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THE ECOLOGY OF THE FUNGI

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INTRODUCTION

Ecology has been defined (104) as the study of the reciprocal relations between organisms and their environment. Fungi are heterotrophic organisms which cannot manufacture their basic food requirements and so are dependent to some extent either as parasites or as saprobes on food materials produced by other organisms. They can thus be placed in five of the six categories included in a recent (104) definition of symbiosis. Disjunctive and conjunctive symbiosis are distinguished by the fact that in the first category the associated organisms are not in constant contact. Each of these two types of symbiosis is divided into social and nutritive groupings. Social disjunctive symbiosis includes the substrate relations of saprobes, but since fungi are dependent on the organism or organic matter with which they are associated, no fungi can be included under the division of social conjunctive symbiosis unless such species as sooty molds, which are parasitic upon insects and only secondarily are anchored upon plant parts, can be included here. Antagonistic disjunctive symbiosis includes those fungi which are predatory on nematodes, amoebae, protozoans and other microorganisms, while antagonistic conjunctive symbiosis includes those fungi which during part or all of their life cycles are parasitic upon plants and animals. Reciprocal disjunctive symbiosis includes those fungi which are cultured and disseminated by insects and other organisms which use them as food; this classification could also include those fungi used by man as food or for the production of specialized by-products. Reciprocal conjunctive symbiosis includes those fungi which participate in the formation of mycorrhizae or of lichens. From this general analysis it will be seen that most fungi are either social disjunctive symbionts or antagonistic conjunctive symbionts.

Most of the fungi have a multicellular thallus or mycelium composed of many fine threads called "hyphae." In some groups the mycelium is not divided into cells but is elongate, branched and coenocytic. In other groups the thallus is unicellular and each cell is a minute single entity. Those portions of the thallus in which the cell wall has not become thickened (337) are in intimate contact with their environment at all times and, where not formed into hyphal strands, rhizomorphs or sclerotia, on all surfaces. Such cells or hyphae may be compared with the root hairs of higher plants in their youngest stages. They may develop their own rhizosphere effects and in addition may develop certain antagonistic effects between other fungi and other organisms in the associations of which they are members.

Spore germination, mycelial development, fruiting body production, spore discharge and dissemination, and the development of rhizomorphs, sclerotia and resting cells all fall within the province of fungus ecology. In addition, cytoplasm and nuclei within the cell walls live in their own environments and help to control the environments in which the fungi possessing them live. It is thought that certain phases of the study of the phylogeny and taxonomy of fungi have application in or may be basic to ecology. Therefore, certain applications of these fields will be included in the following discussion.

EARLY STUDIES

To a large extent fungi comprise a group of ubiquitous and omivorous organisms. Their existence has been recognized almost since the beginning of man's recorded experiences and impressions of nature. They number (33, 275) 80,000 to 100,000 species. They are found wherever they are searched for, and their spores appear anywhere that spore-traps (316) are exposed or soil samples are plated (86).

At first, the study of fungi was devoted to their use as food, medicine or intoxicants (342). The adaptability of fleshy fungi for food was, and still is (406), a matter of trial and error, since most well known poisonous species occur in many parts of the world. In many areas where fleshy fungi of necessity form a food supplement, the native population has learned to recognize many of the common edible species. Mushroom culture has been an industry for a long time (360, 342).

As the binomial system of nomenclature was adapted to the uses of students of life other than botanists, zoologists and paleontologists, mycologists recognized more and more species of fungi. At first this recognition was based largely on macroscopic characters (143, 331), but as the microscope became more adaptable to the study of ever smaller structures, including spores, the larger fungi were better understood and the mold fungi more easily studied (98, 443).

The early history of mycology consists largely of the cataloguing of the various populations in which a student was interested. These were mainly along regional lines, sometimes on national and sometimes on continental lines. Catalogues could be based on limited numbers of specimens, and these would be supplemented by lists of few to many novelties or unusual species or range extensions. This phase of mycology continues to the present day and should not be discouraged. To a limited extent, but with certain improvements as the realization comes to the worker that more information is necessary, such lists and reports include a minimum amount of information concerning the ecology of the species under consideration. Such information is autecologic in nature and usually refers only to a single instance in the distribution of a species which may ultimately prove to be ubiquitous and omnivorous, or to be highly restricted in range and in nutrient requirements (32, 109).

Parallel with the development of systematic mycology, culminating in such universal compendia as those of Saccardo (374) and Oudemans (311), was the realization that certain fungus species are associated with or cause plant diseases. The description of this development (235) and that of plant pathology forms an important portion of the history of fungus ecology.

A very recent development in the systematization of fungi is the suggestion (401) that standard key characters can be initialed, the initials to be built into words which can be used as code names for a species. Another suggestion (165) is for the numerical ordering of genera and species in line with already developed systems of numbered families and orders in such a way that entries can be made in a punch card system for locating a species. In forest pathology, rapid identification of species by cultural characters has progressed to a high degree on a numerical basis. Such sets of numbered characters can readily be transposed to punch cards (309). With the increasing use of punch-card filing systems, it is neither visionary nor unscientific to consider such measures aplicable in other fields of mycology.

CLASSIFICATION AND TAXONOMY

One of the biggest hurdles encountered by the student of fungi is the problem of classification. Within certain groups, classification has become stabilized to a degree mostly because of the dominance of one leader in a school which has gained high rank in the study of the group, or because of the degree of co-operation between two or more leaders and their students. Such work is best exemplified in studies on the Myxomycetes (264, 272) and in some groups of the Phycomycetes (75, 137, 182, 221, 222, 413). However, in higher groups, including the Ascomycetes and the Basidiomycetes, except for the Heterobasidiomycetes (262, 273), possibly the Gasteromycetes (496) and the Laboulbeniales (386), this is not always the case. Order is gradually being brought out of the chaos of Ascomycete taxonomy by students of various groups within the class (25, 26, 263, 293, 305, 464), but disagreement over interpretation of certain portions of the International Code of Botanical Nomenclature (25, 234, 352, 384, 439) is hampering progress in this field. Problems of nomenclature in the Homobasidiomycetes are not so serious, except for corrections of names developed during the controversy between American and International Code adherents, but classification of the whole subclass is in a state of flux because of another controversy. Here the questions of whether to follow the Friesian or Patouillardian school, the importance in systematics of the hyphal system in the fruit body, and the extent to which certain phylogenetic concepts should be emphasized, hamper development of systematics and cause considerable unnecessary controversy during the slow process of study. Recent changes in emphasis placed on microscopic characters in the taxonomy of the higher fungi add additional burdens to the student of local populations, at least until monographic treatments of practically all groups of Homobasidiomycetes have been prepared.

In the Fungi Imperfecti (Deuteromycetes) certain problems of taxonomy and classification seem at present to be almost insurmountable to the beginning student. The changing concepts of classification (207, 374, 450, 451) tend to clarify concepts of apparent relation between form genera and species, but they do not help to solve the puzzles created by lengthy species lists. When each species on such a list is based on a different cultural appearance, different natural substrate or different geographical source, and when most species assigned to a genus can be shown, under uniform conditions (33, 39, 410), also to be one species, the validity of other lengthy species lists can be readily questioned. This situation is most confusing to the student unfamiliar with mycological practice, and results in discussions dealing with the treatment of one or another of the synonymous species as separate species, or more commonly with population groups which are assumed to react as one species, rather than in work which could lead to a broader understanding of the genus or group of species in question.

In the development of our knowledge of fungi, both morphologically and ecologically, it is important that the taxonomy of the group be understandable to all. This and other facts concerning the taxonomy of fungi have been emphasized (229) in a plea for rational development of this science.

Many texts have been written on the morphology and taxonomy of fungi. Depending on the author's background, each text differs in detail or in fundamental principle. From Switzerland comes a well known morphology (151) which has been enlarged in an American translation (154). A work initiated in France and elaborated in Belgium (233) develops a different approach in which all fungi are considered to be unicellular and coenoctic. A detailed American work (30) strongly develops the theme that fungi have arisen from algae. Another recent American text (402) develops the relationships between fungi and bacteria and, as in the French work mentioned above, relates the fungi to their various roles as producers of disease and of certain beneficial effects for man.

Other workers have developed concepts of relationship between groups of species and genera of fungi as a result of lengthy studies in culture and in nature. Of such studies two may be mentioned, namely, the development of a picture of the biology and phylogeny of the fungi (464) which produce their fruiting receptacles in stromata on living or decaying wood, and the morphologic study of a group of Discomycetes, the Sclerotiniaceae (469), whose sclerotia are considered a specialized type of stromata usually associated with the disease of specific host plants.

At the generic level, many monographs have been written. A few of these are pertinent to this discussion. In the development of monographic studies in the genera *Leptosphaeria*, *Pleospora* and *Clathrospora*, familiarity with the many species found in nature, culminating in such studies as one of the species found in Mount Rainier National Park (464), is being coupled with an understanding of the species as they behave in pure culture in the laboratory (393, 394).

After many years of study and work with *Aspergillus* and *Penicillium*, one student of these economically important genera (438) found it necessary to discuss the development of species concepts within the group. *Endogone* (15) is a unique genus in that zygospores are developed within a fleshy receptacle produced beneath the surface of the soil like a truffle. It is possible that members of this genus are mycorrhizal but they are collected infrequently. Species of *Septobasidium* (99) are parasitic on scale insects and inhabit the warmer parts of the world where they apparently grow on the bark of trees, simulating a thin patch of lichen-like growth. The species of the genus *Typhula* develop (359) small sclerotia whose peridial cells have very characteristic outlines. They occur on living or dead plant tissue and may cause the snow mold of grains and diseases of lawns and golf course grasses. The life histories and speciation of certain groups of the genus *Allomyces* have been thoroughly studied (122, 486). Within these generic studies are features of interest to the ecologist and to which he can supply additional information.

PHYLOGENY

The problem of the monophyletic or polyphyletic origin of fungi is not a pressing one for most workers studying the synecology and some phases of the autecology of fungi. However, when one considers the various living states in which organisms assigned to the fungi (7, 30, 151) are found, the problem cannot be ignored and could become of prime importance. Among mycologists it is usually given incidental mention (30:274), but recently a system has been proposed, based on the polyphyletic origin of organisms (97), which cannot be completely ignored. Here organisms usually treated as fungi are thought to have arisen in at least four different places in the kingdom Protoctista. Lines of connection with ancestral forms are thought to have been lost or completely obscured. The Myxomycetes are considered to be related to amoeboid organisms, the Oomycetes (water molds) to be more closely related to heterokont algae than to other fungi, while the chytrids occupy a distinct phylum as do the remaining fungi. Whether this system will hold up under the critical scrutiny of mycology is a question, but in some ways it expresses habitat requirements better than other systems which have been proposed.

On the other hand, it has been suggested (369) that fungi should be maintained as a group distinct biologically from plants and animals on the basis of such factors as method of restriction of water-loss in terrestrial organisms, reproduction without nuclear fusion, nutrition, an extensive generation of cells with a double chromosome complement, and increased certainty of association of gametes. The question "Are fungi plants?" has been asked recently (276). A number of arguments are presented for both points of view and the reader is asked to exercise his own critical judgment in developing an answer.

Within the fungi, a parallelism between the life cycles of certain groups is presented in a demonstration of the apparent similarities between the rusts and the red algae (214). Various arguments have been presented (192) for using phylogeny to develop a natural classification of the fungi.

PALAEONTOLOGY

Fungi have been on earth a long time. Opinion is divided as to the significance of fossil fungi, even regarding their existence. Since woody plants also have a long history and their remains are consolidated only in areas providing special conditions of preservation, it may be assumed that among the microorganisms which reduce wood to its component elements the fungi must be important. Like the decomposition of plant materials that make up coal beds, fungi have played a role in the decomposition of wood or wood-like material prior to its deposition (381). Large conks of identifiable polypore fruit bodies have been found (11) in volcanic ash and lake sediments in the Pliocene or later deposits near Mountain Home, Idaho. *Fomes idahoensis* Brown was found to be very much like modern specimens of *Fomes pinicola* (Sw. ex Fr.) M. C. Cooke. The fragment of the specimen studied was 15 cm. in diameter. Fossil materials indicate that the flora of the region at that time was largely hardwood, while at the present time, with the area in the Great Basin scrub, conifers predominate in the adjacent forests. A large conk of *Fomes applanatus*, which probably occurred on *Umbellularia californica*, has been found in the Pleistocene flora of the Tomales Formation north of San Francisco (278). This specimen measured 15 x 10 x 3 cm. and had four distinctly separate layers of tubes. In the Eocene of Wheeler County, Oregon (383), a fungus assigned to the Aspergillaceae was detected in the lumina of the vessels of two unrelated woods tentatively assigned to *Magnolia* and *Castanopsis*. In a recent book (220) on the microfossils is the following statement: "The organisms in this phyllum (Eumycophyta of the kingdom Protista) are the parasitic fungi; they are found as fossils only in association with other woods as studied in this section. No significant microfossils are known. Devonian—Recent."

FUNGUS GEOGRAPHY

The first statements leading to the development of concepts of mycogeography were made in the United States (109) and in England (32). Certain groups of species have been shown, such as the Phallales and the Xylariaceae, to be more tropical than temperate or arctic, while others are better known in temperate regions. Apparently more micromycetes (249) than macromycetes thrive in the arctic regions (398). A definite series of fungi appears to be associated with melting snowbanks in subalpine western North America (88).

Within a particular group of fungi, the writer knows of only one study in which a specialist has considered state-by-state and region-by-region distribution of the fungi of his speciality. It is a description of the areas in which members of the Polyporaceae (312) exist in the United States.

In general, much more must be known about local fungus populations and about the distribution of individual species in relation to habitat variations before a general fungus geography can be developed beyond the stage of generalizations.

In England a series of plant disease distribution maps (76) has been published. These maps graphically portray the actual and sometimes potential geographic distribution of the important plant diseases of the world.

STATISTICAL STUDIES

Few workers have been able to adapt statistical methods to the study of fungus populations, usually because the methods of population study have been of a survey rather than a quantitative type. In a review of the latter type (87) the seasonal climatic factors which appeared to govern the distribution of fungi throughout the growing season were so erratic that statistical analyses were impractical. However, one worker in England has found conditions to be ideal for developing statistical analysis of various factors in fungal distribution. Because problems differ and have not been treated in the same way, they will be considered separately here.

A theory of anemophilous dissemination of fungi, especially of Basidiomycetes, is presented (320). The mean radius of dissemination depends on the structure of the basidiocarp, the height of the pileus in the case of agarics, the behavior of the spores and the habitat. The present theory applies only to grassland species. "The circumscription ratio is a single-valued function of the mean radius of dissemination, and governs monotonocally the coefficient of inbreeding and all parameters dependent thereon." Results of plotting circumscription ratios on graphs of which the mean radii of dissemination are abscissae indicate that a considerable variation in the general level of heterozygosity is conceivable as a result of purely anemophilous dispersal. It is suggested that if dissemination of small agarics is purely anemophilous, Skokholm Island populations could show incipient speciation.

In presenting the fungus biota of Skokholm Island in tabular form, some floristic and ecological calculations are given (321). The ecological status of each species is described as either prevalent—present more than two times in any one year—or subvalent. In the latter case the species may be preposite—represented by only one record in any one year—or apposite—with at least two records in one year. Habitats, habits, season classes and distribution are tabulated. Statistical analyses have yielded information concerning sampling efficiency, in relation to individuals and species, which may be affected by psychological factors inherent in the observer, the total number of species in the area under study and the various habitats under consideration, and the proportion of species fruiting in any one season.

A statistical analysis of the fungal populations on Skokholm Island is presented (322) under the heading "population densities." Estimate is made of the populations, constancy of the estimated populations is discussed, total populations are summarized, and the population distribution on the island is described. The most abundant species in each habitat together with the communities, hosts or substrata on which they occur are listed according to five principal groups: humicolous, quisquilicolous, coprophilous, metacoprophilous and lignicolous.

Correlation of the occurrence of fungal species with the plant associations of Skokholm Island is discussed (325) statistically. The statistical concept of fidelity is defined and the statistical concepts of 'preference' and 'aversion' are described. One type of fungus may demonstrate a preference for a grassland association and an aversion for a bog community. Certain species have been able to develop in an area to the exclusion of all others. These are considered saturants, a term contrasting with the subvalent species mentioned above.

Experience in England (326) and reports of workers in Colorado (387) suggest a statistical basis for the study of fairy rings and related phenomena. This idea is developed on a geometrical model and considers the rate of growth of impingent groups, interspecific competition, the problem of non-uniform fields, factors of effective reproduction rate, and the longevity of fairy rings. It is concluded that the fairy ring is highly inefficient and that communities in which it arises are open. These are conditions likely to promote the evolution of species of nearly identical ecological requirements.

The fungus foray is an institution in the activities of mycological societies on both sides of the Atlantic. The foray brings together a group of fungus collectors once a year for several days or a week, to collect and study intensively the fungi of the area chosen. In this way much has been learned of fungus floristics. To determine the efficiency of the foray as a means of obtaining floristic information, a test was made of records from one group of forays in England (327) covering a five-year period. Here the statistician was limited, since no experimental design was developed before or during the foray. The foray records showed that collections made on individual occasions yielded only about 25% of the total possible species. This percentage is attributed in large part to the erratic fruiting habits of the fungus species rather than to the inefficiency of the collectors. Thus long periods of time are required in which to obtain an adequate knowledge of a fungus population. The statistical formulae by which the conclusions were obtained may be applied with caution to comparable data from forays in other regions. Fungus forays are as reliable a method of floristic study as can be expected, but results could be improved if the forays were smaller and more frequent.

AUTECOLOGY AND SYNECOLOGY

As with other organisms, the ecology of the fungi may be divided into two parts, autecology (relation of the individual to its environment) and synecology (composition of communities and relation to their environment). To a large extent, the study of fungus ecology has been largely the study of fungus autecology. Such work as has been carried out in the field of synecology has been confined to the larger fungi whose fruit bodies are visible and readily obtainable. Most of the work published on synecology up to 1952 has been reviewed (79, 82). Some of this material and additional work have been reviewed in Holland (206) and Austria (200). Recently work in this field has been published by a student in Czechoslovakia (231). However, work of this type has failed to impress other workers in the field of fungus ecology, according to a recent book published in England (150) which indicates that such observations are superficial and compares them with the study of the vascular plants of a meadow collected by scanning a haystack. Having carried out work of this sort himself (87), the writer admits the validity of this criticism, but for comparative surveys of fungus populations of fields and forests, or of forests of various types, he feels that this type of study is an adequate tool. This is especially true if the technique is not equated with apparently similar techniques used for flowering plants, and if it is supplemented by studies of the whole fungus population and by studies of the types suggested by Warcup (459, 460).

POPULATION GROUPS

Soil

As a natural habitat for fungus populations, the soil has probably been studied more intensively than any other habitat. This is partially because of the importance of fungi as crop pathogens, partly because of their importance in the decomposition of plant and animal remains and thus as agents in the beneficial carbon and nitrogen cycles in the soil in relation to crop plant nutrition.

In a broad sense, the organic layers on the surface of mineral soil are included here as part of the soil complex. Such layers include litter, the fermentation layer, duff and humus. Components of these layers include decomposed leaves, twigs, branches, trunks of trees, stumps, dead and discarded parts of fruits and flowers, and other materials. Throughout the process of decomposition, fungi, alone or in cooperation or in antagonism with other organisms, are among the more active members of the population. In addition to fungi, of course, are bacteria, protozoans, numerous invertebrates and some burrowing vertebrates. In ways to be mentioned below, the fungi may secrete antibiotics or toxins which eliminate competitors and in some instances may in turn be eliminated.

Depending on the parent material and the plant cover of a wild soil, the soil reaction may be acid or alkaline in forest, meadow or prairie. This may be changed as the vegetation cover changes or as the soil is put to different crop uses when recovered from its primitive condition by man. When such changes occur, the fungal population changes. The fungal population may be different for a forest, a meadow or a prairie (87, 121, 156, 482), and as the plant cover changes in any one location, the associated fungi will tend to change (156). The fungi of litter are not those of woody materials. Fruits of nut trees, pine cones and other fruit-parts harbor different fungal populations than do decaying wood. While woody materials usually become decomposed by the same general group of organisms, certain species of fungi are found more frequently on twigs and branches than on stumps and rotting logs. The primary rots and decays of logs on the ground, stumps and snags are usually the same as those of the heartwood of standing timber in the same forest or woodland. In France (258) the mold fungi of decaying wood have been studied on a population basis. The heartwood fungi and some of the fungi causing decay of slash have been thoroughly reviewed in the literature of forest pathology, and in some American work and in a number of recent Canadian reports such fungi have been studied intensively in relation to the decays found in a number of species. Such studies treat the tree as a habitat and consider the forest as a composite habitat so that a type of synecological approach is attained.

As a specific habitat for an association of fungi, the litter has not assumed an important place in ecological or other studies. The ability of certain undetermined organisms to decay portions of the litter has been studied (48), and the ability of certain species of litter fungi to use lignin or cellulose has been considered (250). An extension of forest pathology into this field has been made by the study of the life cycle of pleomorphic fungi which attack the leaves of living plants. During the growing season, most species of herbaceous and woody plants are subject to attack by leaf diseases. Usually the asexual stage of the organism fruits in the leaf during this time, but after the leaf falls to the ground and overwinters, one or more asexual stages in addition to the sexual stage may be produced, and the spores resulting from these fruiting types can reinfect the young leaves in spring. This type of study may also be used in considering various phases in the life cycle of heterocyclic rusts (58).

In addition to the populations of larger fungi on leaves and dead wood on the forest floor or in similar habitats on the ground in meadows and prairies, there is a large population of fungi which grow on the totally unrecognizeable plant remains in the fermentation, duff and humus layers under the litter. The populations of those fungi which produce mushroom-like fruit bodies have been studied by techniques described earlier (28, 200). In addition to these, there are small Discomycetes as well as many other fungi mostly, so far as is known, of the "mold" type. Very little interest has been taken in populations of these fungi, although recent work has been reported in attempts to correlate micro-fungi with forest types (442) and in preparing lists of fungi from as yet little studied areas (131). The habitats of these fungi extend to the deeper mineral soil into which the humus and humic acids have penetrated. It has been found that fewer fungi are present as deeper layers of mineral soils are reached (459). In addition, it has been noted that, of the larger fungi, the mycorrhiza-producing species penetrate the deepest into mineral soils.

Observations of fungi in meadows and prairies have largely been confined to surface areas, although some depth studies have been made. The classic treatment of fairy ring fungi was done in the prairies of eastern Colorado (387). It has been shown in France (156) that long after the forest has been removed from an area which has become meadow, fungi associated with forest types continue to produce fruit bodies in the vicinty of places where trees grew with which they were considered to be mycorrhizal. Studies in eastern Washington and adjacent Idaho (87) have shown that there is considerable difference between populations associated with grasslands and with forests.

Because of the economic importance in the life of crop plants of organisms which produce decay in mulches, fertilizers, crop-remains, weed trash, etc., the fungi of farm soils have received a great deal of attention. Ever since the question "Is there a fungus population in the soil" (454) was answered in the affirmative, work has been directed toward answering questions concerning the members of that population, the activity of certain single members (453) and the activity of the population as a whole. The work of many students of this problem has been summarized by an outstanding soil microbiologist. It was shown in early work (151) that such fungi cannot assimilate free nitrogen. Since 1950 the direction of inquiry has changed in England and Canada toward discovering which nutrient portions the fungi were using rather than how many fungi were present to use them.

Gilman's Manual of Soil Fungi (157) lists 756 species reported from soils up to 1956. These include members of the Phycomycetes, Ascomycetes and Fungi Imperfecti. The species are isolated by techniques to be discussed in a later section. Currently, students of field soils are more interested in the activity of the fungus or microbiological populations than in their specific composition. However, some attention is given to species which demonstrate a hazard to crop plants or which compose part of the populations of the rhizoshpere. A study of forest soils from Finland to Hungary made in Hungary (133) is extensive, covering all members of the soil populations and comparing soils of forest types at numerous latitudes throughout Europe.

Occasionally opportunity is afforded to develop a study on the fungus populations of sand dunes. In France (297) and elsewhere, reports have been published listing species from such habitats but not always correlating them with populations observed on more stable soils.

Water

The fungus populations of water have been studied largely for the various types of interesting species to be found therein. To date, little attempt has been made to obtain complete populations from a single body of water by numerous sampling devices with the possible exception of Douglas Lake, Michigan (390). Sampling for various types of species in other areas of intensive Phycomycete research, such as North Carolina and Massachusetts, has not resulted in species lists for difinite bodies of water so far as available literature indicates. Chytrid populations of planktonic algae have been summarized in England (65, 66, 67), and for North America in a book on fresh water Phycomycetes (413). The fungi which occur in fresh water have been sampled by numerous devices, and usually when cultures have developed in which typical members of soil populations appeared they were considered contaminants (182). Such fungus spores as may be present in water samples appear to have reached the samples in one of three ways: from spore-bearing populations of the bottom and immediate shores, from spores precipitated from air-borne populations, and from run-off water added to the stream from adjacent fields and woodlands. While this type of population has not been studied for clean streams, clean portions of a polluted stream in southwestern Ohio (85) have yielded an interesting population, of which some members may be natural to the stream bank and bottom population, and others may be dependent, at least in part, on the pollution load carried by the stream as a source of nutrients. The more heavily polluted portions of a stream appear to contain larger numbers of fewer species than do the adjacent clean portions.

After water is used in the household or in industry, it becomes sewage or industrial waste. As such it forms excellent habitats for fungi, and from the user to the sewage treatment plant the fungus populations which have been observed are luxuriant. From sampling during the process of treatment (84) or from effluents of a particular process (24), it is evident that fungi can grow and reproduce, at times vigorously, in this habitat. Occasionally fungi capable of producing disease in animals and man (94), or in plants (89), are found to grow and multiply in this environment.

For many fungi, water is the medium of life rather than air. Many Phycomycetes cannot exist without water, since their nutrition patterns and their method of dispersal are adjusted to this environment. Though some of these fungi are found in soils (181), they thrive for the most part in bodies of water (75, 219, 413). In some cases it has been demonstrated that elaborate hormonal systems have been built up by such fungi (347). When they develop parasitism on other aquatic plants, drastic changes in the plankton populations may result (64).

To date no attempt has been made, so far as the writer is aware, to develop a quantitative ecological study of water molds in streams, lakes, ponds or other bodies of water. Many difficulties of technique are involved in such study. Regional species lists at the ordinal (75, 219) or the genus level (218) provide some information about distribution and habitat. Additional information is given in annotated lists and discussions (445). One study has attempted to determine something of the distribution of water molds at various depths in different locations in lakes (202). It was found that species varied at different depths within the same lake.

It has also been noted that aquatic Phycomycetes have two types of cilia on their zoospores (105). These may have various functions in aiding the movement of spores through water, but in these fungi their primary use has been phylogenetic both within the fungi as a group and in attempts to relate fungi with other groups such as algae and protozoans. These types of cilia include: those of the true chytrid line which are simple, posterior whip-like cilia with a thin lash or tail piece; those of the *Rhizidiomyces* line with a single anterior tinsel cilium wherein the cilium appears feather-like; and those of the *Olipiodopsis*, *Lagenidium*, *Saprolegnia* and *Pythium* line with both types of cilia, an anterior tinsel cilium and a posterior whip lash cilium.

In addition to the Phycomycetes, a certain group of Hyphomycetes, of which some have ascomycetous perfect stages (344), occur in pools where there is an organic substratum, e.g., decaying leaves, on which to develop. Such fungi are of interest at present chiefly because of their peculiar spores which are thought to be especially adapted to life in an aquatic environment (211, 212, 344).

Recently there has been an increasing interest demonstrated in the fungi which are able to adapt themselves to a marine habitat. Exposed pilings (22), special wooden sampling devices and other substrates, including algal hosts of disease-producing fungi, have been found to furnish nutrients to such fungi. Most of these fungi are members of the Fungi Imperfecti and Ascomycetes. A fungus parasite of ell grass (*Zostera*) has decimated the populations of this plant, and, as a result of unbalancing food chans, this destruction has resulted in drastic alterations in other marine populations. Fungus parasites of oyster eggs (119), crab eggs (95) and yeast populations of shrimps (332) should be mentioned. To date, the study of marine fungi has been only on a sampling basis. No population or sociologic studies have been reported.

Air

While no fungi are known to grow and reproduce in the air, the spore load of certain areas, especially in relation to allergies and epiphytotics, is usually considered a "population." Most fungi with "dry" spores are transported by air, and when spores of a certain species are released to the air in large enough numbers by explosive forces from basidia or asci, or from conidiophores, or by simple release from pressure of numbers or by air currents, they can result in serious infestations of materiel, diseases of crop plants, allergies of man, or even more serious diseases of man and animals.

Various techniques have been developed for the entrapment and study of fungus spores in the air. Most of the techniques rely on the fall of spores from the air by gravity (296). Various media have been developed (440) for the study of colonies of fungi whose spores have fallen onto the agar plates holding the media. Methods of sampling air populations (228) at high elevations from airplanes have been described in Canada. Here plates containing agar or covered with adhesive material are exposed from the plane in definite time periods. In England (199) an automatic volumetric spore trap and in Kansas (313) a slit sampler have been developed which reportedly entrap spores that can be counted or studied with better results than with earlier type samplers. A New Zealand worker (296) has presented results of comparative researches, in which the gravity and impact methods of sampling air populations have been used.

Surveys of fungus spore populations have been carried out in a number of places over the earth's surface. These usually followed an intensive pollen sampling program and sometimes were conducted simultaneously with the pollen surveys. They were usually made in connection with studies of allergenic populations. Among the common genera found by the gravity technique is *Cladospo-*

rium, and its presence in the air over London has been emphasized. In Israel, in addition to a series of annual gravity plate surveys for allerogenic species (230), the spore content of the air of orange groves and packing sheds has been sampled with particular concern for species of importance in the pathology of the shamouti orange (24). Several surveys of mold spore populations of the air in New Zealand have been prepared separately or in conjunction with studies of pollen incidence. Two such studies (120, 244) may be cited in addition to the one mentioned above. These are of interest not only for the species lists presented, which are similar to those of other areas, but also for the differences in the results obtained by the methods used. In Canada one report (389) lists an aquatic Phycomycete spore as having been found in gravity collecting plates exposed in Toronto.

Canadian workers have been intensively interested in the incidence of fungus spores in the air over seemingly unlikely areas (315, 316). Most of this sampling has been carried out on routine missions by Royal Canadian Air Force planes or in special planes obtained for the study. Plates have been exposed over the Atlantic Ocean and over large areas of the Canadian Arctic regions in an effort to learn something of the distribution of fungus spores in air masses. Fungi of most importance in such studies include rusts and smuts, and others capable of causing damage to crops vital to Canadian and United States farmers. An early report on the fungi of the upper air in the United States was published from work carried on in Tennessee (487).

The relation of large numbers of spores in the air to the incidence of epiphytotics of cereal grasses has received attention in Minnesota (416) and Kansas (314). The techniques of sampling rust and smut spore populations in areas where wheat is a major crop are important to the forecasting of crop disease control measures.

Fungal populations of the air are of great concern to man as possible sources of allergies resulting in asthma or vasomotor rhinitis. One of the more important centers of research for this type of study in the United States has been at the University of Texas (298). English workers (279, 280) have studied this problem from the point of view of the quantitative aspects of allergy to house dust in which the spores in house dusts of various types have been analyzed in relation to sensitization risks from the inhalation of fungal spores. In the air of houses infected with dry rot fungus, spores can be found in large numbers during the time of their active production, especially in the cellar and lower floors. This is important not only in the spread of the fungus itself but also as a possible source of allerogenic sensitization.

In most publications dealing with allerogenic fungi and fungi in the air, the authors are content with presenting lists of species found, together with statements concerning their abundance or rarity. Such work relies on texts based on general monographic studies, regional biotas or Saccardoan compilations. One departure has been made in Argentina where a manual (493) published in Spanish is devoted to the listing and description of the fungi associated with allerogenic studies.

Deterioration of Commodities

Practically everything man uses for shelter, nourishment and communication is subject to deterioration by fungi. It has been suggested (467) that in the study of some of these commodities and their contaminants, a new concept of association be applied to the study of fungi. For example, in molding of butter or leather there may be succession of fungi, one species overlapping another as a particular nutrient is exhausted or as competition becomes more aggressive. The idea expressed recently (150) that a fungus succession proceeds on a substrate from a fungus able to use simple compounds to a fungus able to use complex compounds to finally a complete depletion of the substrate with nothing left for a fungus to use, can apply readily to commodities used by man if the succession is permitted to run its normal course. However, in most of man's activities any decaying matter is usually destroyed before the succession is complete. Usually, today, attempts are made to prevent the molding of clothing, foodstuffs, housing materials, paper, insulation and other substances in use by man. If molding results from a particular type of storage, the condition is usually corrected; if it results from methods of handling between production and market, the methods are modified. It is rare that food poisoning results from the eating of moldy bread or other food stuffs in this day of precautionary measures against infection or deterioration.

The most elaborate precautions against natural contamination of manufactured commodities are those taken in pharmaceutical industries where unwanted strains of organisms could cause irreparable damage to the final product. In the preparation of foodstuffs for market the use of mold inhibitors in bread and of relatively aseptic techniques in other preparations tends to reduce the incidence of natural contamination or the development of natural populations in such products. It is no longer a common event for a batch of rye flour to be contaminated with powdered ergot sclerotium which causes the disorder known as St. Anthony's Fire or ergotism.

Other products are less fortunate. Cloth from cotton fibers is still subject to molding and mildewing (399) without superficial chemical or physical treatment. The cellulolytic activity of various fungi (356, 357, 455, 470) has been studied intensively. This work has been carried over to degradation of woolen fabrics (472). At least one of these fungi, *Memnoniella echinata*, has been studied intensively (471), and it has been shown (498) that spores of this fungus and of *Stachyhotrys atra*, another cellulolytic fungus, may be produced on the same mycelium. Seeds of crop plants are consistent carriers of molds, and when these are stored improperly the seed can be rendered useless by the activity of many kinds of fungi. Untreated seeds are also the carriers of spores or mycelium which can reinfect the new crop. Lumber, when stored improperly or when cut from infected trees, is subject to a number of fungus disorders. White pocket rot and other sapwood and heartwood decays develop if the lumber is not properly dried. Various kinds of stain fungi make sapwood for window frames, sills and other uses unsightly. The natural contaminants of poles, posts and other wood products which touch the ground, as well as local populations of fungi, can actively destroy the wood in relatively brief periods unless it is treated. A number of types of fungi can attack wood pulp during storage, causing discoloration and deterioration. In the processing of pulp and paper products a number of types of fungi can develop which are difficult to control, since some of the ultimate product comes in intimate contact with foods and control agents usually include chemicals potentially poisonous to man.

Dung and Sewage

The fungi which inhabit dung comprise a special group made up of members of several classes of fungi. In most cases the spores of such fungi must be ingested by an animal. During the course of passage through the digestive tract they are exposed to the activity of gastric juices which hasten their germinability. Upon passage from the animal they germinate, develop rapidly in the dung, and produce fruiting bodies, on or in which spores are produced. These spores may be liberated in such a way that they become attached to adjacent or nearby herbage, to be ingested, by another grazing animal to continue the cycle.

To date, attempts which have been made to study the succession of development of these fungi are weak except the little attention which is given to the matter in certain laboratory exercises. The greatest interest has been shown in their morphology (63), the peculiarity of their fruiting structures (48, 56), and the germinability of their spores in artificial nutrients in the presence of special growth-promoting substances found in manure, artificial media in which other fungi have grown, and developed synthetically in the chemical laboratory (335).

If sewage is considered a type of dung, a recent listing of the fungi found in this habitat should be mentioned (90). Here the fungi were considered in relation to their ability to exist in the habitat. Coprophilous fungi were considered as organisms restricted to sewage and dung habitats. Fungi and other organisms restricted to this habitat were called "lymabiont"; those which preferred this habitat but could live elsewhere were "lymaphiles"; those which preferred other habitats but could live in the presence of sewage and dung were "lymaxenes"; while those which could not survive in such habitats were "lymaphobes." Species were assigned to one or another of these categories, on the basis of their occurrence in the habitat, the number of colonies isolated from one or another type of sample in sewage treatment plants or polluted waters, and the number of colonies isolated from clean areas in contrast with polluted areas.

Burned Areas

The ability of fungi to grow on burned areas or areas sterilized by intense heat has been recognized for some time. Such fungi have been called "pyrophilous" (384). More recently this term has been redefined (299) on the basis of a study carried out on fungi, Bryophytes and higher plants growing on areas burned over by forest or camp fires in the Austrian Tyrol. Four types of response to such habitats were found, and organisms giving such responses were defined as "anthracobiont," "anthracophilous," "anthracoxenous" or "anthracophobous." The first two categories included pyrophilous fungi. A number of anthracobiont fungi were found. These could grow only on burned areas, and this restriction was attributed to certain unexplained changes in available nitrogen. Most of the mosses, liverworts and vascular plants could and do pass the initial stages of growth on burned areas and continue to develop on the area after the influence of the fires has been eliminated.

Living Plants

The literature of plant pathology (189) is full of data and information concerning plant disease fungi, both obligate and facultative. A somewhat different approach to plant disease has been presented from Switzerland in both German (152) and English (153) editions. Here the ability of the plant to accept or withstand infection is considered important.

A few examples will suffice to indicate the breadth of activity required in the study of fungi in relation to the diseases they cause in higher crop and wild plants. In monographic treatments of various groups of pathogenic fungi, much information can be drawn concerning life cycles, host plants, geographic distribution and cross-inoculation studies. Such monographic treatments as those dealing with rusts (13), smuts (136) and the Plasmodiophorales (221) give comprehensive information concerning the species they treat. Certain generic monographs present different types of approach to the various problems presented by fungus genera to the plant pathologist. A study of the genus *Pythium* (289) presents, in addition to morphological characterizations, the host ranges and geographic distribution of the species in this widespread and important genus. The genus *Synchytrium* (224) has presented problems in method of treatment. One worker based his classification on the reaction of the host tissues and the galls which were produced. More recent workers adopt a more natural method of approach. In studying the diseases caused by members of the genus *Septoria* on grasses (415), the possibility of one species causing a disease on many related or unrelated species of grasses was explored extensively through field collections and greenhouse cross inoculation studies. In studying the genus *Mycosphaerella* (14) it was found that a large number of species had been erected unnecessarily on the basis of the idea that one species of fungus is confined to one species of host plant. An example of the type of study carried out in relation to the effect of one fungus species on its host plant is the study produced (10) on the disastrous effects of the *Endothia parasitica* infection of American chestnut.

Root rots and root-disease fungi have been studied intensively. Reviews of the various aspects of this work have appeared and need only be mentioned here. The relation of soil fungi to root infection was discussed in an early review (59). Root rots of cereals (391, 392) form one of the more important groups of this general type of disease, but root rots of non-cereal crops (28) and of deciduous fruit trees (96) are also important to these groups of crop plants. Much of the current knowledge of these types of disease-producing fungi has been summarized in a recent text from England (150). Here it is thought that the more primitive types of root-disease fungi are those which invade juvenile or senescent root tissues that have not yet gained or have lost the ability to resist such attack. As the pathogenicity of fungi evolves, it progresses through those root-disease fungi which attack only vascular tissues producing wilts, those fungi which cause hypertrophy of host tissue without killing the host, finally to those fungi which live in harmony with their host, causing minimum distortion of host tissues but apparently unable to live without the host plant, as in certain types of endotrophic mycorrhizae.

Specialized studies dealing with various problems of plant pathology, such as the cytology (362, 363) and physiology (50) of host-parasite relations, and physiologic specialization of parasitic fungi (353, 354), have been adequately reviewed. General host-parasite relations have been discussed more recently (2). Because of their great importance in relation to loss of crop by disease incidence, the rusts (217) and the smuts (74, 204) have been studied intensively in relation to physiologic specialization, hybridization and genetics. In attempting to control certain diseases by breeding disease resistance into a host, it is also important to learn how rapidly a pathogen can mutate to a disease-producing organism on hosts resistant to earlier strains. Vegetable crops, too, may be subject to breeding for disease resistance (458). Progress in various types of breeding experiments for disease resistance in wheat, oats, barley and flax (17), and in breeding for resistance to *Verticillium* and *Fusarium* wilts (388), has been reviewed.

Environment is very important in the development of epiphytotics caused by fungi. A crop may not be economically introduced to a new area if the climatic conditions are conducive to the development of certain types of disease fungi. Various phases of the relation of environment to cereal smuts have been reviewed (436). Maximum, minimum and optimum temperatures in which many disease-causing fungi are known to grow have been summarized in a recent book published in Tokyo (441). The relation of weather to the fungus diseases of plants has been critically reviewed in England (138, 139).

Flood-fallowing of land in an attempt to control the Panama disease of bananas caused by *Fusarium oxysporum* var. *cubense* has received much attention from workers in Honduras. To understand the problem in the field, the colonization of banana roots by the pathogen and other soil fungi has been studied (433). The effect of soil moisture (428, 429) on the pathogen and related species of *Fusarium* has been examined in various laboratory tests. Techniques of flood-fallowing and the effect of various factors in the altered environment (430, 432), including that of the oxygen supply (431), have been described. While flood-fallowing has achieved a certain amount of control, a residual inoculum appears to remain in the soil or in dead and decaying plant parts, so that infection of a new crop may take place.

The presence of fungi in seed has been of concern to plant pathologists, for various types of disease may be carried in this way and different types of fungal infection are initiated through seed. Types, methods and reasons for seed treatment have been reviewed (241). The types of fungi found in association with seeds have been monographed in Canada, starting with a paper on *Stemphyllium* (170). The significance of seed-borne fungi was of importance to the president of the British Mycological Society, as indicated by his 1949 presidential address (304). A number of species of *Fusarium* has been found in close association with cereal seed in Canada (163).

Sooty molds, which occur more commonly in subtropical and tropical regions, appear to be leaf parasites to the casual observer. Species similar to those in the southeastern and southwestern United States have been studied in Australia (142), and it has been shown that they are more closely associated with insect parasites, such as aphids, than with the leaf tissues on which they appear to be found.

Control of plant disease has been discussed for many diseases in the textbooks of plant pathology and in the literature of the control of each disease. Various control methods, which are departures from usual methods, have been described (424, 425). Some workers have approached plant disease control from the point of view of chemical control agents. The chemotherapy of plant disease has been summarized (427). Various chemical elements are required in very small amounts by most living organisms, but some can be used in plant disease control when applied in large or toxic amounts. The nature of the fungicidal action of copper and sulphur has been considered extensively (281). The use of fungicides for control of disease in forest and shade trees, and for control of fungal activity in forest products has been discussed (180). The definitive text on the action of fungicides was written in Connecticut (205).

The occurrence of plant disease in the United States is subject to fluctuations according to climatic conditions, soil variation, crop rotation and other factors. These factors and their effects on plant disease fluctuation have received much attention (426). Plant quarantine is designed to prevent the introduction of plant disease into the United States. The methods of operation, their successes and failures have been described (282). Plant diseases which have not yet been introduced into the United States and problems associated with preventing their introduction have been adequately covered (176).

The fact that plant-disease control can become the object of legislation has been pointed up (148) in an extensive review of the laws man has enacted to aid in the control of black-stem rust of wheat by removal of barberry, the control of whitepine blister rust by removal of currants and gooseberries, and the control of apple rust by removal of cedar trees. Methods and results of forecasting the occurrence and incidence of plant diseases have been reviewed (295).

In the field of forest pathology the fungi causing diseases of forest trees and the fungi associated with staining or deterioration of forest products have been treated extensively in several texts and many separated reports and papers. Two texts published in the United States (23, 43) and one in England (70) cover the field extensively. The occurrence and type of heart rots in living trees has been reviewed recently (452). In studying the fungi which cause decay in forest trees, the ability of the observer to identify the causal fungus is important. Keys to the identification of cultures of fungi obtained from heart and sap rot specimens (309) have been published. In the further removal of dead wood from the forest, other wood-decay fungi such as molds are operative. The studies of a worker in France (271) help to show the quantitative and qualitative occurrence of various mold fungi in decaying woods. The content of nitrogen in sound and decayed conifer wood has been related to loss in weight during decay (200). The decay caused by *Polyporus versicolor* is speeded up in the presence of nitrogen. It was found in Maine (196) that as wood decays the potential heating values decrease. Many fungi cause stain reactions in woods used for building, crating and other purposes, resulting in unsightliness. Some of the species which cause such stain reaction have been discussed (106) as a result of studies on cultures of species from the southeastern United States. Control of the growth of fungi in wood products during seasoning is an important factor in developing a merchantable product. Problems of control of such fungi during the seasoning have received adequate attention in a recent review (449). Extensive researches on the decay produced by the dry-rot fungus have been carried out in Germany (130).

The effect of air currents on the transportation of air-borne spores of fungi, especially those which cause plant disease, is important in the etiology of plant disease. Study of the sporal populations of the air (416) yields much information for plant pathologists concerning the origin and distribution of various types of plant disease. In confined areas an abundantly sporulating fungus can fill the air with its spores. In England the spore content of the air in buildings infected with the dry-rot fungus, *Merulius lacrymans*, has been found to be high, a potential source of allerogenic reactions in the persons associated with such habitats.

In the development of the pulp, paper and rayon industries, fungi have found a different medium for growth. In many cases pulping processes are carried on seasonally and the raw materials are stored until the manufacturing plant can use the excess supplies. During the storage process, if conditions are right, fungi causing stains in the pulp can develop relatively rapidly, increasing costs and bleaching problems. Most of these fungi can cause deterioration of the cellulose; others cannot. In some cases the stains are caused by a select group of soil fungi whose spores contaminate the air of the plant; in other cases the usual fungi causing bluing and other stain reactions in finished lumber can cause the troubles. Control of humidities, moisture and temperature of storage bins has been recommended for protection against such loss-producing fungi. Much research on this subject has been carried on in Sweden (36, 283) and Italy (159).

As a result of information gathered on plant disease fungi in a number of areas in the world, from the northern temperate regions to desert and tropical regions, an idea has been developed (42) in which an attempt is made to apply synecological techniques to the study of plant disease fungi. The author's examples are mostly obligate parasites and rather than relate these to specific hosts or host crops, he relates them to general areas over which the weather is generally uniform. For instance, he finds that powdery mildews are more prevalent in areas approaching desert conditions than in tropical areas, while rusts present a reversal of this pattern.

Living Animals

INVERTEBRATES

Insects and spiders are subject to fungus diseases of various types. The Entomophthorales includes several fungi which are parasitic on numerous species of insects and these eventually become masses of fungus tissue (421). Members of the Laboulbeniales (386) are entirely parasitic on insects. Members of this order are usually attached to one or another chitinous part of the outer skeleton. Members of the Cordyciptaceae sclerotize insect bodies and puppae, from which elongate stalks producing clusters of perithecia are produced. It has been suggested (132) that, because of their susceptibility to certain diseases, insects causing disease of plants may be controlled by the introduction of fungus epizootics of these insects. Insects and spiders are also prey to a number of hyphomycetous fungi (269). Except as the host insect is an incidental member of the biota of one or another location, it is difficult to place such fungi among others in a given population.

The Eccrinales is an order including organisms considered by some to be fungi, not definitely placed by others (274, 243). This order embraces organisms parasitic in the hind gut and other hind parts of worms. Recent monographic treatments and notes have come from France and from Illinois.

VERTEBRATES AND MAN

Fungi which cause diseases of fish have been known for a long time. A taxonomic study including such species (75) has been published in North Carolina. These fungi form a white fuzzy mass on the fish which may be parasitized, or the fungus may be a secondary invader in diseased tissue or in wounds. A recent study from Germany (358) indicates that fish may be subject to systemic diseases caused by fungi. Material thought to be similar to *Alternaria, Cladosporium* and two other mold fungi has been obtained from tissues of fish in fresh and salt waters in northern Europe.

One of the more interesting phenomena associated with fungi pathogenic on man and higher animals, especially those causing systemic mycoses, is their ability to develop as yeasts in the body and at body temperatures in the presence of special media or cultural conditions, and their ability to develop as molds at room temperature on standard mold culture media. *Histoplasma capsulatum, Blastomyces dermatidis, Coccidioides immitis* and *Candida albicans* are able to develop in this way. The phenomenon is referred to as "dimorphism" in the literature (378), and its occurrence in yeasts, *Candida* for instance, is discussed fully in a recent review. Data concerning this phenomenon as well as other physiological properties of pathogenic fungi have been considered extensively in a text on the subject (306). Intensive studies on the physiological bases and experimental control of morphogenesis in animal disease fungi have been carried on at Rutgers University (307, 308). One of the basic controls of the phenomenon is thought to be enzymatic. When the enzymes controlling cell division and cell elongation function normally, a mycelial type of growth is produced. Apparently at higher temperatures and under certain conditions of nutrition present in blood agar or other media on which morphogenesis occurs, the enzyme for cell elongation is inhibited and a budding type of cell division producing short oval single cells occurs.

The diseases of animals caused by fungi are best known in relation to man. Veterinary mycology is at present hardly more than an off-shoot of medical mycology. A recent text on animal pathogens (284) emphasizes the importance of bacteria and viruses but devotes only 18 of its 850 pages to fungus diseases. During and since the Second War the science of medical mycology has developed from a ponderous pre-war text (115), in which many hundreds of separate fungus cultures were considered etiologic agents of disease, to simplified post-war texts (77), in which many strains and multiple species are reduced to synonymy, decreasing the number of earlier recognized disease-causing fungus species to a relatively small number. Handbooks and reviews (77, 124, 395) discuss the broad phases of the subject, while more restrictive treatments (390) indicate the approaches possible when studying the various phases of particular diseases.

Most of the fungi causing important fungus diseases of man and animals have been isolated from soils. This indicates to some workers (3, 125, 155) that the soil is a natural reservoir of disease agents. In some cases the air one breathes is definitely the source of infection, especially when it contains large numbers of spores of the etiologic agent. In other instances the air borne nature of the infectious agent is still suspected. Study of such fungi and of the contaminants which may be associated with them has resulted in the publication in Argentina of a unique manual (494). In some cases the body population contains cells of organisms capable of causing disease, and when the balance between the different members of the population is upset by therapeutic agents or other means, the cells present are reported to be able to produce the disease.

Whether or not these fungi play an important role as members of soil fungus populations is as yet undetermined. They are found only with special techniques, or, when located with the usual soil-sampling techniques, their importance is minimized or their presence is unrecognized, since many of them take longer to fruit, some may be considered sterile mycelium, some may be unknown or confused with other species, and some are of only sporadic occurrence.

The fungus *Histoplasma capsulatum* has been studied intensively in relation to its natural environment and to the disease, histoplasmosis, which it causes in man. The disease has been thoroughly reviewed (390, 485), but in the present survey it might be well to mention some of the types of study carried out on this fungus in relation to its environment. It is only within the last ten years that we have learned (125) how to obtain this fungus from its natural environment. The technique used at first has been modified and expanded so that at present a revision (238) has been described. That the technique is not too effective is shown by the fact that even after shaking or beating the soil sample suspected of carrying spores, the spores and their carrying mycelium are so tightly adherent to the soil that only 10% recovery is effected. To be sure that the strain of the fungus being sought is pathogenic, it is routine now to inject suspensions of the suspected sample into four or more mice (236), with the added precaution of using antibiotics, and to permit the fungus to incubate in the mouse for as much as four weeks. Following the incubation period the mouse is sacrificed and portions of its liver and spleen are streaked on Sabouraud agar usually made with neopeptone. After such slants have been incubated under room conditions for two or more weeks, the fungus is considered to be present in the sampled substratum in a pathogenic form when it develops on the agar. In addition to the mouse technique, the membrane filter (162) has been used, but with the method suggested the spore is collapsed, is not viable, and pathogenicity cannot be proved. The spores of this fungus will remain viable and pathogenic after 500-600 days storage in waters of different types (93, 364). Spores of this fungus have been studied in reference to size, since large spores may not be effectively inhaled. In the strains studied, most of the spores were small, although large ones were present and there were both smooth and tuberculate spores. Various soil studies have been carried on with relation to this fungus. In one type, soil samples are surveyed (237) for presence of the fungus; again, an attempt is made to correlate the more common soil types (497) in which the fungus is found with the potential distribution of it.

The Environmental Complex

That the environment in which a fungus grows is exceedingly complex has been demonstrated in a series of proposed outlines to be used in the study of ecological life histories of fungi (81). This is also indicated by the extent of numerous researches to indicate one or more phases of the life cycle of fungi being studied specifically as plant or forest-tree pathogens, as saprobes in the deterioration of various types of materiel, and as organisms accountable for the reduction of dead organic matter to simple compounds or elements in forms assimilable by the plants or other organisms filling the ecological niche once inhabited by the decaying organism.

In the study of the ecology of higher plants a number of concepts have arisen which may, in the development of a nearer complete picture of the ecological life history of fungus species, become adopted by the mycologist. One such study presents a functional, factorial approach to the study of plant ecology (270). The functional equation used was based on a soil development equation and includes those factors considered paramount in the development of the vegetation of an area. Components of the equation include variations of five basic functions and sequences. Such data can be applied to the development of fungal populations of one type or another.

In a further extension of the environmental complex to include all factors operative on the organism (31), it has been shown that a very wide range of habitat and environmental influences is operative during the development of an individual, a species, a community or a population of organisms. Such factors are operative on all organisms in the population complex, and this complex is only one of the factors in the environmental complex.

The relationships between fungi in respect to mutual pathogenicity, i.e., symbiosis, have been critically reviewed (108). It was found that some fungi are parasitic on others to the extent that one species may be restricted to one strain of another species or may have a wide range of selectivity for species within an order. Pathogenicity of one fungus on another may be expressed in reduction in size of a fruit body or in elimination of the ability to sporulate by the host in favor of the parasite. The whole question of the relation of one fungus to another was developed on the basis of the MacDougall pattern of symbiotic relationships.

Yeasts

As a group, yeasts have received little attention ecologically. Since 1940 several books and reviews have been written concerning their classification and biology. With intensive study, information about the ecology of yeasts can be gathered from the various topics which have been presented in this way. In France the sexuality, development cycle and phylogeny of yeasts have received exhaustive attention (171), while in California many phases of the biology of these organisms have been studied (301). The genetics and cytology of the yeast cell have occupied workers in St. Louis (253). The taxonomy, biology and distribution of *Hansenula* have occupied workers in Peoria (477), and the most comprehensive manual of taxonomy of perfect and imperfect yeasts has come from Holland (260). A comprehensive volume on the biology of the yeasts from England (213) indicates that little is known about the ecology of them, especially on a quantitative basis and in relation to other organisms in the same environment and habitat.

In the last ten years studies have indicated that yeasts occur in a number of locations throughout the natural scene. Some of these studies include the following types of information. Yeasts were found in increasing numbers as the fleshy fungus fruiting body matured and started to decompose (9). Different mushrooms harbor different species of yeasts. In France, yeasts were detected (40) in liquors derived from plant materials used for tanning. In studies on the surface populations of shrimp obtained in the Gulf of Mexico off Texas (332), yeasts were in considerable numbers. During the ripening of apples in Quebec yeast populations changed (483) so that low numbers occurred in August, high numbers in October, and different species prospered in the changes of seasons. No fermenting species were common. The human body has been found (78, 403) to be a habitat for yeasts. *Lipomyces starkeyi* was commonly present in many areas of the skin, and populations were found to develop within three hours of bathing. The pigmented genus *Rhodotorula* gave considerable taxonomic trouble to this group of workers. A system has been developed in Holland whereby five carbohydrates, two nitrogen sources and other tests are employed to separate species. This system has revealed that at least five species of *Rhodotorula* occur on the human body. However, if a larger number and variety of carbohydrate sources were used, there was not special pattern of utilization and it was concluded that the genus is monotypic, consisting only of *Rhodotorula glutinis* which is made up of a number of strains, each able to use varying types of carbohydrates.

In New Zealand (112) a search has been made for yeasts in soil samples, especially for those which might be of interest as human pathogens. In Canada yeasts have been isolated from soils by various techniques. To reduce the numbers of bacteria and other fungi, the workers (294) used acid, rose bengal and oxgall. Of these the last was perferred.

In the Yosemite region of California an intensive study has been completed on the occurrence of yeasts in the same habitats as species of the fruit-fly *Drosophila* (69, 113, 333). A number of species have been found in the alimentary canal of the flies and of their maggots, indicating that the yeasts may form part of the food supplies of these insects. The natural breeding sites of the flies have been studied intensively for their yeast populations. Factors of microclimate of the habitats and the nutrient supplies were considered. Finally in this series of studies attention was given to the differential attraction of species of the fruit-fly to various species of yeasts.

Work done in St. Louis indicated (251) that if vegetative yeast cells can be induced to store excess materials of fats and carbohydrates, they can be induced to become dormant. Conditions for reactivation such as starvation were also discussed. The same workers (252) analysed the mechanism of budding in yeast cells based on structural considerations. Various explanations for the dimorphism phenomenon in yeasts have been considered (378) in a recent review.

NUTRITIONAL GROUPS OF SOIL FUNGI

The fact that numerous groups of soil fungi can be based on nutritional requirements (257, 16) indicates that such fungi form a large and heterogeneous assemblage. Such groupings can go beyond the soil as such into the litter, dead wood, and almost any material in or on which fungi grow. At present it is more convenient to consider these grouping under soil fungi, since this is the substratum in which they have been most intensively studied (150, 16).

The simplest of these groups, as to carbon requirements, includes the most widespread and abundant in numbers of species and colonies encountered. This has been referred to as the "saprophytic sugar fungi." The species of this group use simple sugars, especially hexoses, and other simple carbohydrates.

Cellulose-decomposing fungi form a large group (399) capable of reducing the cellulose molecule to simpler carbohydrates, thus reacting with a substance which forms the basis of many manufactured textiles in common use throughout the world, as military supplies, clothing, tentage and rope. A large amount of work has been done in an effort to prevent the activities of such fungi, at least on man-made materials.

A number of substances in nature are composed of pectin and cutin or pectin-like and cutin-like materials. Leaf and stem surfaces are covered with a layer of such materials which bind cells together and may include cutin or pectin. Apples and citrus fruits include pectin substances together with cutins in their surface layers. In dew-retting of flax (480), pectin-decomposing fungi play an important role. Techniques for the study of such organisms (479) and the distribution of such substances in nature (478) have been described recently. Such materials are considered (405) to be prevalent in litter, and the organisms which are primary invaders of litter are thought to be those capable of using cutin, for instance, *Pullularia pullulans.* This fungus can use other materials of this general type in nature. In a study of the microbiological populations of buds (226) this was one of the more important fungi in such populations. This fungus is also very important in the deterioration of paints and plastic surfaces in Florida (361) and elsewhere.

Fifteen to 25 percent of woody tissue is made up of a cementing substance called "lignin." This material does not lend itself to ready analysis so that its chemistry is still doubtful, although a large text (45) on the subject presents a number of hypotheses concerning its origin, development, possible constituents and degradation. A large number of wood decay fungi (91) are known to use lignin slowly in nature, but few fungi and no bacteria are known to use it in pure culture in the laboratory, except very slowly over periods of months. In Sweden it has been found that many soil Hymenomycetes use the lignin present in litter materials (250). A basic study method on the use of lignin and other materials in the soil has been developed (48) in West Virginia. Here litter materials are incubated over long periods of time with suspensions of forest floor materials, and rates of decomposition are determined during the exposure period. Certain soil fungi (193) are able to utilize some of the building blocks suspected of eventually forming lignin, such as para-hydroxybenzaldehyde, ferulic acid, syringaldehyde and vanillin.

Keratin is a common substance in many soils, especially in the vicinity of cemeteries, in soils in which animal remains are included, and in other places. A special group of fungi is more or less closely restricted to this substance as a nutrient substrate (3, 223). It is possible that fungi growing on many types of proteinacious materials should be placed here, and those fungi like *Onygena* which grow on hooves, feathers, owl pellets and other substrates involving skin and similar habitats also belong here. The fungus *Keratinomyces* which strongly resembles the *Microsporum*-type of ringworm fungus, isolated from soils in Belgium (446) and the United States, is a member of this group.

Predaceous fungi are usually considered a group with specialized nutrition. Their habitat, aside from the soil surface and litter in which they are usually found, is the bodies of protozoans which they entrap with special appendages and then proceed to devour. Such fungi are among the Phycomycetes, Fungi Imperfecti and possibly the Basidiomycetes, since species are known which produce clamp connections. Entrapment mechanisms may be of two types: a lasso is formed by one type and a nematode swimming through it is caught by the enlargement of the cells forming the lasso; special appendages may trap amoeboid organisms by secreting a sticky substance which holds the amoeba while the fungus mycelium penetrates its body and consumes its substance (117).

The rhizosphere is a highly specialized habitat in the soil. Here, exudates from root cells and sloughings of root tissues form a nutrient or toxic complex, to which many bacteria and some fungi are constantly exposed. Summaries of the biology of this habitat have been published from Canada (225) and England (150). Work in England (463) with plant succession on sand dunes has demonstrated the existence of a succession of microorganisms associated with the rhizospheres of the various successive groups of colonizing plants.

The fungi which form mycorrhizae with higher plants constitute another group in a special nutritional environment. In addition to utilizing carbohydrates and possibly lignins in the soil, these fungi from mycorrhizae with roots in the soil. In a recent book on mycotrophy (227) these structures are described, and they are depicted in detail in a book published in Germany early in 1941 on the anatomy of fungi (261). Recent work in England (177, 178) and in Sweden (37) has given modern views regarding the function and types of mycorrhizal development. Some Hymenomycetes which form mycorrhizae with *Pinus strobus* have been identified and proved as mycorrhiza formers (184). In a recent volume (150) on root-infecting fungi, mycorrhiza-forming fungi are considered to be parasitic on their host plant. Some of these are weak parasites which can be obtained in culture; others, difficult to culture, are considered obligate parasites. The weak parasite can exist without the plant with which it forms a union and it can be brought into pure culture. The obligate parasite can be brought into pure culture with great difficulty, if at all, and in nature appears to require the presence of the plant with which it makes its mycorrhizal union. The weak pathogen produces an ectotrophic mycorrhiza in which the fungus tissue is extra cellular to the root tissue, the endotrophic mycorrhiza is formed by the obligate parasite whose hyphae penetrate the root cells, although it is reported (261) that the host plant produces defensive mechanisms without arresting the natural flow of nutrients between the two organisms.

HABITAT GROUPS OF SOIL FUNGI

There are four principal types of soil fungi (150): *a*) those living saprobically in the soil where they develop only on dead organic matter; *b*) weak plant pathogens living in the soil, capable of using soil organic matter but developing as occasion arises on young roots or senescent roots; *c*)ecologically obligate plant pathogens, including those species which can parasitize the actively growing roots of plants, produce diseases like vascular wilts, and, following the death of the host, utilize its tissues as nutrients until their activity is arrested by more actively competitive sapropic fungi; and *d*) obligate plant parasites such as endotrophic mycorrhizae, rusts, powdery and downy mildews which apparently require living plant materials for their substrates.

RHIZOMORPHS

Certain fungi, during their growth processes, develop accumulations of mycelia which permit the actively growing and assimilating mycelium to grow where the best nutrients are available but to fruit in much different areas where the best fruiting conditions occur. Such structures are termed "rhizomorphs." In structure they range from simple aggregations of few to many hyphae elongating together in one direction, to complex affairs whose growing points superficially resemble a meristematic tissue and whose internal make-up presents a picture of fused hyphae with spiral and scalariform parts which remind one of water-conducting elements in vascular plants. These structures are best developed in *Armillaria mellea, Serpula lacrimans* var. *lacrimans* and *Meruliporia incrassata.* Other fungi have also developed rhizomorphs but these are of more primitive nature. A summary description of these structures has been presented in a text on fungal anatomy (261), and recent papers have developed concepts concerning the ability of fungi to use such structures to colonize new areas of nutrient supply (149).

SCLEROTIA

One type of response to an unfavorable habitat is the development of small to large agglomerations of cells, with or without structure, which have been referred to as "sclerotia." Several types of such bodies have been described in the fungal anatomy referred to above (261). Chlamydospores and *Papulospora*-type cell aggregations may be primitive developments in the pathway toward sclerotium formation. In some organisms, *Aspergillus* and *Eurotium* for example, the sclerotium may be a predecessor or a replacement of the perithecium (439). In other fungi, such as the Sclerotiniaceae, the fruiting bodies may arise from sclerotia which are considered as stromata (469) and which serve as overwintering storage organs. In *Cordyceps, Claviceps,* the Sclerotiniaceae, *Poria cocos* and other fungi there are small to large sclerotia of varying types and functions. The small sclerotia of *Typhula* are quite characteristic and have been described in detail (359).

NUTRITIONAL REQUIREMENTS

General

The filamentous fungi are organisms with restricted or elaborate hyphal systems whose cells are formed of either cellulose (rarely) or chitin, the latter usually referred to as "fungus chitin" (38, 261). They are aerobic, only rarely anaerobic, require carbon, hydrogen, nitrogen, the macro- and all the micro-elements to varying degrees. They are set apart from other organisms (369) in that they do not ingest food as animals do, nor do they produce their own types of photosynthetic pigments, but they secrete enzymes into their environment which break down bulk materials into substances readily assimilable by the fungus cells. Preferred habitats are acidic, but they will grow in pH levels higher than neutral, and some species have been known to grow at pH 11. Many species are able to produce their own vitamin supplies but others require an outside source of vitamins for growth. A plea has been made for the integration of research on nutrition and metabolism in microorganisms (489). Too much work has been done on either one or the other aspect of physiology without attempts at correlation, which could be useful.

Studies of general or specific nutrient requirements have been made on specific fungi or groups of species. Some of these studies will be mentioned here, although most of the studies which have been made have been summarized in general reviews and texts. The general subject of the growth of fungi in nutrient solutions has been summarized in two reviews (419, 420). In studying the growth of wood decay fungi, one technique was developed in which submerged growth in liquid synthetic media was used with success (216). Here the correct combination of nutrient materials can spell the difference between success and failure. Four unrelated species of cellulose-decomposing fungi (396) were studied in determining the optimum environmental and nutrient requirements of such fungi. It has been found that nutrient factors and vitamin supplies may be critical (239) in promoting pycnidia formation in some species of Sphaeropsidales. In other cases no factors have yet been revealed which will promote the formation of pycnidia or even spores in sterile mycelia isolated from many habitats. Many species of fungi in such diverse groups as the Basidiomycetes (365), the Fungi Imperfecti (367) and the Dermatophytes (366) have been studied in large-scale screening experiments for their ability to use vitamins and for their inability to grow without vitamins in the media. Other studies on vitamin requirements include additional factors influencing the growth of thiamin-requiring fungi (240) and the relation of vitamin deficiencies to growth rates of fungi (246). The requirements of growth factors in the nutrition of fungi has been reviewed, and a classification has been proposed (146), based on requirements for various vitamins and combinations of vitamins. Following studies with a number of species of Hymenomycetes (492), their requirements for essential metabolites were found. A wide variety of fungal species (248) was screened for their ability to use a number of different simple to complex sugars. Whether or not fungi could use three different oils as carbon sources (355) was determined by a series of experiments using filamentous fungi known to use cellulose.

The water mold *Leptomitus lacteus* has been used (376, 377) in a series of tests to determine its specialized nutrient requirements. It uses amino acids rather than ammonia or inorganic nitrogen sources. This characteristic may be related to the environment in which it is most commonly found—waters polluted by sewages. That this condition is a relatively derived state of existence is shown in a recent survey of the nutrient requirements of Phycomycetes (68) in relation to their possible phylogeny.

The subgenus *Euallomyces* of *Allomyces*, another water mold, has been studied intensively, and recent work on its physiology has been carried out to discover its growth factor requirements in optimal and minimal nutrient media (265), the optimal composition of a minimal medium in which it can be grown extensively (266), and the sources of carbon used most readily by the strains of the fungus under study (267).

In the study of the nutrient requirements of fungi two approaches can be used. These are two papers, each of which serves a different purpose. For a general survey, the techniques in a study of the nutrient requirements of two species of aquatic Hyphomycetes (343) can be useful as a guide. A more intensive study has been reported in connection with experiments on the species *Stachybotrys atra* and *Memoniella echinata* (328).

In the use of complex substances as foods, the fungi secrete a series of exoenzymes which break down the more complex materials into simpler materials that can be assimilated by diffusion. Within the cell other enzymes continue the metabolic porcesses. In early work on enzyme systems (495) at least 22 different enzymes have been found in the wood decay fungus *Lenzites sepiaria*. This work was carried out before such metabolic processes as the Krebs cycle were discovered, and other enzymes may also be involved.

Spore germination presents numerous interesting problems in physiology. Many of these have been reviewed (164) earlier. In the study of mold infestation of book bindings and paper, humidity of the atmosphere played an important part in the germination of mold spores (385). Most spores would not germinate below 65% humidity, while many species germinated at humidities between 85% and 95% with some not germinating until nearly 100% was reached. In many cases the germination of spores and development of mycelium of those species of soil hymenomycetes and Gasteromycetes (144, 145) which may be mycorrhizal but which apparently are not obligate mycorrhiza-formers are encouraged by the presence of yeasts on the culture plates. Species of red yeasts, members of the genus *Rhodotorula*, were found to be most effective.

Oxygen Requirements

It is generally assumed that all fungi are aerobic organisms which, under certain conditions, may produce anaerobic fermentation. Very few reports (187, 247) concerning oxygen requirements have been published. The threshold point of lowest oxygen tension required for growth is still uncertain.

According to an experiment with *Penicillium roquefortii* (292), growth is inhibited when oxygen in the air is reduced from the normal 21% to 2.1% by addition of nitrogen gas to the incubation chamber. Later work has dealt with six species of filamentous fungi. Growth was completely inhibited at pressures to produce 0.015 to 0.118 ppm of oxygen in the medium.

It has been found that the water mold, *Blastocladia pringsheimii*, could grow as well under the partial pressure of oxygen of less than 1.0 mm. Hg. as in air. Large numbers of mature resistant sporangia were produced under 99.5% carbon dioxide, while few, if any, were produced in air without the addition of special nutrients to the medium.

Using manometric techniques (103) and pressures of less than one atmosphere of oxygen, the effect of reduced oxygen pressure on *Myrothecium verrucaria* has been studied. Hydrogen gas and oxygen-free nitrogen gas were used in experiments where, under less than one atmosphere, the rate of utilization of oxygen was a function of the oxygen pressure. At pressures between 0.21 and 0.40 atmosphere of oxygen, consumption was increased while no further increase was noted above 0.40 atmosphere, and there was not any inhibition in pure oxygen. Under anaerobic conditions, no matter how obtained, no carbon dioxide was produced, no fermentation was observed and organic acids were not produced.

Recent texts (187, 247) are not in disagreement with the following statement from a tabular summary of nutritional requirements of organisms (6): "Fungi require oxygen, obtainable from gas dissolved in the culture medium, or, in the case of surface growth, from the atmosphere." In human or animal pathogenic fungi it is indicated that under certain conditions such fungi, especially yeast-like species or species with yeast-like phases, can produce anaerobic fermentation in culture under varying conditions of nutrition, temperature and other factors. It has been stated (141) in part: "One of the major metabolic differences between molds and bacteria is that there are no anaerobic molds . . . Indeed, there is general concurrence with the idea that molds are highly oxidative organisms. This is not to say that molds will not metabolize carbohydrates anaerobically (fermentation), but rather that this is accomplished by preformed cell material and growth at the expense of fermentative metabolism exclusively does not occur."

Heavier mushrooms can be produced in excesses of oxygen (187), while certain types of wood decay (360) proceed more rapidly in excesses of oxygen. It has been indicated (247) that certain types of fungi can survive as long as 13 weeks in waterlogged soils, while in Honduras it has been shown that some fungi survive 18 months under flood-fallowed soil. Even when fungi (including yeasts) are used in anaerobic fermentation, they cannot survive without introduction of oxygen at some stage in their life cycle. Evidence has been cited (408) to indicate that fungi will, at some point in their life history, need oxygen for continuing growth and activity. Studies in England (61) indicate that in different stages of development in the Mucoraceae, oxygen supplies are critical, especially during sexual reproduction. Spores in a deep liquid culture take a long time to germinate and grow to the air, after which they develop rapidly.

In classifying the yeasts, fungi used most extensively in anaerobic fermentation process in industry, no species are based (260) on anaerobic characteristics alone, although the ability to ferment certain sugars anaerobically is used to distinguish between certain species within a genus.

Growth of fungi has been obtained in dilute media (95) in which the only oxygen present was dissolved in the aqueous medium. The oxygen was dissolved without the use of pressure. At the beginning of the experiments as much as 8 ppm oxygen was present in the solution; at the end of ten days three-five ppm of oxygen were still present and growth had not ceased.

Special emphasis has been placed on oxygen requirements because the literature appears to be weak on this phase of fungus nutrition, since the fact that fungi are aerobic is taken for granted or treated as a dogmatic fact.

Requirements for other Nutrients

Other nutrients are required by fungi in varying degree. Summaries of carbon and nitrogen requirements are presented in recent texts (187, 247), while elsewhere (399) additional carbon sources which can be attacked by cellulolytic fungi are listed. The nitrogen requirements of fungi are summarized by the texts as are requirements for macro- and micro-elements. The nitrogen metabolism (147) of microorganisms has been described in a recent book from England. Recent reviews have summarized the requirements of fungi for micro-elements (329), the heavy-metal nutrition (140) and the requirements for vitamins. Books on the chemistry of microorganisms (44) and the chemical activities of fungi (141) have recently been published in England and the United States.

TERMINOLOGY OF MATING SYSTEMS

Few people have tried to integrate the study of sexual systems in the diverse organisms called "fungi." An early work (254) tried to develop a terminology of the sexual processes as they were understood in 1929. In the intervening 27 years a large amount of information has been developed on the genetics and physiology of the processes involved in mating in fungi and a new set of terms has been proposed (62). Only 28 of the 171 references cited were published in 1929 or earlier.

"*Heteromixis* is the condition where sexual reproduction only results from the fusion of genetically different nuclei normally derived from different thalli. It includes: (a). *Dimixis.* The heteromictic condition where there are two and only two types of complementary nuclei which control mating. The nuclear types are determined by two allelomorphs at a single locus. (b). *Diaphoromixis.* The heteromictic condition where several types of complementary nuclei occur which control mating. The nuclear types are determined by multiple allelormorphs at one or two loci, the bipolar and tetrapolar conditions respectively. (c). *Homoheteromixis.* This is an essentially heteromictic condition where sexual reproduction results only from the fusion of genetically different nuclei derived normally from the same thallus. Such forms are derived from dimictic or diaphoromictic forms, hence the derived terms 'homo-dimictic' and 'homo-diaphoromictic.' *Homomixis* is the condition where sexual reproduction can result from the fusion of genetically similar nuclei derived normally from the same thallus. *Amixis* is the condition where the essential events of sexual reproduction are lacking but the pre-conjugation and post-meiotic events normally associated with sexual reproduction may occur." "Amixis" is chosen here rather than "apomixis" which is a term usually associated with flowering plants.

Numerous pre-existing terms are tabulted in comparison with the newly suggested terminology, and examples of fungi demonstrating each term are given. As many as seven pre-existing terms may be replaced by one new one. The new terms have the advantage that, in addition to being well documented, they have easily understood bases in stem, suffix and prefix words from the Greek which have universal application in genetic and botanical literature. The older terms tend to compartmentalize the phenomena they describe unnecessarily, are composed of multiple words in some cases, and in other cases too loosely define the phenomena they describe by the use of analogy with conditions as they occur in higher plants which may not be truly comparable.

GENETICS, SEXUALITY, VARIATION

General summaries of work on genetics and sexual mechanisms in the fungi have been developed in both North America (71) and Europe (349). A general discussion of natural selection in the microbes includes discussion of certain fungi (449) and the elaboration of principles applicable to fungus studies.

In the group of organisms commonly brought together to form the Phycomycetes there is a wide diversity of sexual phenomena, and some of these have been made the bases for studies of genetics in the fungi.

In the Blastocladiales the life histories, sexuality and variability of several genera have been studied intensively (122, 123, 185, 186). Morphological variability of a species in the Saprolegniaceae has been observed, in which many sporangial types could be produced under varying conditions of the culture medium. The fact that there are several sexual hormones in species of *Achlya* each active in a different phase of sexual development, has been demonstrated by Raper (346, 347, 348). Most genera of the mucoraceous fungi include heterothallic species requiring two opposing strains before sexual processes can occur.

In the Ascomycetes sexual phenomena are developed in quite different ways. Five principal groups of fungi have been studied in this class with reference to genetic phenomena. Nuclear bahavior has been reviewed earlier (310). The yeasts are fairly simple and much of the work with them has been published in St. Louis (253). In England the biology of yeasts (213) has been brought up-to-date, and recent developments in cytology and genetics are included. Continuing studies on *Glomerella* (e.g., 472) in Louisiana, in which sexual hormones have been demonstrated (109), and on *Venturia* (e.g., 41) in Wisconsin have been used for various types of genetic analyses, including chromosome-mapping techniques; such studies are related to the genetics of the pathogenicity of strains of these fungi. *Pyronema* has been used, together with related genera, in the study of sexuality and nuclear condition in various phases of the life cycle, and in investigations of heterothallism and homothallism. *Neurospora* has been considered in a large number of experiments dealing with genetic variation, with special emphasis on variants deficient in the ability to grow in one type or another of nutrient in the absence of one type or another of required nutrient source. The genetics of *Ascobolus stercorarius* (34) have been described recently.

Studies of sexuality in the Basidiomycetes have been of several types. Many of those on rusts have been summarized (58), including both the kinds of rusts which require more than one host upon which to complete their life cycle, such as the white pine blister rust and the black stem rust of wheat, and those kinds which complete their cycle on only one host. Heterothallism and its manifestations in the smuts have been summarized (476). The genus *Schizophyllum* (350) has received attention in genetic studies dealing with various kinds of mating. Summaries of the literature on bipolar and tetrapolar sexuality in the Basidiomycetes (473-476) have been presented. The types of tetrapolar sexuality in the genus *Coprinus*, in which as many as 16 combinations of monosporous mycelia can be made within one species, have been worked out in Canada. An outgrowth of the studies on social organization in the Hymenomycetes (51) was work on diploidization in the higher fungi (57). The pairing of monosporous mycelia derived from two apparently different fungi (300, 448) is commonly used to determine whether the two strains are members of one species or not in the Homobasidiomycetes. The component strains of dicaryotic mycelia can be recovered (290) by special techniques.

In the Fungi Imperfecti recent studies have resulted in a completely new alignment in the genus *Fusarium* (412). This is based on studies in which the concept of the "dual phenomenon" in fungi (172) was developed. This has been found to be associated with heterocaryosis (173) in these fungi. Work with this phenomenon has been carried over into studies in *Trichophyton* (481) of the Dermatophytes, species of *Penicillium* (19), *Botrytis cinerea* (174) and other genera. Work with the fungus which produces penicillin, *Penicillium chrysogenum*, in which methods of obtaining high producing strains of the fungus are described, has been summarized as a geneology (18). Additional manipulations with heterocaryosis, leading to the elaboration of the theory of the parasexual cycle (338) in fungi, have been described.

The steps in the parasexual cycle in fungi (338) are described as: *a*) fusion of two unlike haploid nuclei in a heterokaryon; *b*) multiplication of the resulting diploid heterozygous nucleus side by side with the parent haploid nuclei in a heterokaryotic condition; *c*) eventual sorting out of a homokaryotic diploid mycelium which may become established as a strain; *d*) mitotic crossing-over during multiplication of diploid nuclei; and *e*) vegetative haploidization of the diploid nuclei. The most important events here are considered to be the fusion of unlike nuclei, mitotic crossing-over and haploidization. The important results of such a phenomenon are three: *a*) production of haploid strains like the starting ones; *b*) production of haploid strains which recombine in all possible ways the chromosomes and chromosome parts of the initial strains; and *c*) prduction of a small proportion of diploid strains homozygous and heterozygous for all possible associations and recombinations of the members of *a* and *b*.

In a series of studies in England several problems in the distribution of higher fungi have been worked out on a statistical-genetic basis. Most of these studies have been conducted on species of fungi in the population of Skokholm Island, a small island off the coast of Wales. In most cases the species in the island are compared with similar material on the mainland. Two species, *Panaeolus campanulatus* and *Leptonia solstitialis*, were studied (317) to determine whether spore size could be used to indicate the presence of a distinct insular biota. In favorable cases a comparison of the variance and higher cumulants of distributions of spore measurements from different populations might indicate the degree of inbreeding in an area. In both species evidence was found that the insular populations are more highly inbred than those on the mainland. It is thought that some barrier exists to prevent free interchange of genes between the insular and mainland populations, and on this basis it is suggested that small animals play more of a role in the distribution of these species than has been commonly suspected. It is suggested that this type of separation may result in the appearance of insular subspecies in certain species.

In a study of *Panaeolus papilionaceous* (318) an analysis of spore breadth, using tetrasporic clusters for comparison with related species, was developed. The population of Skokholm Island was significantly more homozygous than the mainland population, and the specimens examined were probably heterozygous for at least one pair of alleles having a major effect on spore breadth. It was concluded that probably the two miles of water separating the island from the mainland produced a satisfactory barrier to wind distribution of spores, at least in this species.

A species of *Psilocybe* occurring on rabbit and horse dung on Skokholm Island was intermediate between two previously well known species (319). By statistical analysis of spore tetrads from the hybrid and its suspected parents it is thought that the new hybrid has become stabilized in recent times and that it is a disinct genetic entity, although capable of back-crossing to the parent species.

Intramycelial variation in the agaric *Hygrocybe turunda* var. *lepida* collected in Orchid Bog on Skokholm Island has been investigated (323). One hundred spores were measured in length and breadth from each of a number of basidiocarps. Characters employed in the statistical analyses of the data were spore length and shape; the latter was measured as the ratio length/breadth. As a result of this analysis it was concluded that the mycelium was genetically heterogeneous, containing more than one diplont.

Mycena galopus (324) has been chosen as an example of a Basidiomycete in which to demonstrate deme structure in the fungi. From a number of collections obtained in England, 100 or multiples of 100 spores were measured as to length and shape ratios. The collections studied represented a series of phenodemes which on a statistical basis were distinct but which could not be distinguished morphologically, even by the measurement of a few selected spores. Following a discussion of the significance of genetic barriers between colonies of apparently identical individuals, and the possibility of a lack of barriers between other individuals, the following statement is made: "It is one thing to discover what is *possible*, by laboratory experiments, but quite another to work out how these possibilities actually work out in nature, which is usually what most closely concern us."

SPORE DISPERSAL

The fungi are highly ubiquitous organisms. This is more true of those species whose spores are carried by air. Mechanisms of liberating spores into the air, of discharging zoospores into water, and many highly specialized processes of spore liberation, have been described recently in an excellent monograph (211). The splash-cup mechanism of spore discharge has been described (49) in many groups of plants in addition to the fungi. The fact that spores can be washed down through layers of relatively coarse materials, such as sand which form soils in some areas, has been studied (60). It was found that "dry" spores, those produced in dry chains or clusters instead of moist spore balls, can be carried downward by water for considerable distances in sandy soils. Should human and animal disease fungi produce spores in such a way that they can be carried in water, the fact that they could get into municipal water supplies has been shown in experiments (285) with spore passage through slow and rapid sand filters in Kansas. It was demonstrated that tuberculate macroconidia of *Histoplasma capsulatum* could pass through a 30-inch rapid sand filter. Eighty to 99% removal of such spores was effected by plain sedimentation or by alum flocculation and settling. On the other hand, in other experiments the same workers (286) have shown that spores of this fungus can be removed by using a combination of several standard water treatment methods. If 413,000 spores per 100 ml of raw water are passed through plain sedimentation beds, 16,900 per ml are left. After passing these through coagulation and settling, 205 spores per 100 ml are left. After filtration and before chlorination, none is left, as is true after chlorination. These values have been obtained with a membrane filter. If the agar plate technique for recovery of spores is utilized, no significant difference in the number of spores is noted except that no spores are found with this technique after ocagulation and settling. High counts of spores were obtained with either technique from sediment and sludge samples.

FRUITING HABIT

The importance of position of fruit body with reference to gravity in relation to fall of spores after discharge have been emphasized (52) in the Homobasidiomycetes. This importance was demonstrated by experimental evidence as well as by evidence based on the use of physical laws relating to various phases of ballistics. In the Homobasidiomycetes, where the hymenium is not amphigenous, a fruiting body had to be produced in such a way that, for effective liberation, the basidia could discharge their spores into air spaces large enough so that the spores would not become lodged against opposing sides of the spaces. Thus the tubes of a polypore of a bolete, the gills of an agaric and the teeth of a hydnaceous fungus must be arranged in positions perpendicular to the earth's surface for maximum efficiency of spore discharge from a particular fruit body. Accidental change in such a position, or deliberate variations as may be induced in laboratory experiments, or distortions in the production of a pileus, result in loss of spores for effective wind distribution. Such fruit body arrangements were considered geotropic. It has been shown (211, 261) that in the Ascomycetes, certain structures are phototropic or light sensitive. The asci in a Discomycete fruit body may be oriented in such a way that they are directed toward the light. In this way no spores are lost in the violent discharge process by having them aimed at the wall of the cup. The cupulate type of fruit body is found in both the Ascomycetes and the Basidiomycetes. While in the Ascomycetes the cups are always facing upward and the asci in some are phototrophic, in the Basidiomycetes the cups face downward and the basidia may be considered to be arranged in a geotropic manner. The theory (397) has recently been proposed that in cupulate Basidiomycetes of the cyphellaceous type, at least in some species, the cupulate habit is a response to regressive evolution. According to this theory, what may be presumed to have been an agaric developed a resupinate habit, as in certain genera. Degeneration progressed beyond this resupination to a breaking up of a pileus into numerous pilei both along and across gill lines, resulting in numerous irregularly arranged cupules.

Club-shaped and gelatinous fruit bodies are in general amphigenous with the hymenium borne on all sides. Here the spores are shot from the basidia or asci into the air currents which always surround such fungi.

TECHNIQUES

For the study of many fungi, especially those whose fruit bodies cannot be collected by hand, various types of techniques have been developed for obtaining them in pure culture. Most of the large fleshy or woody mushroom or bracket-type fungi can be cultured with proper care. This is done from tissues of the fruit bodies, spore prints, or from the wood or other material in which the fungus is causing decay. Handling these fungi with aseptic techniques is important, for the surface of fruit bodies is an excellent habitat for yeasts (9) and bacteria as well as mold fungi, and the surface of wood is an excellent habitat for molds which can penetrate deep into decaying wood as secondary or tertiary users of the nutrients available (271), as well as other organisms such as yeasts and bacteria. Potentially contaminated surfaces can be removed, and relatively pure culture material can be obtained, by inserting chisel forceps into the decay from which cultures are desired, and singeing the surfaces in open flames.

For fungi of smaller size other techniques have been used. These will be discussed for most types of organisms for which a technique has been described.

The most concise statement of the soil mold plate count technique is that published by English workers (47). This has been modified several times by changing the number of plates used, the amount of material sampled, certain nutrients in the medium, and the method of completing the dilution. However, the basic technique remains the same. These workers found that within a certain ratio of material to be sampled to optimum growth medium developed by Waksman (456), in a 9-cm. plate using eight replicates and at certain dilutions, plates with discrete colonies which can be read and studied with little difficulty can be obtained. The Waksman medium requires that the reaction be maintained low enough so that bacteria are not troublesome. A reaction of pH 4.1 gave good results but did not retard growth of rapidly spreading fungi. An early compilation of many types of culture media (242) has been replaced recently by more concise summaries (21, 11) of commercially prepared multi-purpose and dehydrated media. With the availability of antibiotics it was found (277) that by omission of acidification and by addition of rose bengal and streptomycin, bacteria could be eliminated or reduced to a minimum and spreading fungi could be slowed down in their growth speed so that plates could be adequately counted and colonies picked for future study or use. This medium was further modified (84), since aureomycin was preferable to streptomycin for sewage because of the bacteria present. Sources of organic nitrogen other than peptone (a hydrolysate of beef), such as phytone (21) or soytone (111) (hydrolysates of soy beans), could be used to good advantage.

A tube has been developed in England (72, 73) in place of soil for study of soil organisms. It is a test tube, culture tube or centrifuge tube with openings on the sides. The tube is filled with sterile soil and placed in the ground in soils whose microbiological characteristics are to be examined. The organisms developing in the new soil migrate from the test soil and can be studied by direct observation or plating. In addition, recolonization of sterilized soil by micro-organisms can be studied by similarly prepared tubes (127).

In England (461, 462) a "soil plate" technique has been developed in which small quantities of soil materials are placed in Petri dishes to which agar is added in which the fungi developing from the soil sample can be studied. It can be determined by microscopic observation of the plates whether the fungus colonies originate from spores, chlamydospores or pieces of mycelium in chunks of soil which could be agglomerates of soil particles and organic matter or organic matter alone. In this way a more adequate idea of what is happening in the soil and whether the fungi in question are actively participating in reduction of organic matter in the soil at the time of sampling can be obtained. Such observations can more adequately be used to determine the qualitative and quantitative fungus populations of the soil than the direct soil mold plate count technique previously used. It has been said (150) that in one technique we observe what cannot be seen; in the other we are able to identify what otherwise cannot be studied. With a little familiarity with the populations in the area under study, the species composition can readily be determined regardless of whether the fungi are on clear agar or on agar containing dyes or pigmented materials such as rose bengal, crystal violet or ox-gall. A comparison (404) has been made between direct and plate count techniques for quantitative estimates of soil fungi. Other workers have shown (349) that soil plating techniques must be carefully handled to avoid large statistical errors.

In a text on micropedology, direct observation of soil samples by a special microscope has been described (232). In addition to the use of a special microscope, examination of soils has been carried out by a modification of the Rossi-Cholodny technique. A recent review (92) has covered several modifications of the use of glass slides in the study of soil populations by direct observation. In work with cellulose-decomposing fungi (400), potato dextrose agar acidified with lactic acid, as well as other media, has been used to advantage. In studies in progress on the fungi in stored mattresses the rose bengal-aureomycin technique mentioned above has been used in tandem with the actidione technique mentioned below. Other techniques have been described (179) for study of active mycelia on living roots and other surfaces in the soil.

For isolation of human and animal pathogenic fungi from natural materials, in surveys for their occurrence as members of a population, two basic techniques are in current use. For fungi causing systemic mycoses, a portion of a sample of the suspect habitat is suspended in water or saline (238), the suspension shaken and allowed to settle. The supernatant is used for injection of susceptible animals, commonly mice (236). One milliliter of the supernatant is injected, usually intraperitoneally, into a mouse. After two to four weeks the mouse is sacrificed and portions of such internal organs as liver and spleen are streaked and left on neopeptone-dextrose agar slants. After one to two weeks or more of incubation the tubes are examined for the presence of the suspected fungus. In this way such fungi as *Histoplasma capsultatum* and *Coccidioides immitis* have been found in soil and substratum samples. The second basic technique involves plating samples of suspected materials such as soils, scrappings from shoes and shower stalls (4) and other types of materials in plates in which a Sabouraud-type medium is fortified with actidione, penicillin and streptomycin (4), or in which an enriched medium is fortified with ox-gall, gentian violet and streptomycin (255). Penicillin and streptomycin reduce the bacterial contaminants, although aureomycin was found to be an acceptable substitute, while actidione reduces the numbers of filamentous fungi which crowd such plates, preventing observation and study of the slower growing and less definitive pathogens. In this way various dermatophytes have been found in areas where their appearance was suspected but otherwise not demonstrated.

In the study of aquatic fungi, including chytrids, various types of baits (100, 218) have been used, but at present the most generally accepted bait for saprolegniaceous fungi is hemp seed. In Germany (202) such additional seeds as rice, corn and rye are employed. These seeds are handled in two basic ways: materials are brought to the laboratory and placed in culture dishes with the hemp seeds (182), or the seeds are placed in containers, such as tea balls (218) or cloth sacks (202), and allowed to remain in the test water for various periods of time. Two to six days have given varying degrees of effectiveness. Upon completion of the exposure time, the seeds are brought to the laboratory in a still moist condition and re-exposed with fresh hemp seed, in water in which carbon has been boiled and filtered off. When the usual halo of fungus growth appears around the new seed it can be studied during its development. As the fungus develops it can be studied under the microscope, and various techniques have been described (218) for preservation of such material. In addition to hemp seed, rosaceous fruits, meat and whole dates have been used in trapping such fungi. These are exposed in hardware cloth or other wire containers, buoyed with cork stoppers, in the bodies of water from which samples are desired. Additional sampling baits include cellophane, human hair, pieces of human skin peeled from sunburn blisters, other keratin-containing materials, and materials reasonably uncontaminated with the fungi for which one is searching. Such baits are exposed in the laboratory in culture dishes to which the sample is added, with water in which spores of the fungus being sought can swim.

In the study of different products to determine their mold populations, special media have been developed. For instance, in the study of citrus fruit juice preparations for microbiological content it was found (302) that most available media were inadequate and that a better medium containing citric acid or citrus concentrates could be prepared. This medium was later (423) developed as a dehydrated agar medium which could be used in any laboratory.

Various techniques have been developed to study fungi on materials in which they were suspected of causing deterioration. For the study of fungi on cloth, the papers mentioned under this topic include techniques for study. Other materials are also subject to deterioration. Study of fungi on leather (107) is particularly difficult. In addition to getting fungi to grow on such substrates in pure culture it is important to know how to evaluate (444) this information.

To get good growth of fungi in the laboratory it has been suggested that, rather than depend on synthetic media, like those described above, whose formulae include known concentrations of known chemical nutrients, and on semi-synthetic media including potato dextrose agar, natural materials, such as pieces of healthy or rusted or otherwise diseased plant parts (411), can be used. Such materials need not be autoclaved but may be sterilized dry at room temperature by small amounts of highly toxic volatile materials (175).

A further refinement of technique, the molecular or membrane filter, has had little use as yet in the study of fungi. With this technique, a suspension of the sample being tested is filtered and washed through the filter; the materials, including spores and other fungus fragments to be tested, remain on the filter which is transferred to a nutrient soaked pad in a suitable receptacle, on which the spores are allowed to germinate and grow (105) or are fixed and stained (162). In the study of the passage of *Histoplasma capsulatum* through water treatment processes (286), the membrane filter technique was more useful than the agar plate technique. That broths have somewhat different concentrations of nutrients than solid media may have played some part in the final results.

A wide variety of methods have been developed for the use of workers in many fields, including plant pathology, medical mycology, fungus genetics and others, for the isolation of single spores and the development of cultures from single hyphal tips. The techniques developed have been thoroughly reviewed (197, 198). A common and popular technique is still the simple flooding of an agar plate with a dilute suspension of spores and the cutting out of agar blocks bearing single spores or the lifting of single spores from the agar to another plate.

To purify cultures of fungi that either have become contamnated accidentally or are mixtures in which one or more species of importance to a study are to be separated, the van Tieghem cell technique has been developed (12, 345). A van Tieghem cell is placed on the agar and the mycelium of the desired fungus allowed to grow under it and outside its limiting area. The tips of the outgrowing hyphae are removed to clean agar plates and the colony is maintained in pure culture.

One of the techniques available for developing a fungus colony on a slide and mounting the whole preparation, including the agar, has been described from England (118).

A Committee of the Society of American Bacteriologists (188) has recently presented general statements concerning methods of maintaining culture collections of industrially important microorganisms. Such techniques apply to bacteria, yeasts and filamentous fungi, and are becoming standardized as the genetic implications of heterocaryosis in imperfect fungi are better understood.

A number of years ago in Boston two doctors found that by use of ultraviolet light, photomicrography of fungi and bacteria could be improved (126). This information lay fallow for a long time except that ultra-violet light was used under certain rare conditions for the study of occasional organisms. With the improvement of equipment and development of a certain amount of interest in the subject it has been shown more recently (201) in Vienna that the ultraviolet light techniques, especially when secondary fluorescence is induced with stains, can be used in mycology with good results. Certain anatomical and morphological characteristics not readily demonstrated otherwise can be brought out with stains which produce a secondary fluorescence. Primary fluorescence has functioned in a very limited way in microscopic analysis of fungus struture.

SPORE PRESERVATION AND LONGEVITY

Several methods have been devised for the maintenance of fungal spores and cultures in as compact and viable condition as possible. Such methods arose primarily from a desire to retain the large numbers of fungus cultures in collections developed during and after the Second World War as a result of cellulolytic activity and as the culture collections on which identifications are based increase in size. The principal techniques which have been described are lyophilization (134, 182), preservation under mineral oil (5, 418), preservation in sterile soil pans (20), and preservation at sub-freezing temperatures (287). Holding cultures in the laboratory at room temperature, in the experience of the writer, necessitates transfer at intervals of three to four months, depending on the humidity of the air. Keeping cultures in refrigerators when tubes are stoppered with cotton requires transfer once a year for maintaining viable cultures, and somewhat less often when tubes are covered with paraffin or screw caps to prevent drying. The longevity of spores kept under these conditions has been described, based on samples removed after varying periods up to five years.

The longevity of fungus spores in nature is a problem incompletely solved and rarely mentioned. It has been indicated (150) that fungus spores remain dormant until a piece of material carrying nutrients favorable to its development is deposited beside it. In most cases this would be rarely longer than the interval between two growing seasons of a crop. It has been shown (51) that collections of *Schizophyllum commune* can produce turgid spores after more than a year of complete desiccation. Assuming that a turgid spore is a viable one, spores of this species can withstand considerable desiccation.

Collections of spores representing species of the Ustilaginales have been surveyed (135) for their longevity in herbarium collections. Seventy-nine collections of 23 species from North America and Europe were tested on potato dextrose agar; species from the Ustilaginaceae were held as long as 12 days; from the Tilletiaceae, 30 days. Collections ranging in age from two to 25 years were used. Thirteen-year old spores of *Sphacelotheca sorghi* germinated to the extent of 40% after two days incubation. Of a ten-year old collection of *Ustilago bromivora* there was 95% germination after two days; and of an 11-year old collection of *U. hordei* 90%, germination occurred after one day incubation. In a 16-year old collection of *Tilletia trictici* there was 90% germination after 12 days, and a four-year old collection of *T. levis* gave 95% germination after seven days.

MISCELLANEOUS

Luminescence

A number of species of fungi produce luminescent mycelium or fruit bodies bodies. Among these the most pronounced is the jack-o' lantern fungus (*Clitocybe illudens*) which produces fruit bodies on decaying stumps and which, under certain conditions, is luminescent. These fruit bodies are heavily laden with phosphorous, and because of this the species is one of the few inedible fleshy fungi growing on decaying wood. *Panus stypticus* grows in both Europe and North America, but in one country luminescence is displayed in the other it is not. That these two geographic races are of the same species has been shown by Canadian workers (268) using monosporous cultures.

Pigmentation

In observing a series of general isolates from soils or other substrates where mixed populations occur, it is readily noted that different fungi produce various colored pigments, some of which are confined to the mycelium, others of which are soluble and diffused in the agar. An intensive study (195) of one species *Coccosporium* presents a review of pigment formation and shows that temperature, aeration, pH and carbon source are important variables in the development of the red pigment in that species. In yeasts and other fungi the carotenoid pigments have been described in a recent review (161).

Force

Data have been presented to show that fruiting bodies of fungi develop under considerable hygroscopic pressure (49). As a mushroom is elaborated rapidly, it can raise a piece of cement sidewalk. In *Coprinus* an actively developing colony can destroy a tennis court covering by pushing its fruit bodies up through the asphalt (385). Fungus spores can be discharged under pressure from both asci and basidia. The pathways of the projectiles thus produced correspond to those of projectiles fired from guns. The fungus gun, the trajectories and the sporabola have been carefully studied (48, 50). In the Ascomycetes such violent discharges are accompanied by audible sound (53).

Size

Most of the mold fungi are microscopic. An indication of this can be gained from data presented in an elementary text on soil science (291). A comparison is given between numbers of colonies or individual organisms of bacteria, Actinomycetes and fungi with their equivalent weights in an acre of good soil seven inches deep. While 0.3 to 95 million colonies of bacteria per gram of soil are present, representing more than 500 pounds live weight per acre seven inches deep, the fungi are represented by only 8,000 to one million colonies or 1000 to 1500 pounds per acre seven inches of soil, and 0.1-36 million Actinomycetes or 700 pounds per acre seven inches are present.

Of the macro-fungi there are wide variations in size. Among the smallest are species of hypogaeous fungi, almost microscopic, which are uniloculate (371) in contrast to the larger hypogaeous species and the puffballs in the multiloculate Gasteromycetes. Among the largest fungus fruit bodies are the puffballs of *Calvatia gigantea* which may exceed one meter in diameter (29). A specimen half meter in diameter is estimated as having produced more than seven trillion spores (52). Bracket fungi have fruit bodies which vary in size between species. In many cases the size is fairly constant but in some species, under supraoptimum growth conditions, a fruiting body may exceed the dimensions of the average for the species. *Ganoderma applanatum* has been found in Ohio (194) to produce conks three feet across, while this size has been exceeded in Alaska (129). The Alaskan conk measured 111 cm long, 311 cm in cirumference, 75 cm wide and 81 high. It weighed 52.1 kg and had at least 64 layers of tubes. It has been estimated (52) that a specimen of *Fomes applanatus*, having a spore surface of one square foot, can produce 5.5 trillion spores in the six months period in which it is active. In the Cascade mountains of southern Washington and northern Oregon, a large fungus has been found which reaches five feet in height and three feet across (80). *Oxyporus nobilissimus* has been located on rotting hemlock stumps and on the ground near noble fir trees, but no connection with living trees has been established.

Translocation

The phenomenon of protoplasmic streaming has been known for at least 25 years (52). In those fungi which demonstrate this phenomenon it can readily be seen, especially when the cytoplasm is granular. Because of the ability of protoplasm to stream readily between cells of the mycelium of the Ascomycetes and Basidiomycetes, it has been thought (233) that not only the Phycomycetes but all fungi are unicellular and coenoctic.

An elaborate study on translocation (382) of nutrients and dyes through fungal mycelia has been made with species selected from the Phycomycetes, Fungi Imperfecti and Basidiomycetes. No translocation occurred in certain species of mold fungi and thus no protoplasmic streaming. In all agarics studied there was translocation in certain undifferentiated series of cells which could not be distinguished from other non-functional cells.

Translocation and protoplasmic streaming were closely linked and always occurred together. Efficient bi-directional streaming was absent.

Transpiration was found to be a vital function in the fruit bodies of agarics. It occurred under conditions of complete saturation, although at a reduced rate. The rates of transpiration and of translocation were similar. The behavior of fairy rings appears to bear out the theory that transpiration and translocation are closely connected.

It is apparent that translocation is very important in the fleshy and in some mold fungi. While the morphology of fungi may appear to be rather simple, the physiological processes within the cells are highly complex.

Temperature

Optimal temperatures for growth of a large number of fungi have been compiled in a book published in Japan (441). In almost all studies of plant-pathogenic fungi, optimal growth temperatures are determined (150). It has been said that in soils in cooler parts of the world the populations of fungi are dominated by species of *Penicillium*, those in the warmer areas by *Aspergillus* species. The extent to which temperature controls the fruiting of fungi, especially of those that produce macroscopic fruit bodies, is only surmised. In Scotland (166) it was thought that such fruiting resulted from the concomitance of such favorable factors as temperature, precipitation, light, day length and nitrogen supplies. In eastern Washington and adjacent Idaho, where fruiting occurred primarily in the fall, no correlation (87) was found between these phases of the habitat. In a study of the synecology of plant-pathogenic fungi (42), correlations with moisture were more pronounced than those with temperature. It has been shown that *Oospora lactis* (*Geotrichum candidum*) will not survive the temperatures of pasteurization (160), although it is a common contaminant of dairy products.

Few fungi are thermophilic. Most of these are associated with compost heaps during the active stages of decomposition or curing of the compost. It is possible that those species which tolerate high temperatures during spore germination are thermophilic.

Certain fungi pathogenic for man and other animals have yeast-like stages in their life cycle. The mycelial phase is encountered in nature and is obtained in pure culture in the laboratory at room temperatures, but in the pathogenic phase and on certain media under temperatures approximating those of the body, the mycelial phase converts to a yeast-like phase. The reversion to mycelial phase results when the temperature of incubation is reduced. This change has ben attributed (307) to inactivation at higher temperatures of the enzyme system controlling mycelial elongation. Two enyzme systems controlling cell elongation and division are considered to be active. The system controlling the yeast-like budding of cells of limited size is dominated, under cooler temperatures, by the system controlling cell elongation and the usual type of cell wall formation.

Moisture

The problem of the relation of moisture to the production of fungus fruit bodies and the development of fungus mycelium has not yet been satisfactorily studied. It is well known that various types of plant disease respond differently to the moisture content of the air (atmospheric humidities), but the nature of the reaction to soil moisture in soil fungi, or of aquatic fungi in the soil, is as yet incompletely understood. In Scotland (166) moisture was considered one of the important aspects of the environment which controlled fungus fruiting. In eastern Washington and adjacent Idaho (87) fungus fruiting was correlated as much with precipitation as with any other phase of the environmental conditions studied. In Austria fungus fruiting was correlated with the moisture content of the soil. On Mount Shasta (86) and in subalpine western North America (88) it was noted that the fruiting of certain groups of fungi was correlated with moisture resulting from melted snow. From various observations it may be assumed that development of fungus activities of the soil is correlated as much with soil moisture as with any other factor. When soil moisture drops below the wilting coefficient for higher plants, i.e., when the humidity in soil air-spaces becomes less than 100%, fungus activity decreases or ceases. When soil air-space humidity reaches 100%, the soil may not be water-logged, but sufficient moisture is present to satisfy the moisture requirements of fungi. Such requirements are high, since there are few, if any, checks on the loss of water by fungi through evaporation. Aquatic fungi can also become active in soils at such high humidities, since they require films of water for movement of zoospores and oospores, and for other activities.

Water in Fungus Spores

Recent studies (491) on conidiospores of powdery mildews and other fungi have shown that while the conidia of powdery mildews contain 52-75% of their fresh weight as water, spores of six miscellaneous air-borne fungi contain only 6-25% of their fresh weight as water. Correcting for hygroscopic water, these figures indicate that the physiologically active water content of *Erysiphe polygoni* conidia may be 15 times that of *Uromyces phaseoli* uredospores. This high water content may explain the ability of such spores to germinate in areas of low atmospheric humidity. Calculations based on conidia of *Monilinia fructicola* and its increase in volume during germination in water indicate that its water content at germination may be about the same as for powdery mildew conidia. These data may apply to other fungi requiring free water for germination.

Diurnalism and Day Length

In the development of certain plant diseases caused by downy and powdery mildews, it has been shown that day length and diurnalism are important phases of the habitat. Whether such conditions can be translated into natural requirements of other fungi is as yet an unanswered question. It is a difficult matter to control light, temperature and moisture conditions in pure culture in the laboratory to simulate those to which the fungus has become adapted in nature. The culturing of fungi in cases outside laboratory windows, on media containing various plant parts (natural media) (411), and similar techniques used in the laboratories of the Department of Plant Pathology at Berkeley, California, are steps in this direction. Use of culture chambers with too rigidly controlled conditions of either single temperatures and humidities or of alternately applied temperatures and humidities may not give any more natural conditions than use of simple laboratory room conditions.

Fungus Foods and Poisons

Fungi have served as food for a long time, probably since before the dawn of history (342). It has been reported that fungus poisons have also long been in use to eliminate enemies and as stimulants.

The culture of mushrooms is one of the more specialized phases of horticultural science. A number of books and pamphlets have been written on this subject. To increase production without loss of flavor, the use of liquid culture has been proposed (209). A number of edible fungi have been adopted to liquid culture (434). The culture of truffles has become an industry of some importance in Europe where it is necessary to develop mycorrhizae with oaks in forest plantations. As yet, techniques and media for growing the morel and truffle in artificial culture have not been perfected.

Use of poisonous fungi as intoxicants has been practiced for a long time (342), and other fungi which are not deadly poisonous but whose edibility is questioned by many connoisseurs are used for similar purposes. The intoxicating effect of such fungi is not felt for long periods, and immunity to the poison is built up gradully by increasing dosages. The edible inky-cap *Coprinus atramentarius* is reported from France (208) to have produced intoxication in at least one case.

Many animals also depend on fungi as food sources. Workers in Austria (379) have shown that definite relations can be established between fungi and the beetles which use them as food. Here the same degrees of dependence on fungi as food sources have been noted as are shown between fungi and burned areas mentioned above. Slugs and rodents use fleshy fungi as incidental food sources, as has been noted in Canada (52) in a study of the hypogaeous fungi of Mount Shasta (86) and in *Endogone*, a fleshy fruited hypogaeous member of the Phycomycetes (110). Observations in tropical Africa (191) have shown that termites are able to grow certain agarics as food sources.

The relations between species of the fly *Drosophila* and yeasts growing in habitats from which these flies have been taken in the Yosemite region of California have been carefully studied (113, 333).

That there is an important dependence between nematodes and fungi has been noted in a recent study made in Holland (288). Here it was noted that, as in the case of beetles, there is a dependence between the nematodes and the fleshy fungi on which they subsist, in which some species of nematodes require the mushroom as a habitat while others do not.

COMMUNITY ADJUSTMENTS

Under this heading two principal types of activity may be considered. In the normal course of activity, when groups of organisms live together, certain degrees of associative ability are experienced. The fungi may form a complex of hyphae through the soil, in the litter, or in a mass of decaying wood without interfering with each other's activities, or some species may secrete substances inhibitory to the activity of other fungi or other organisms. A certain amount of symbiotic activity also occurs among the fungi. Species expressing this type of activity may live exclusively with another organism as in a lichen, or their activity may be less exclusive as in mycorrhizae, where the mycelium may be in active competition with other fungi in the soil.

With the development (351) of the antibiotic, penicillin, produced from such fungi as *Penicillium chrysogenum* and *P. notatum*, searches have been instituted by workers all over the world for antibiotics which may be produced by other fungi as useful, more useful, or supplemental to the first "wonder drug." The various antibiotic products of fungi have been reviewed (203). Compendia devoted to a listing of antibiotics (334) and their properties have appeared on both sides of the Atlantic. The problems encountered in the search for antibiotics, using screening procedures for all fungi found in habitat samples (372), have been outlined by one group of industrial workers. American workers (368) screened large numbers of wood decay fungus cultures for their ability to produce antibiotics in culture. In Portugal (336) it was noted that at different stages in their life cycle certain Hymenomycetes were capable of producing more or less antibiotic substances. English workers (46, 484) screened large numbers of fungus cultures, listing variations in technique as the screening process was developed. In Holland it was found that Discomycetes (169) are able to produce antibiotic substances.

The study of fungi producing antibiotics and of their ability to yield these substances in increasing amounts, as genetic manipulation (18) was used to change strain characteristics, has developed into a major field of effort on the part of mycologists (416) and biochemists (330). Paper chromatography has a place (8) in the study of various kinds of antifungal antibiotics.

The study of the production of antibiotics under natural conditions in the soil and the use of antibiotics in the control of forest tree disease (35) has developed in the last few years. Using very sensitive techniques it has been found that, under special conditions, as in sterile soil without competing organisms, strains of *Trichoderma viride* which actively produce gliotoxin in the laboratory could produce this substance in the soil. The amount and type of gliotoxin produced by *T. viride* have been investigated in England. It appears that it may be possible eventually to purify this antibiotic so that it may be used without the toxic effects now observed. Certain fungi are able to produce antibiotics in English heath soils. Proponents of the idea that fungi, actinomycetes and bacteria can produce effective antibiotics in soil (150) suggest that the amount of such substances required by the fungi is very small and need be secreted only in the immediate vicinity of the mycelium producing them.

The subjects of fungus antibiotics in relation to the occurrence of the organisms producing them in association and in competition with other soil organisms (466), and in relation to fungus antagonisms (339) have been covered in earlier reviews. In the therapy of fungus diseases of man, a number of papers have been published in symposium form (422), in which newly developed antibiotics are discussed in relation to the control of several of the more difficultly treated mycotic infections.

In Holland (341) and Switzerland (440) the role of the fungus in the formation of a lichen has been intensively studied. According-ing to these workers, the fungus components of lichens require complete vitamin supplements when grown in pure culture outside the lichen thallus. Furthermore, it is difficult to synthesize a lichen from its known fungus and algal components when these are grown in pure laboratory culture (341, 340). The relationships of lichens with their environment and other organisms have been described (407), and the biologic and economic significance of lichens has received recent attention (256).

PREVENTIVE MEASURES

There are three principal reasons for considering measures for the prevention of fungus growth. All are based on man's economy and the interruptive nature of certain fungus activities in this economy. The literature of plant pathology (189, 205) and of human and animal pathology (77, 395) is full of references to methods of controlling disease caused by fungi. That control of human diseases, especially of the types referred to as "deep mycoses," has progressed less rapidly than control of plant diseases is based on the lack in availability of adequate amounts of test materials, as few people are willing to undergo the elaborate and extensive tests used on thousands of plants annually in plant-disease control experimentation. Utitization of copper and sulphur compounds (205, 240), of organic compounds (205) and of heavy metals in fungus nutrition, and the combatting of fungus disease are reviewed and discussed in the literature. Legalistic aspects of plant disease control have been reviewed (148).

A more recent method of soil treatment to prevent disease organisms from attacking crop plants is sterilization. Much of the work on this subject has been reviewed in a recent text (150). This type of treatment is applied on an increasing scale, not only in the laboratory and greenhouse but also in the field. It is interesting that the ubiquitous *Trichoderma viride* is one of the few fungi to survive sterilization treatments, that under certain conditions it can be used to control other fungi, while under other conditions it needs control, and that following such treatments the soils can be "reseeded" with fungi harmless to crops and can remove crop debris from the soil without infecting the living crop.

USES FOR FUNGI

It has been implied above that there are several uses to which fungi can be put for man's benefit. The earliest of these was the culture of mushrooms and the collection of wild mushrooms for food sources. Possibly older than this was development and manufacture of fermentation products from natural yeasts. More recently, as fermentation processes have become more elaborate and refined, additional fungi have been found useful in the production of various types of commodities (340, 408), such as penicillin and other antibiotics, food (437) and feed materials, drugs and chemicals (259, 373). When other sources fail, fungi have been employed in the manufacture of fats for food supplements. Fungi have been surveyed (488) and fat production techniques have been improved (303) recently. The potentialities of fungi for biosynthesis of many products have been discussed (167).

While development of pure culture techniques has taken place in the last 75 years (114, 258, 259), it is only in the recent 25 years that techniques have become refined to the extent that certain species can be employed in the assay (245) of various types of compounds. Techniques have recently been developed to assay vitamins and other highly concentrated substances. Fungi are sensitive to the amount of elements, for instance, molybdenum, in soils and in solutions.

The development of sewage treatment facilities has led quite by accident to further use for fungal populations. Both on the trickling filter and in the activated sludge tank (90) fungi are one type of organism which contributes to the treatment process. Recent work (95) has indicated the probable extent of this activity, but the whole problem of biological treatment of sewage is full of problems based on questions concerning how this activity takes place, what contribution each group of organisms makes and related inquiries.

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