that easily assimilable non-polymeric compounds including glucose, fructose and xylose, are utilized by virtually all fungi which have been investigated in this connection. Also widely utilized are sucrose (although some common fungi lack invertase) and starch, which is relatively easily hydrolysed. By contrast, less common or more complex, and so more refractory, substances are utilized much more selectively, and the fungi involved often show marked specificity for substrata containing such substrates. However, there may be some circularity in this statement in that ability to utilize uncommon or complex substrates is probably usually ascertained only in ecologically appropriate cases. For example, cellulolytic ability may not be expected (and therefore not investigated) in fungi colonizing animal tissues; similarly keratinolytic ability may not be expected in fungi colonizing plant tissues.

Table 1.1. Some substrates available to fungi as major carbon sources

Degree of assimilability and persistence	*Substrate*	*Major sources*	*Major utilizers*
Readily assimilable, non-persistent	Glucose, fructose, mannose (and other hexoses), xylose (pentose)		Probably all fungi except certain Oomycetes (Leptomitales)
	Sucrose, maltose, cellulose (disaccharides and polysaccharides)	Living or dead plant and animal tissues, living or dead microbial cells	Probably most fungi with some notable exceptions, e.g. sucrose not utilized by many Chytridiomycetes. Zygomycotina (Mucorales) and some Ascomycotina
	Organic acids		Some fungi, but ability highly specific
	Fatty acids		Some Chytridiomycetes (Blastocladiales) and Oomycetes (Leptomitales)
Readily to fairly readily assimilable, non-persistent to fairly persistent	Starch *Polymer of glucose*	Plant tissues	A wide range of fungi including some Oomycetes
	Inulin *Polymer of fructose*	Plant tissues (Compositae, Liliaceae)	A wide range of fungi including some Oomycetes
	Glycogen *Polymer of glucose*	Animal tissues, and microbial cells	Probably a wide range of fungi
	Hemicelluloses *Short-chain polymers of glucose, mannose, xylose uronic acids and other residues*	Plant cell walls, especially higher algae	A wide range of fungi, possibly particularly marine Ascomycotina

Table 1.1 cont'd

Degree of assimilability and persistence	*Substrate*	*Major sources*	*Major utilizers*
	Pectins *Polymers of galacturonic acid*	Plant primary cell walls and middle lamellae	A wide range of fungi
	Lipids (fats and oils) *Complexes of glycerol and fatty acids*	Animal and plant tissues, microbial cells, animal secretions	A wide range of fungi
	Proteins (non-keratinized) *Polymers of amino acids*	Living or dead plant and animal tissues, microbial cells	Many fungi, but release of ammonia may be quickly inhibitory
Slowly or very slowly assimilable, fairly persistent to very persistent	Cellulose *Microfibrillar aggregates of glucose polymers*	Plant cell walls	A wide range of fungi but few Zygomycotina
	Cutin *Polymer of fatty acids and hydroxy-fatty acids*	Plant cuticles	Little information, but cutinases possibly widespread among Ascomycotina
	Lignin *Complex polymer of phenyl propanoid monomers*	Plant cell walls	Some Ascomycotina (Xylariaceae), many Basidiomycotina
	Suberin *Complex corky material containing high molecular weight fatty acids and their oxidation-condensation products*	Plant bark and endodermises	Undoubtedly some fungi, but information scanty

Table 1.1 cont'd

Degree of assimilability and persistence	*Substrate*	*Major sources*	*Major utilizers*
	Chitin *Polymer of N-acetyl glucosamine combined with protein*	Arthropod exoskeletons, fungal cell walls	Many soil-borne fungi, and species of Ascomycotina that inhabit living arthropods
	Keratin *Cross-bonded protein rich in sulphur-containing amino acids*	Dermal tissues of animals; hair, fur and feather, hoof and horn	Many Ascomycotina, including species that inhabit living animals
	Waxes n-*alkanes and* n-*alkyl esters*	Plant cuticles	Many leaf-surface fungi
	Other hydrocarbons (oil, bitumen, kerosene, petrochemical products)	Mainly industrial	Many Ascomycotina

The relatively refractory polymers cellulose and lignin are among the most abundant organic materials on earth, and are formed in vast amounts annually by primary producers. Fungi are probably the principal agents responsible for degrading these substances, and as such fulfil a vital role in the carbon cycle and in humification processes. Partly this is due to their possession of suitable enzyme systems to break down these substances (Figs 1.1 and 1.2). Indeed, only certain fungi, notably Basidiomycotina and xylariaceous Ascomycotina causing white rot of wood and other plant litter, have been unequivocally shown to have the enzymatic capacity for complete, rapid breakdown of lignin, although partial or slow breakdown may be accomplished by other organisms, including certain bacteria. Also crucial is the ability of fungi to gain access to these substrates within natural substrata, and, as will be seen later, this is largely attributable to their mycelial organization. Some abundant refractory polymers, such as chitin and keratin, may be more physicochemically accessible