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ECOLOGY OF FUNGI IN WILDLAND SOILS ALONG THE MAUNA LOA TRANSECT

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ABSTRACT

The distribution of fungi in soils along the Mauna Loa Transect was determined by an approach employing specific fungal reference genera, selective isolation methods, and a combination of analytical techniques. Two sets of transect zones were determined on the basis of fungal distribution. The influence of environmental factors, particularly those relating to soil, vascular plant communities, and climate, are interpreted according to distribution patterns. The distribution of fungal groups coincided clearly with vascular plant communities of the transect as defined by other studies. Features of the structure, stability, and development of fungal communities, and of the ecological roles of certain fungi are indicated by the results. The composition, spatial distribution, and environmental relationships of fungal communities along the Mauna Loa Transect are compared with situations in other insular and continental ecosystems in order to further characterize and elucidate the ecology of the Hawaiian soil-borne mycoflora. An overall evaluation of the research indicates that the selective methods employed to evaluate fungal distribution represent an effective approach to ecosystem analysis on a broad scale.

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INTRODUCTION

The fungi generally are ubiquitous and important, although often inconspicuous, components of functioning ecosystems. As heterotrophic organisms with various roles and capacities for degrading sugars, cellulose, lignin, proteins and other biochemicals, and for participating in symbiotic relationships with plants and animals, the fungi contribute importantly to decomposition, nutrient cycling, soil-building, the welfare of other biota, and other essential aspects of ecosystems. The importance of fungi prompted mycological studies as integral projects of the Hawaii IBP, Island Ecosystems Integrated Research Program (IRP).

An understanding of the purposes and design of mycological work within the IRP might be best understood after a brief review of the scope and objectives of the Hawaii IBP (Mueller-Dombois 1975). The broader research aims of the IRP are to elucidate unique aspects of island ecosystems to facilitate effective management of wildlands and the conservation of natural resources. The general, long-term objectives which have guided the program point to an ultimate understanding of the mechanisms of speciation, the stability and fragility of ecosystems, and the rates of evolution in different groups of organisms. Specific research projects have been focused on the spatial distribution and temporal relationships of island biota; on community structure and niche differentiation; and on the genetic variation within island species. Study areas are in the general vicinity of Kilauea Volcano on the east flank of Mauna Loa, a geologically young, volcanic mountain on the island of Hawaii (Fig. 1). Several transects and study areas on Hawaii were established for the IRP and allied studies. One major transect is an altitudinal, environmental gradient known as the Mauna Loa Transect, which extends from a rain forest at 3920 ft (1195 m) through mesic forests, savanna, and scrub to an alpine area at 10,000 ft (3050 m) (Fig. 2).

Research on the ecology of soil-borne fungi reported herein has dealt primarily with the spatial distribution of island species along the Mauna Loa Transect (Fig. 2), the structure of fungal communities, and certain aspects of niche differentiation. The research was designed to satisfy the concepts of spatial integration and hierarchical sampling defined for the IRP (Mueller-Dombois 1973) in order to contribute to a synthesis of understanding of the biota, thereby facilitating the delineation, further investigation, and management of island ecosystems.

Research on the nature and ecology of root- and soil-borne fungi associated

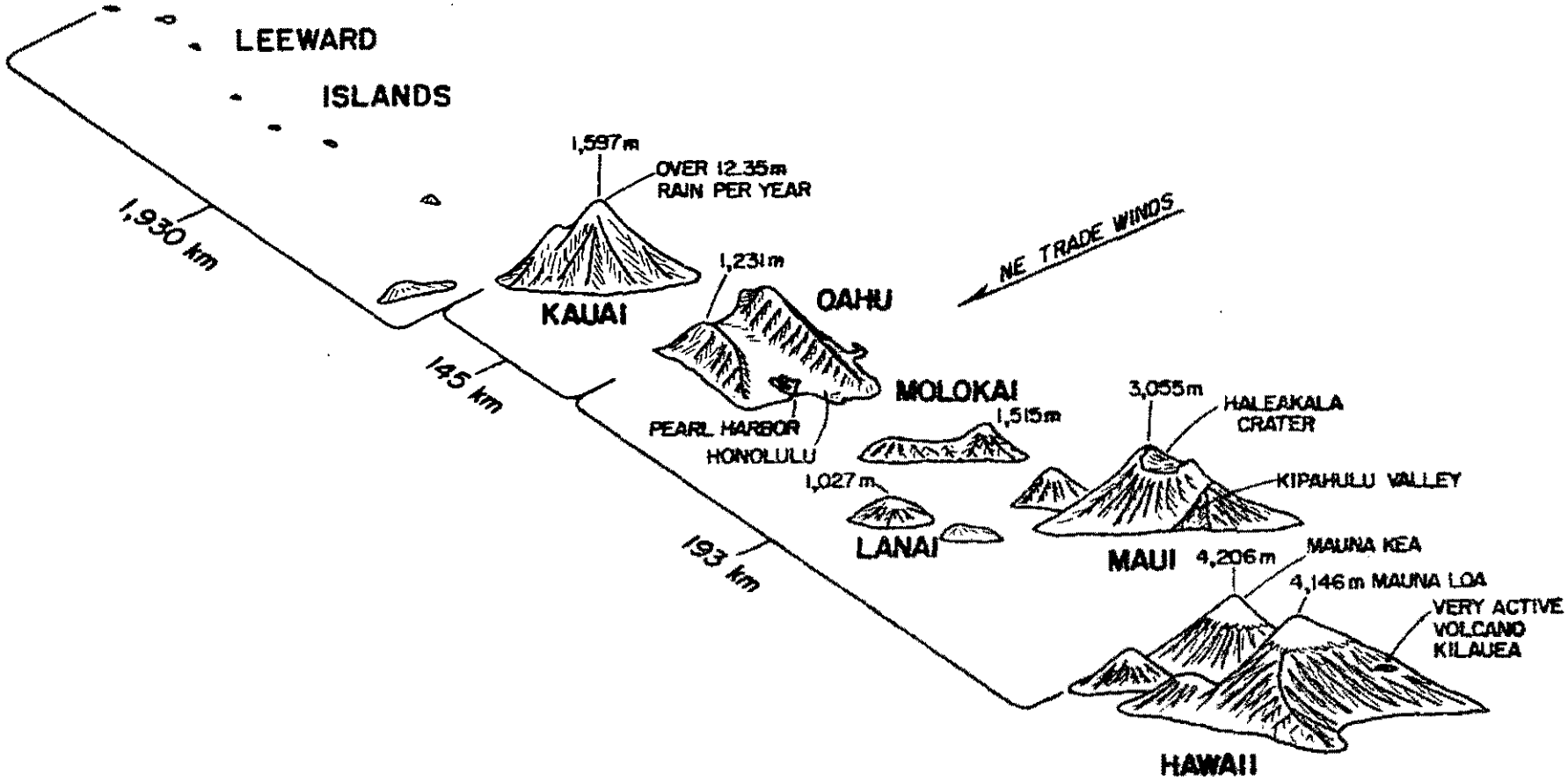


FIG. 1. Generalized topographic profile of the Hawaiian Islands. (From Mueller-Dombois 1975.)

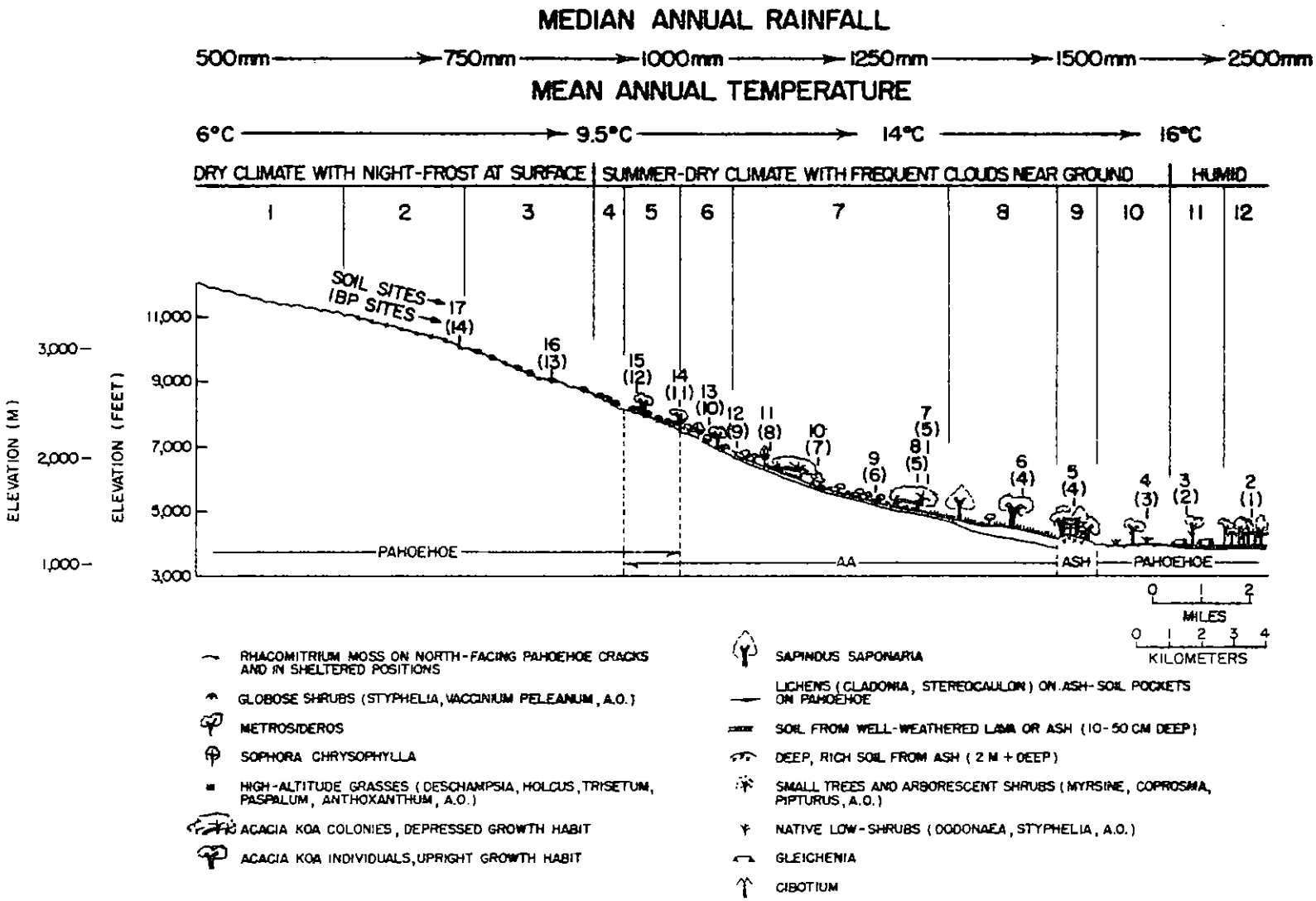


FIG. 2. Profile diagram of the Mauna Loa Transect indicating the locations of soil collection sites. For geographic location, see Figure 10, transect 1. (From Mueller-Dombois, Berger, and Gressitt 1972, as revised by Mueller-Dombois and Bridges 1975.)

with noncultivated soils in montane, endemic plant communities of Hawaii has been very limited (Aragaki, Laemmlen and Nishijima 1972; Baker 1964, 1968; Laemmlen and Bega 1974). Baker (1964) presented an appraisal of knowledge on Hawaiian fungi before the inception of the IRP and other projects. Most recent studies have been connected with the IBP (Baker, Dunn and Sakai 1974; Stoner 1974a; Stoner, Baker and Stoner 1973) or with research on ohia forest "decline" (Bega 1974; Kliejunas and Ko 1973; Petteys, Burgan and Nelson 1975).

BASIC RESEARCH PLAN

This research included two major, interrelated phases: (1) a preliminary study for the selection, evaluation and/or refinement of field sites, methods, materials, and groups of fungi to be investigated; and (2) the subsequent, principal research on fungal distribution along the entire Mauna Loa Transect. Phase 1 (Stoner, Baker and Stoner 1973) was especially important in the determination of which fungi would be studied in Phase 2. In Phase 2, data regarding the distribution of fungi was analyzed by objective and subjective techniques to determine the location and structure of fungal communities and to reveal other ecological relationships.

The principal research plan was based on a working hypothesis that the altitudinal distribution and ecological significance of soil fungi and fungal communities on the Mauna Loa Transect could be meaningfully determined and evaluated by studying the individual or group-occurrence of a limited number of selected "reference" genera and species. Reference fungi are defined as those genera or species that are sufficiently represented and distributed along the Mauna Loa Transect to support statistical and subjective analyses; that belong to major taxa generally associated with key ecological roles (e.g. cellulose vs. simple sugar decomposition) or habitats (e.g. root-inhabiting vs. humus-decomposing) in the soil-plant root environment; that support intersite comparisons; that could be detected accurately by methods that would support a realistic, feasible approach to the extensive sampling area; and that could support intercomparisons of island and continental ecosystems based on available literature.

The approach used in this research, which focuses attention on predetermined reference fungi and employs methods that ensure their selective isolation, is a substantial departure from previous methodologies in soil-fungus ecology

(Griffin 1972; Parkinson 1960; Parkinson, Gray and Williams 1971; Warcup 1960). This is essentially opposite to the general, floristic analyses of earlier studies wherein any selectivity was unintentional or accepted as a limitation of techniques that frustrated the basic goal of achieving a more complete account of fungi.

In some earlier studies, such as those made by Tresner, Backus, and Curtis (1954) and by Christensen (1960), the number of fungi employed in ecological comparisons of soils was limited according to predetermined limits regarding the frequency of occurrence in isolation plates. However, the kinds of fungi isolated in these studies were determined largely by the very limited range of media employed rather than by any planned selection of genera or species. Other studies, such as those performed by Warcup (1950, 1951), Mueller-Dombois and Perera (1971) and others, have been aimed at broader and more complete (less selective), floristic determinations of the soil mycoflora. While some techniques used in such studies may have promoted the isolation of genera or species missed by other methods, the factor of unintentional selectivity was still involved, and the fungi found were limited primarily by the methods, not by specific plan of the investigator.

These earlier, standard approaches have produced much useful ecological information. In most cases, however, they have been influenced to some extent by floristic concepts and their attendant, relatively cumbersome methods. The nonselective, floristic approach, while especially useful in the earlier stages of soil mycology, is no longer considered as an essential, most advantageous, or realistic avenue in the ecology of soil-borne fungi (Griffin 1972). In view of current mycological knowledge, it is clear that even the most intensive floristic surveys of fungi in soils probably do not detect a large number of the fungi present. While earlier methods are still valid and important in many applications, new approaches are needed to facilitate a broader range of advanced ecological studies. Considering the foregoing and, specifically, the point that any method or medium used to study soil fungi is inherently species-selective to some degree, it would seem appropriate and practical to harness selectivity and utilize it in a planned approach to fungal ecology. The reference group-selective approach reported herein is considered as an effective alternative to older techniques for mycological ecosystem analysis, particularly for extensive research projects such as the Hawaii IBP.

PRELIMINARY STUDY

Considering the paucity of knowledge on the mycoflora of noncultivated soils of montane, endemic plant communities in Hawaii, it was necessary at the onset to determine by a general survey which fungi existed in A_1 soils along the Mauna Loa Transect. This preliminary survey was the principal basis for the selection of reference genera for Phase 2.

Methods and Materials

Selection of Sites

Following a review of information on the Mauna Loa Transect and field inspections of the gradient in 1972, four soil collection sites were chosen for the preliminary study. These sites, which are described in detail in Appendix 1, were selected primarily for the determination of the general fungus flora on the transect. Since a relatively exhaustive series of isolations and identifications was anticipated, the sites for Phase 1 were deliberately limited in number. It was assumed that a few sites located at intermediate low and high elevations and climatic areas on the transect and in the vicinity of dominant vascular plants would provide a reasonable sampling of the mycoflora for the purpose of selecting reference genera. Sites 1 and 2 were at Kipuka Puaulu (Bird Park) at 1224 m (4000 ft) elevation. Soil at Site 1 was in the root zone of koa trees (Acacia koa var. hawaiiensis Rock) and some shrubs (Appendix 1); Site 2, in the root zone of ohia trees (Metrosideros collina (Forst.) Gray var. polymorpha (Gaud.) Rock). Sites 3 and 4 were at the 2040 m elevation. Again, the sites differed with respect to the root zone influence of koa and ohia.

Additional inspections of the transect in July and August 1972 were performed to select additional sites for Phase 2 of the research.

Collection and Handling of Soil Samples

The A_1 or uppermost mineral horizon, which is darkened by incorporated organic matter (Griffin 1972, Wilde 1966), was selected for study. Previous studies have shown that a majority of soil fungi found in the various horizons of many soils usually can be recovered from the A_1 horizon (Griffin 1972; Tresner, Bachus, and Curtis 1954; Warcup 1951). Furthermore, there is strong evidence that fungal activity generally is highest in this horizon (Griffin 1972; Warcup 1951).

Collection

The procedures for handling and storage of soil used in this research were selected to minimize changes in the viability and detectability of the soil microflora, and are supported by previous research (Chu and Stoner 1971; Stotzky, Goos and Timonin 1962).

Soils were collected at 5 different points or relevés within a square area approximately 10 m x 10 m at each site. The litter, humus, and about 6 mm of surface soil were removed from each collection point to avoid contamination of the pit area. A small pit with vertical walls was dug at each point to permit the collection of a sample and the study of the soil structure. Soil was collected with a clean (washed and dried), metal tool which was inserted horizontally into the A_1 horizon of the pit wall about 50-75 mm below the surface. Ample soil for biotic and physical analyses was placed in Whirl-Pak plastic bags which were sealed and stored in a cool, shaded place; within a few hours of collection the soil samples were stored at 4-6°C until used (up to one week) for isolations.

All soil samples were collected in July 1972 during the driest period of the year with no recent rain (Bridges and Carey 1973). Without recent, major fluctuations in moisture content and related biological activity, the soils along the entire transect were in a preferable state for biotic comparisons.

Preparation of Composite Soil Samples

Each site was represented initially by five separate soil samples. Just prior to analyses, portions of samples were passed through a 2-mm soil sieve to remove roots, stones, and concretions. Gravimetrically equal portions of each of the five samples from any site were thoroughly mixed to form the composite sample. Biotic and physical analyses were conducted using composite samples. Each geographic site was then represented by one composite sample which, in turn, was expected to furnish a general consensus of the biotic and physical characteristics of the area.

Dry Weight Equivalent

The moisture content of each composite sample was determined by the oven drying procedure (Black 1965; Johnson and Curl 1972; Thies and Patton 1970) so that assays of microbial populations could be performed on oven-dry-weight-equivalent amounts of fresh, field-moist soil. Use of the dry-weight-equivalent

allowed population comparisons between different sites based on propagules per gram of oven-dry soil, thus correcting for differences in the fresh weight of soils attributed to moisture content at the time of collection.

Mycological Media

A number of culture media, which are defined in Appendix 2, were employed in Phase 1 to facilitate a general assay of fungi present in collected soils. The media were evaluated also for potential use in Phase 2. All fungal isolation media contained antibiotics (designated by +) to inhibit bacterial growth. Some contained Tergitol NPX, a surfactant that retards mycelial growth in some vigorous fungi such as Trichoderma and Mucor (Lee 1970; Steiner and Watson 1965). The general isolation media for fungi included corn meal agar (CMA+), diet-food agar (DFA+), potato-dextrose agar (PDA+), sodium caseinate agar (SCA+), and soil-grass extract agar (SGA+). General actinomycetes and bacteria were isolated and identified on SCA. Two very selective media, alpha-cellulose agar (ACA+; with cellulose as the sole source of carbon for isolating cellulose-degrading fungi) and V-8 juice agar with benomyl (an anti-Ascomycete chemical) (V-8A+, for Phycomycetes, particularly the Oomycetes and Mucorales) were evaluated. All media were stored at 6°C until used. Sodium caseinate agar (SCA+) was used to provide information on the general population levels of actinomycetes and bacteria in order to furnish an overview of microbial distribution in studied soils.

Some fungi were identified directly on isolation media; others were sub-cultured onto media without antibiotics or surfactants. CMA, DFA, PDA, and V-8A were used for general identifications. Aspergillus, Gliocladium and Penicillium species were identified on Czapek (CZA) and malt extract agars (MXA) according to standard procedures (Raper and Fennell 1965; Raper, Thom and Fennell 1968). Fusarium species were cultured on PDA made from fresh potatoes (Toussoun and Nelson 1968).

Isolation, Identification, and Quantitation of Fungi

Isolation Techniques

From the standpoint of feasibility, a decision was made at the onset of Phase 1 to test standard, proven techniques (Griffin 1972; Stoner 1974b, Warcup 1960) that could facilitate the extensive sampling of the Mauna Loa Transect and the isolation of reference genera anticipated for Phase 2. Three related

techniques were tested: a modification of the standard dilution-plating method, referred to here as the spread-plate technique; the soil-plate method; and the soil-washing method. The inherent fungal selectivity in these methods was not considered a significant limitation because of the basic research plan. These methods were modified slightly to expedite and improve sampling procedures. Tests of these methods were incorporated in the preliminary survey of soil-borne fungi.

Soil-Dilution Spread-Plate Method

This method is a very useful variation of the standard dilution-plating technique described by Johnson and Curl (1972). Rather than mixing portions of diluted soil with melted agar just prior to plating as in standard dilution plating, 0.5 ml aliquots of measured sample suspensions prepared in 0.1% water agar instead of pure water (Snyder, Nash and Trujillo 1959) were spread uniformly over the surface of solidified agar media in petri dishes (Paharia and Kommedahl 1954). The use of 0.1% water agar as a diluent helped to keep the entire soil sample in suspension. This offered a distinct advantage over the use of pure water, thus virtually eliminating one significant disadvantage of classic dilution plating of soil.

Media in petri dishes were allowed to "dry" (age) for about 72 hr prior to use (Paharia and Kommedahl 1956) to eliminate free surface water on the plates and thus to promote optimal distribution of propagules and separate, clear colony development. The water agar suspensions were pipetted onto plates and distributed uniformly by sterile, bent, 3-mm diameter glass rods. Other modifications of the basic method are discussed under Isolation and Quantitation of Fungi.

Soil-Plate Method

In this method, small crumbs of soil (approximately 0.005-0.01 g) were mixed by crushing and stirring with melted but cooled (45-50°C) agar media in petri dishes (Warcup 1950). This method places propagules within the medium as well as at the surface. It also ensures that the whole soil sample is added to plates, something that is not always easily achieved in older dilution-plating techniques using pure water as a diluent.

Soil-Washing Method

This method (Watson 1960) is similar to the dilution-plate technique. However, prior to preparation of the dilution series and plating, each measured

soil sample was subjected to a series of washings until the decanted (discarded) wash water was clear. What remained of the soil sample to be plated were the larger, but still mostly fine, soil particles. The method was aimed at detection of particle-bound propagules that might be "overshadowed" by more numerous free elements in soil. In this research, the washed soil was diluted with 0.1% water agar and plated by the spread-plate technique onto aged media. In addition, washed soil was processed by the soil plate technique.

Incubation of Soil Plates

Plates were incubated unstacked, on flat table tops, under 12-hr/day illumination from fluorescent lights in a room with an ambient temperature of 23-25°C. Most colonies were ready for counting and isolation in 3-10 days from the time of plating; a few fungi appeared in 15-20 days. All plates were observed for at least 30 days. The speed of growth was partly a function of the selective media. Specific comments are included in Appendix 2.

Identification of Fungi

Individual fungi were numbered and isolated into axenic culture on suitable media (Appendix 2) for identification. Similar fungi were grouped early to expedite identification.

Many manuals and other references were used for general identifications (von Arx 1970; Barnett and Hunter 1972; Barron 1968; Dennis 1968; Domsche and Gams 1972; Ellis 1971; Gams 1971; Gilman 1957; and Hughes 1951). Groups identified primarily by standard methods or references included Aspergillus (Raper and Fennell 1965), Chaetomium (Ames 1963; Seth 1970), Cylindrocarpon (Booth 1966), Fusarium (by the Snyder and Hansen system: Messiaen 1959; Synder and Toussoun 1965; Toussoun and Nelson 1968), Mucorales (Gilman 1957; Zycha, Siepmann and Linneman 1969), Penicillium (Raper, Thom and Fennell 1968), Papulaspora (Hotson 1942), Pestalotia (Guba 1961), Pythium (Waterhouse 1967, 1968; Hendrix and Papa 1975). Information on media used in identifications is provided in Appendix 2.

Actinomycetes and bacteria were not specifically identified.

Detection and Quantitation of Fungi

The soil-dilution spread-plate technique, by nature, was the only method that supported accurate measurement of microbial populations. It is realized, of course, that what is considered a measurement of the population is based on

countable colonies on isolation plates. These numbers may not accurately represent actual soil population levels; they are interpreted at least as relative measurements of population sizes which can be used for intersite comparisons within a species.

To support accurate quantitation, 10 g (dry-weight equivalent) of each composite soil sample was used to make the initial 1:10 (w/v) dilution of a series. The 1:10 mixture was first shaken by hand and then stirred for 10 min on a magnetic stirring unit to ensure complete homogenization and suspension of soil in the 0.1% water agar carrier. Additional dilutions were initiated immediately after stirring. This procedure ensured that the original, whole soil sample was well represented in all dilutions.

For fungi, serial dilutions of $1:10 - 1:10^4$ were used; for actinomycetes and bacteria, dilutions up to $1:10^6$. A range of dilutions was used in all studies to obtain optimal colony counts per plate (Garrett 1951) and thereby maximize the determination of populations and the recovery of potential reference species. The inclusion of high dilutions which yielded few counts per plate was intended to promote the isolation of species that might be otherwise inhibited or masked by competing species (Warcup 1960). As could be expected, the more selective the fungal media, the lower the optimal dilutions. In a very selective medium such as V8-A+ for Phycomycetes, dilutions of 1:10 and 1:100 were generally optimal. The 1:1000 - 1:5000 dilutions were usually optimal for the nonselective fungal media and counts of "total fungi." Counts of actinomycetes and bacteria were routinely done on the $1:10^5$ dilution plates.

Results and Conclusions

Fungi and Fungal Communities

Over 500 fungi were isolated. Some fungi were isolated repeatedly, so the total number of different species identified was 67. Of these, approximately 3% were Oomycetes; 3% Ascomycetes; 10% Zygomycetes (Mucorales); 82% Fungi Imperfecti; and 2% Mycelia Sterilia and Basidiomycetes. The distribution of these fungi according to the four transect sites is shown in Table 1. Detailed information on the fungi and the relative population sizes is presented in Appendix 3.

The most common genera were Absidia, Cylindrocarpon, Fusarium, Gliocladium, Mucor, Mortierella, Penicillium, Pythium, Trichoderma, and Verticillium. Certain fungi, such as Cephalosporium, Cordana, Pyrenochaeta, and Pestalotia were very limited in distribution.

TABLE 1. Distribution of fungi among soil collection relevés on Mauna Loa Transect, 1972.

Acacia koa relevé only	At both relevés	*Metrosideros* relevé only
Kipuka Puaulu (1224-m level)		
13 isolates	20 isolates	9 isolates
Chloridium chlamydosporis	*Absidia spinosa*	*Anixiopsis* sp.
Cordana pauciseptata	*Cephalosporium acremonium*	*Chalaropsis* sp.
Cylindrocarpon destructans	*Cylindrocarpon lucidum*	*Coniothyrium* sp.
C. obtusisporum	*Fusarium oxysporum*	*Cylindrocarpon candidum*
Doratomyces microsporum	*F. solani*	*C. ianthothele*
Penicillium diversum	*Gliocladium deliquescens*	*Gliocladium vermoeseni*
P. implicatum	*G. roseum*	*Mortierella isabellina*
P. lanosum	*Gliomastix murorum* var. *felina*	*Myrothecium verrucaria*
P. lilacinum	*Humicola fuscoatra*	*Sphaerosporium* sp.
Phialophora sp.	*Mortierella ramanniana*	
Pythium spinosum	*Mucor globosus*	
Stilbella bulbicola	*Paecilomyces carneus*	
Verticillium chlamydosporium	*Penicillium janthinellum*	
	P. nigricans	
	P. rugulosum	
	P. variabile	
	Pyrenochaeta decipiens	
	Pythium sp.	
	Spicaria violacea	
	Trichoderma viride	

TABLE 1 Continued.

Acacia koa relevé only	At both relevés	*Metrosideros* relevé only
End of Strip Road (2040-m level)		
19 isolates	7 isolates	18 isolates
Absidia glauca	Absidia spinosa	Cephalosporium curtipes
Aspergillus sydowi	Cephalosporium acremonium	Chaetomium fusisporale
Colletotrichum sp.	Gliocladium roseum	Cladosporium cladosporioides
Cylindrocarpon destructans	Mortierella ramanniana	C. oxysporum
C. obtusisporum	Paecilomyces carneus	Curvularia verruculosa
Fusarium oxysporum	Penicillium nigricans	Fusarium sp.
F. solani	Pestalotia planimi	Humicola fuscoatra
Gliocladium deliquescens		Myrothecium verrucaria
Gliomastix murorum var. felina		Papulospora irregularis
Mucor hiemalis		Penicillium clavigerum
M. jansseni		P. commune
Penicillium aurantio-virens		P. funiculosum
P. chermesinum		P. janthinellum
P. citrinum		P. lanosum
P. corylophilum		P. psittacinum
P. frequentans		P. variabile
P. kapuscinski		Verticillium chlamydosporium
Pythium sp.		V. lecanii
Trichoderma viride		

The major cellulolytic fungi, as determined by isolation on ACA+, were Chaetomium, Gliocladium, Paecilomyces, Penicillium, and Trichoderma. Penicillium and Gliocladium species were isolated from all soils on ACA+. Gliocladium deliquescens was very common. Fusarium was noted infrequently.

Additional comments on the differential occurrence of fungi are included under Selection of Reference Fungi.

General Microbial Populations

Table 2 indicates the comparative levels of general microbial populations in the assayed soils. At both elevations, the koa relevés showed greater populations of actinomycetes, fungi, and bacteria than the ohia relevés; this was more pronounced at the higher elevation. No definite explanation is offered for this difference. Subsequent research did not support the hypothesis of a tree-related effect.

Evaluation of Methods and Materials

Isolation Methods

The soil-dilution spread-plate method was judged best for Phase 2 research for several reasons. First, the soil-plate and soil-washing techniques, as tested, offered no real improvement over the soil-dilution spread-plate method in the detection of fungi. The former methods detected only 9 identified species that were not found on spread plates (Appendix 3). Moreover, an even greater percentage of the total identified species were not detected by the soil-plate and soil-washing techniques. Only 3 genera were found exclusively by the soil-plate or soil-washing methods, and these fungi were not in the major groups which qualified well as reference types for Phase 2. The soil-plate technique has no definite advantage over soil-dilution methods as an indicator of fungal activity in soils (Warcup 1960). The results of this research, compared with comments in the literature, suggest that the value of the soil-plate technique as reported by Warcup (1950) depends a great deal on the particular soil studied.

Results show that the soil-dilution spread-plate technique used together with specially formulated, selective isolation media and 0.1% water agar as the diluent and carrier for soil supported the most uniform, reproducible counts and isolations. The technique allowed for quantitative estimation of propagules per unit of soil. The advantages of the technique were further enhanced by the

TABLE 2. Comparative levels of general microbial populations in soils along the Mauna Loa Transect, as determined by the use of relatively non-selective media. Populations are expressed as propagules per gram oven-dry soil.

Soil Site	IBP Focal Site (No.)	Actinomycetes	Bacteria	Fungi
Kipuka Puaulu	(5)			
Acacia koa relevé		8,300,00	18,100,000	448,000
Metrosideros relevé		1,800,000	4,800,000	100,000
End of Strip Road	(12)			
Acacia koa relevé		8,200,000	16,860,000	500,000
Metrosideros relevé		7,100,000	14,400,000	260,000

fineness of the soils, which contributed to uniform suspension of the samples in the 0.1% water agar diluent. The use of 10 g of soil (dry-weight-equivalent), which constitutes a relatively large volume of sample, for each dilution series should have compensated for effects of localized propagule distribution. Some important genera which have been cited as not occurring often on dilution-plates, such as Mortierella, Pythium, and Trichoderma (Warcup 1960), were detected regularly by the spread-plate technique.

Dilution-plating techniques have shown qualitative fungal differences between root-free and rhizosphere soil (Katznelson 1965). This was considered another potential advantage since the basic research plan called for the study of reference fungi differing in part according to habitat or substrate within the soil. Additional merits of dilution-plating procedures have been discussed by Montegut (1960).

Selective Media

Diet-food medium (DFA+) was judged to be the best general isolation medium. It was especially effective in the detection of both Penicillium and Gliocladium species. In addition, the medium supported many other fungi, including Cylindrocarpon, Paecilomyces, Verticillium and, occasionally, Fusarium. This medium supports excellent differentiation of colonies and rapid, prolific sporulation in many species. Colonies are readily distinguished by color (hyphae and/or spores) and mycelial habit, a feature lacking to a large extent in other media tested. A clearing of the medium itself under some fungi also aids in differentiation.

PDA+ was similar to, but not as effective overall, as DFA+. CMA+, SCA+, and SGA+ were useful in the isolation of many fungi but did not support good differentiation of colonies; this factor made the separation and counting of colonies much more difficult. It should be noted that CMA+ often yielded the largest count of colonies per plate at each dilution; however it is doubtful if the species number was increased. Also CMA+ proved least useful in colony differentiation. V-8A+ was very effective in the isolation and quantitation of the Phycomycetes Absidia, Mortierella, Mucor, and Pythium. ACA+, a medium with carbon as the sole source of carbon, supported primarily species of Aspergillus, Gliocladium, Paecilomyces, and Penicillium. This medium gave relatively high counts of cellulose-degrading fungi and, therefore, was chosen for use in Phase 2.

SCA was considered acceptable for general estimations of actinomycete and

bacterial populations.

Selection of Reference Genera

Reference genera for Phase 2 of this research were chosen on the basis of results obtained in the preliminary survey, and according to established roles and other characteristics of fungi reported in the literature. These genera, which conform to the definition of reference fungi stated under Basic Research Plan, include Absidia, Cylindrocarpon, Fusarium, Gliocladium, Gliomastix, Mortierella, Mucor, Paecilomyces, Penicillium, Pythium, Trichoderma, and Verticillium.

Reference genera were selected in part according to probable habitat- and substrate-specialization. It is difficult to determine the complete capabilities for substrate utilization, or the habitat limitations for individual fungi. The ecological roles or behavior of fungi in soil can vary with conditions, and may not be readily revealed by in vitro studies (Griffin 1972; Wilhelm 1965). The particular roles or capabilities associated with reference genera here are not intended to represent the entire nature or potential of the organaisms but, instead, to indicate some features that make these fungi particularly suited to ecological comparisons based on differential distribution. Members of the Mucorales and other Phycomycetes, for example, are generally considered to be so-called sugar fungi whose carbohydrate nutrition appears to be primarily limited to the lower molecular weight compounds (Garrett 1951). Absidia, Mortierella, Mucor and Pythium fit this classification, and therefore differ significantly from species of Gliocladium, Penicillium, and Trichoderma which are all capable of utilizing compounds such as cellulose. Certain species of Fusarium and Cylindrocarpon might be considered as somewhat intermediate in nutritional specificity (Stoner, unpublished data). While Penicillium has on occasion been placed with the sugar fungi, this research suggests that at least some members of the genus are vigorously cellulolytic. The cellulolytic activities of Penicillium and Trichoderma species were noted by Jensen (1931).

Some fungi are frequently associated with living roots and the rhizosphere and, therefore, might be used as indicators of the effects of vascular plant influences on the distribution of fungal communities. Species within the same genus may show different levels of dependence on or association with the rhizosphere. More frequent association with roots is known as the rhizosphere effect (Clarke 1949; Katznelson 1965). Fusarium and Cylindrocarpon are recognized

as common fungi of the rhizosphere (Katznelson 1965; Kubikova 1968; Waid 1960). Thorton (1960), in a comparison of grassland and forest soils, showed that Cylindrocarpon and Mortierella were commonly associated with roots with secondary thickening. Mucor and Penicillium have been cited also (Katznelson 1965). Pythium and Verticillium are well-known also as root-inhabiting fungi. Soil-borne fungi, such as certain species of Fusarium and Pythium with a necessary parasitic phase in their life cycles which requires a close relationship with plant roots,belong to the ecological group known as soil invaders, as opposed to the less dependent soil inhabitants (Waid 1960).

It is probable that a majority of soil-borne fungi are influenced in some way by the factors of the rhizosphere. Some genera, however, by nature of their scope of nutritional specificities, are considered to include species whose roles encompass decomposition of organic matter somewhat independently from influences of, or direct dependence on, living roots. Such species, which fit the definition of true soil inhabitants as opposed to soil invaders (Waid 1960), belong to Absidia, Paecilomyces, Penicillium, Trichoderma, and many other genera.

Other investigators have related differential distribution to various broad or narrow environmental influences. For example, in a study of temperate hardwood forest soils, Tresner, Backus and Curtis (1954) cited species of Mucor, Penicillium, and Spicaria as indicators of pioneer vs. climax communities. Mortierella ramanniana (= Mucor ramannianus) and Penicillium species have been cited as widely distributed fungi in forest soils (Wright and Bollen 1961; Jensen 1931; Tresner, Backus and Curtis 1954). Aspergillus has been collected more frequently from warmer soils, while Penicillium and Mucor have been associated with cooler areas (Thorton 1960; Warcup 1951). Soil pH in its broad sense has been related to the overall distribution of species of Penicillium (Warcup 1951), Trichoderma, and the Mucoraceae (Jensen 1931). Wet soils tend to have or lack certain fungi (Warcup 1951). The genus Fusarium is cosmopolitan and includes species with a variety of ecological roles from decomposition to parasitism (Booth 1971).

It was hoped that in this research, the independent, overlapping, and interrelated ecological roles and other features possessed by designated reference genera would be reflected in the differential distribution of these fungi along the Mauna Loa Transect.

PRINCIPAL RESEARCH

Methods and Materials

Collection Sites

Soil was collected at 17 different sites, 16 of which were on the Mauna Loa Transect. These sites are described briefly on Table 3 and in detail in Appendix 4. Their locations on the transect are indicated on Figure 2, above. Fourteen sites were selected to match the IBP focal sites for purposes of spatial integration (Mueller-Dombois 1973). Two additional sites were selected within the general ranges of IBP focal sites: soil site 5 at Bird Park for comparison of a closed kipuka forest with nearby savanna; and soil site 7 at 1485 m (4900 ft) elevation, near site 8, for comparison of a Styphelia scrub area (at 7) with a koa colony community (at 8). One additional site was established at Kipuka Nene (864 m; 2850 ft), an ohia forest area downhill from the lowest point on the Mauna Loa Transect. This area was included for comparative purposes.

It should be noted that the collection sites at Kipuka Puaulu and at the 2040-m (6700 ft) level were different in 1973 than during the preliminary study in 1972.

Soil collection sites are referred to here simply as sites, while the IBP focal sites, if mentioned, are identified as such.

Collection and Analyses of Soil Samples

Collection

Soils were collected within approximately 10 x 10 m square areas at the sites. Slight increases in the collection areas were necessary at the 2440 and 2745 m (8000 and 9000 ft) elevations (sites 15 and 16) because of the discontinuous distribution of soil. Samples were taken in all cases from the A_1 or equivalent horizon in the root zone of dominant vascular plants in the area, according to techniques described under Preliminary Study. At sites such as 7, 8, and 9 where the effects of feral pig activity were particularly noticeable, soils were collected from areas which were apparently free of recent disturbance and where the soil horizons appeared to be intact.

All samples were collected during one week in July 1973, in the middle of a very dry period (Bridges and Carey 1974). Since there had been no recent rain on any sites, the soil samples were judged to be especially good for qualitative and

TABLE 3. Soil collection sites on Mauna Loa Transect and at Kipuka Nene.*

Soil Site No.	IBP Focal Site (No.)	Location (name abbreviation)	Vegetation and A_1 Soil
1	Not on transect	Kipuka Nene (KN) 2850 ft (864 m); near Radovsky arthropod-pitfall site	Open Metrosideros (ohia) kipuka forest with grass-vine understory; fine, light-brown, sandy soil
2	(1)	Thurston Lava Tube (TH) 3920 ft (1195 m); near arthropod pitfall and IBP climatic station	Closed Metrosideros-Cibotium (ohia-tree fern) forest; dark, stony muck soil
3	(2)	Sulphur Bank (SB) 4000 ft (1220 m)	Open Metrosideros-Gleichenia (ohia-matted fern) forest; dark, stony muck soil
4	(3)	Tree Molds area (TM) 4000 ft (1220 m); near arthropod-pitfall	Open Metrosideros-native shrub-lichen forest; light-brown, sandy soil
5	On transect, treated as a relevé of (4)	Kipuka Puaulu (KP) 4000 ft (1220 m); near arthropod-pitfall	Closed kipuka forest; Sapindus with Psychotria-Sophora-Coprosma understory; deep, fine, dark brown forest soil
6	(4)	Kipuka Ki (KK) near climatic station, 4200 ft (1280 m); near arthropod-pitfall	Acacia koa-Sapindus savanna; fine, brown forest soil
7	On transect, treated as a relevé of (5)	Power Line Trail (ST) 4900 ft (1485 m); Styphelia-fern-grass zone	Mt. Parkland ecosystem; Styphelia-fern-grass zone; light, rusty-brown, granular soil with scattered, small rocks
8	(5)	Power Line Trail (PL) 4920 ft (1500 m) near arthropod-pitfall	Mt. Parkland ecosystem, Acacia koa colony; light-brown, granular soil, with scattered, small rocks
9	(6)	IBP Climatic Station (CS) 5250 ft (1600 m); near arthropod-pitfall	Mt. Parkland ecosystem, Acacia koa colony; fine, rusty-brown soil
10	(7)	Keamoku Flow (KF) just above, 5650 ft (1720 m)	Mt. Parkland ecosystem, Acacia koa colony; fine-granular, brown soil

* Detailed site information is presented in Appendix 4.

TABLE 3 Continued.

Soil Site No.	IBP Focal Site (No.)	Location (name abbreviation)	Vegetation and A_1 Soil
11	(8)	Above Goat Exclosure (GE) 6200 ft (1890 m)	Mt. Parkland ecosystem, Acacia koa colony; fine, rusty-brown soil
12	(9)	End of Strip Road (ER) 6700 ft (2040 m); near arthropod-pitfall	Mt. Parkland ecosystem, Acacia koa colony; fine, brown, apparently shallow soil
13	(10)	7000-foot level, (2130 m)	Open Metrosideros scrub-forest; ohia-Styphelia area; fine, light-brown, shallow soil with lava outcroppings
14	(11)	7500-foot level, (2290 m)	Open Metrosideros scrub-forest; ohia-Styphelia area; fine, light-brown, shallow soil with lava outcroppings
15	(12)	8000-foot level, (2440 m)	Metrosideros tree line ecosystem; open scrub with scattered trees; light, rusty-brown shallow soil with lava outcroppings
16	(13)	9000-foot level, (2745 m)	Vaccinium-Styphelia low-scrub desert (very sparse scrub); fine, light-brown soil in pockets separated by lava
17	(14)	10000-foot level, (3050 m); Puu Ulaula area	Vaccinium-Styphelia low-scrub desert (very sparse scrub), scattered grasses; reddish sandy-gravelly ash

quantitative intercomparisons of fungal content.

Composite samples for each site were prepared as previously described.

Analyses

Each composite sample was analyzed for pH, water and organic matter content, and available mineral nutrient levels.

Soil pH was determined by using a 1:2 (w/v) soil: 0.01 M $CaCl_2$ suspension (Schofield and Taylor 1955; Smiley and Cook 1972). This method is believed to indicate pH values that are more representative of the rhizosphere.

Organic matter content was determined by the ignition method (Booth and Barrett 1971; Hesse 1971). Samples were held at 600°C for 3 hr in a muffle furnace.

Levels of available calcium, magnesium, phosphorus and potassium were determined by the University of Hawaii-U.S.D.A. Cooperative Soil Testing Service using a 0.3 N HCl extract and the Hellige-Truog method (Hellige, Inc., Garden City, New York). Other available mineral levels were determined by Edward S. Babcock and Sons, Riverside, California, using a 1:5 water extract for chloride, nitrate, and sulfate; a diethylene triamine pentaacetic acid extract for iron, copper, molybdenum, manganese, and zinc; and a saturation extract for boron, sodium, and determination of electrical conductivity. Mineral nutrient levels were expressed in concentrations of parts per million based on a suggested density of 35 lbs/ft^3 for the soils tested (Oran F. Bailey, Soil Conservation Service, Honolulu, personal communication).

Selective Isolation Media

Media used are discussed under Preliminary Study and described in Appendix 2. The selectivity of the media is indicated in Appendix 7. DFA+ was employed as a general medium for fungi. ACA+ was used to selectively isolate cellulolytic fungi. ACA+ supported some of the same fungi found on DFA+, and was therefore useful in checks on the population counts of those fungi. Interestingly, ACA+ was the only medium which supported consistent coremium development by Gliocladium catenulatum. V8-A+ selectively isolated Phycomycetes (Oomycetes and Zygomycetes). PCNB (Nash and Snyder 1962) was employed to selectively isolate Fusarium. Interestingly, this was the only medium to support isolation of Mortierella hygrophila var. minuta. The media used to measure "total" populations of soil-borne microbes were SCA (actinomycetes and bacteria) and DFA+ (fungi).

Isolation, Quantitation, and Identification

The soil-dilution spread-plate method was used for all isolations. In some cases the soil-plate technique was used to confirm the absence of fungi such as Trichoderma from samples.

Identification and quantitation procedures followed the methods already discussed. Spread-plates were surveyed exhaustively for at least 30 days to ensure maximal isolation of reference species as well as other fungi. Most isolations were completed within 15 days of plating. Population levels were expressed as propagules (colony counts) per gram of dry soil.

Analysis and Interpretation of Data

The data were analyzed by relatively objective statistical techniques and by subjective mycological-ecological analysis.

Reference Fungi

Isolations were not restricted to reference genera. Therefore, a number of additional fungi were recorded. Importantly, however, the reference fungi were the focal point of this study and were the only species employed in statistical analyses. Subjective analyses did take into account all of the isolated fungi.

The reference fungi studied included species of Absidia, Cylindrocarpon, Fusarium, Gliocladium, Gliomastix, Mortierella, Mucor, Paecilomyces, Penicillium, Rhizopus, Trichoderma, and Verticillium. Rhizopus was added to the list because of its isolation in 1973 and its ecological and taxonomic relationships with other Mucorales.

Statistical Analyses

Two statistical techniques involving computer programs were employed in this research to determine zones of the Mauna Loa Transect on the basis of differential distribution of significant groups of fungi. The principles and applications of these techniques have been summarized by Mueller-Dombois and Bridges (1975). Only presence/absence information was used with these techniques since recorded population levels were deemed useful only for subjective intraspecific comparisons. The first method, sample ordination by the dendrograph technique of McCammon (1968), using a modification of Sørensen's index (1948), was used to determine the pattern of similarity among the soil sites according to fungal distribution. The resulting dendrograph diagrammatically illustrated the similarity between groups of species.

All of the reference species, regardless of their occurrence pattern, were employed in this technique.

The second analysis used was a species ordination by a two-way table technique based on the Ceska-Roemer program (1971). This method identified groups of fungal species with similar distributional ranges. The designation of groups was controlled by imposed rules that specified required frequencies of association of species and sites. This technique, unlike the dendrograph, excluded reference species with very limited or ubiquitous distribution. This characteristic of the program is valuable, but limits the usefulness of the method in evaluation of so-called species-poor sites. This limitation is an important justification for subjective evaluation of fungal distribution. Since the dendrograph and two-way table technique are different, they serve to complement and support one another in the final analysis. A two-way table technique not involving computer analyses was employed by Mueller-Dombois and Perera (1971) in a study on fungal distribution in montane grasslands of Ceylon.

Subjective Analysis

The qualitative and quantitative data on fungal communities, populations, and distribution were examined subjectively according to mycological and ecological considerations, taking into account especially information that was not used or sufficiently evaluated by the statistical techniques. In this sense, the subjective analyses were mainly useful in confirming and clarifying statistical evidence. For example, species which were excluded from the two-way table analysis because of very broad or narrow distributions were studied in light of major distributional patterns. The absence of certain fungi from sites was carefully noted and evaluated. Population levels were interpreted as possible indications of distributional limits and the importance of individual species in statistical groups. Additional analyses were performed to determine the existence of correlations between environmental factors and fungal distributions.

Results and Discussion

Figure 2 illustrates the locations of sites discussed herein.

Properties of Soils

The measured properties and tentative classification of soils on the Mauna Loa Transect and at Kipuka Nene are presented in Figure 3, Table 4, and Appendix 5. Additional descriptions of soils are given in Appendices 1 and 4.

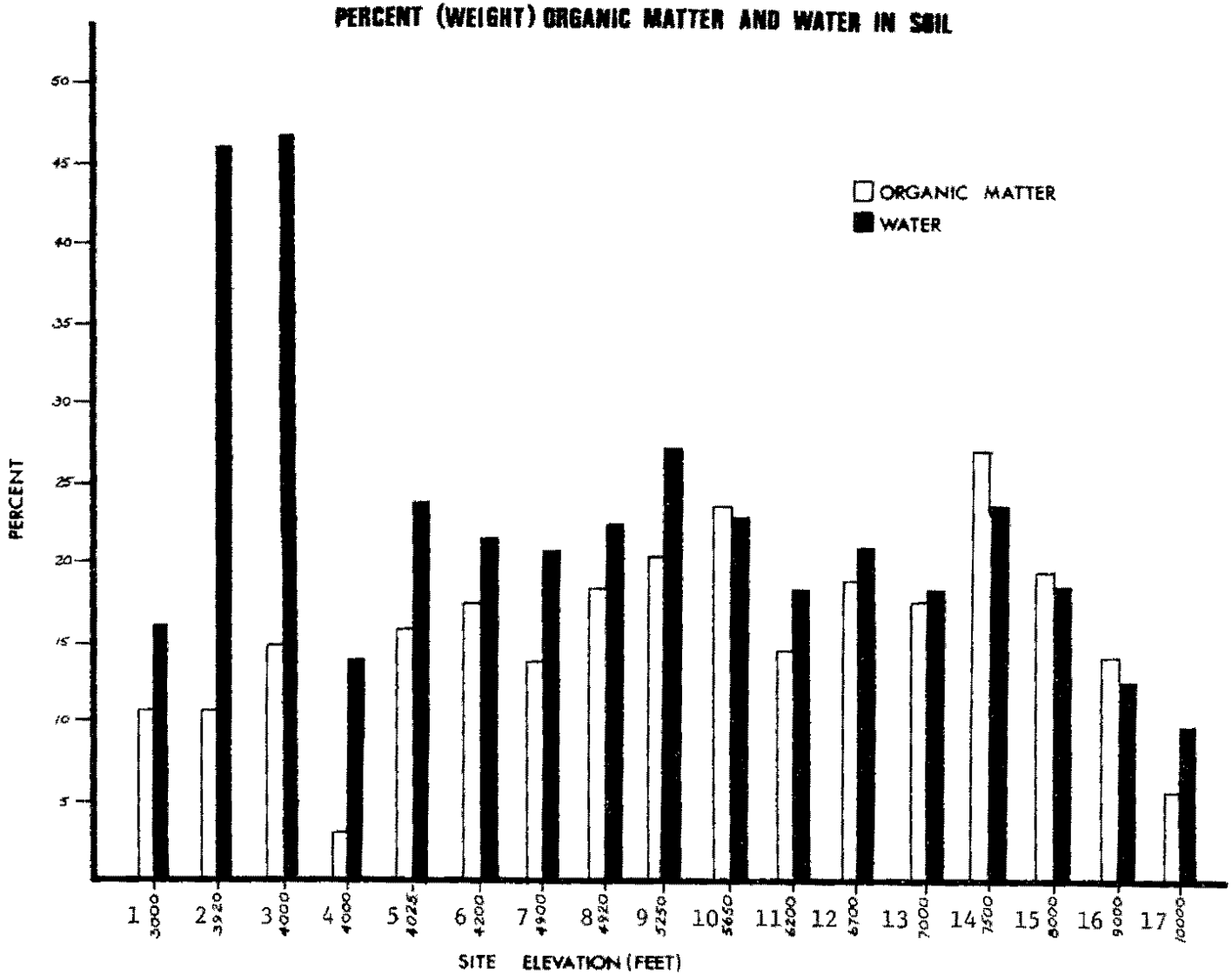


FIG. 3. Percent (weight) of organic matter and water in soils along the Mauna Loa Transect in July 1973.

TABLE 4. Properties and tentative classification[7] of soils at collection sites along the Mauna Loa Transect.

Soil Site No.	IBP Focal Site No.	pH[1] of A_1 Soil	Soil Temperature[2]	% Organic Matter[3]	% Moisture[4]	Order[5]	Subgroup of Soil[5]	Family Information[5]	Probable Related Soil Series	Related 1938 Great Group Name
1	—	6.4	24.5	11	16	Inceptisol	Typic Dystrandepts	Euic, isothermic	Hanipoe?	Latosolic brown forest ?
2	1	5.3	16.0	11	46	Histosol	Lithic Tropofolists	Euic, medial isothermic	Keei	Lithosols
3	2	5.4	17.0	15	47	Histosol	Lithic Tropofolists	Euic, medial isothermic	Keei	Lithosols
4	3	5.2	20.0	3	14	Inceptisol	Lithic Dystrandepts	Euic, medial isothermic	Heake	Regosols
5	4	5.9	17.0	16	24	Inceptisol	Typic Dystrandepts	Euic, medial isomesic	Hanipoe	Latosolic brown forest
6	4	5.7	19.0	17	22	Inceptisol	Typic Dystrandepts	Euic, medial isomesic	Hanipoe	Latosolic brown forest
7	5	5.2	19.5	14	21	Inceptisol	Typic Dystrandepts	Euic, medial isomesic	Hanipoe	Latosolic brown forest
8	5	5.4	22.0	18	23	Inceptisol	Typic Dystrandepts	Euic, medial isomesic	Hanipoe	Latosolic brown forest
9	6	5.0	18.0	23	27	Inceptisol	Typic Dystrandepts	Euic, medial isomesic	Hanipoe	Latosolic brown forest
10	7	5.2	18.5	23	23	Inceptisol	Typic Dystrandepts	Euic, medial isomesic	Hanipoe	Latosolic brown forest
11	8	5.0	19.5	15	18	Inceptisol	Typic Dystrandepts ("Very Stony Land")	Euic, medial isomesic	Hanipoe	Latosolic brown forest
12	9	5.3	17.0	19	21	Inceptisol	Lithic Dystrandepts ("Very Stony Land")	Euic, medial isomesic	Hanipoe	Latosolic brown forest
13	10	5.2	20.0	18	19	Inceptisol	Vitrandepts ("Rock Land")	Euic, medial isomesic	?	Regosols
14	11	5.5	16.0	27	23	Inceptisol	Vitrandepts ("Rock Land")	Euic, medial isomesic	?	Regosols
15	12	5.2	13.0	19	19	Inceptisol	Vitrandepts ("Rock Land")[6]	Euic, medial isomesic	?	Regosols
16	13	5.2	12.0	14	13	Inceptisol	Vitrandepts (Pahoehoe Flows)[6]	Euic, medial isomesic	?	Regosols
17	14	6.5	14.0	5	10	Entisol	Psamment ("Cinder Land")	Euic, cindery isomesic	--	Regosols

[1] $CaCl_2$ method, using field-moist soil

[2] °C at time of collection (July 1973)

[3] Ignition

[4] At collection

[5] Based on pH, temperature, observations, analyses of collected soils

[6] Aeolian soil?

[7] According to classification system used by Sato et al. (1973)

Soil pH values were in the 5.0-6.5 range. The highest pH values were at the lowest site, Kipuka Nene (6.4), and at the highest site, 17, the Puu Ulaula area at 3050 m (10,000 ft) elevation (6.5). All other sites were in the pH 5.0-5.9 range. The adjacent kipuka sites 5 and 6 shared a similar pH, different from surrounding areas.

Organic matter content ranged from lowest levels of 3% and 5% at sites 4 (Tree Molds, 1220 m) and 17 (Puu Ulaula, 3050 m), respectively, to the highest amounts of 23% and 27% on sites 9-10 and 14, respectively. It should be noted, however, that because of the very stony character of the muck soil at rain forest sites 2 and 3, the organic matter content determined for these whole soils is probably less than the actual content which exists in the fine material between the tiny stones. Most sites were in the 11-19% range. Levels of organic matter were generally highest in the intermediate range of the transect; aside from this no pattern is evident.

Since there had been no rain during or prior to the period of soil collection, recorded moisture levels (Fig. 3) are considered as valid for relative comparisons of the sites. Soils of rain forest sites 2 and 3, with 46-47% water, contained at least 76% more moisture than at any other site. Aside from these two rain forest sites, soils of the other sites contained 10-27% water, with the values decreasing roughly toward either end of the altitudinal gradient. Site 17 (3050 m = 10,000 ft elevation) was driest. In general, the water and organic matter levels of the soils appeared to be positively correlated, a common situation in many soils. While sites 2 and 3 may appear in the data as exceptions to this rule, it must be remembered that the moisture holding portions of soils in those areas probably has a much higher organic matter content than is indicated by analysis of the complete, stony samples.

The mineral abundance values in Figure 4 and Appendix 5 are based on agricultural standards, with consideration to the nature of Hawaiian soils. It is clear that soil (site) 17 has the lowest overall levels. Soil 17 differed from all others in having only a trace of calcium. This soil had very low levels of 8 of the 14 elements tested, including phosphorus (P) and potassium (K), 3 other major elements, and 3 minor elements. Soils (sites) 13-17 were low in sodium. Soils 11, 13, 17 were low in both P and K. All soils had low to very low concentrations in some major elements and at least one minor element. Soil 5 (Kipuka Puaulu) had the best overall mineral abundance, including the highest N, P, K levels, of any site. Nitrogen was most abundant in soils 2, 5, 6, 8-10, and

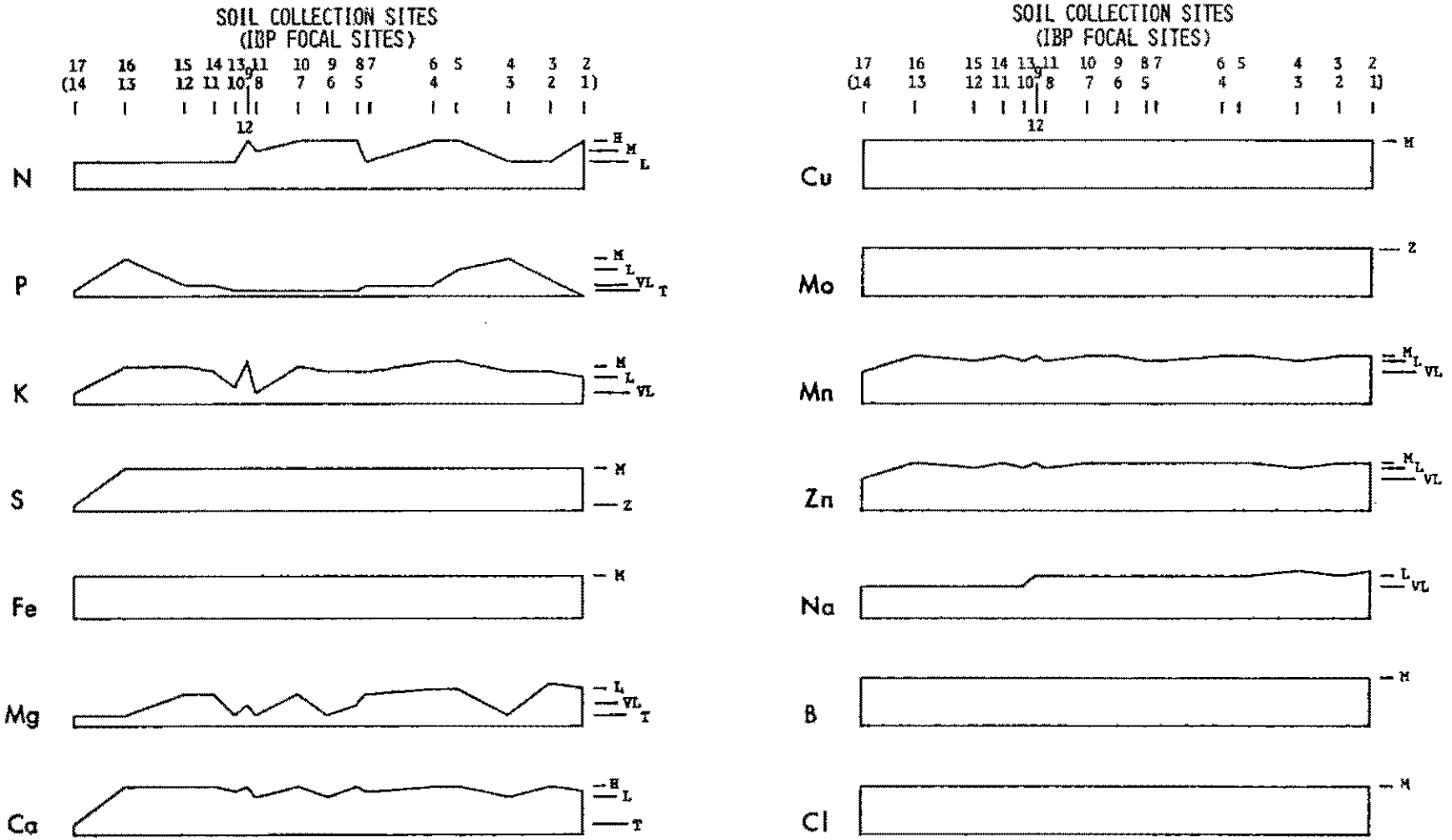


FIG. 4. Mineral abundances along the Mauna Loa Transect plotted as values relative to optimal agricultural levels. For positioning of the sites, see Figure 6. H = high, M = medium, L = low, VL = very low, T = trace, Z = zero (not detected). Site one is not included. (See Appendix 5.)

12. The two rain forest soils, 2 and 3, differed considerably in available nitrogen but not in any other elements.

The condition of the litter and humus at each site is given in Appendix 4. Soils of rain forest sites 2 and 3 show a reasonably clear differentiation between the litter, fermentation and humus layers. Sites 4 and 13 had no definite humus layer; sites 1, 5-12, and 14-16, slight humus layers; and 17, very little litter and no humus layer. These conditions indicate active mixing of decomposing organic matter with the mineral soil by soil animals such as earthworms. At higher elevations, wind or the porous nature of the Vitrandepts could explain the lack of surface accumulation of fine, decayed material.

General Microbial Populations

Table 5 and Figure 5 indicate the general or overall population levels of actinomycetes, bacteria, and fungi according to sites. Some trends are evident. Bacterial counts were highest in the wet soils (sites 2, 3) and at sites 5 and 9. Site 5 was in a closed forest. Site 9 had the highest soil moisture percentage of the mesic sites. These factors suggest a general, positive correlation between moisture content and overall bacterial populations. Organic matter probably could be included also in this relationship. There is a general indication that overall fungal and actinomycete populations are highest in the mesic sites (Fig. 5); these populations are lowest in the very wet soils (sites 2, 3) and the drier soils at the highest elevations and at site 4 (Tree Molds area). It appears that in wet soils the populations of fungi and actinomycetes have an inverse relationship to bacteria. With the exception of wet soils, actinomycete and fungal populations in general appear to be positively correlated with moisture and organic matter levels in soils. Soil temperature (Table 4) has to be considered here as an interacting variable, particularly at the extremes of the transect.

Fungi and Fungal Communities

The fungi isolated from soil samples, together with their population values, are listed alphabetically, according to site in Appendix 6. The species comprising fungal communities are presented according to site in Table 6.

The fungal taxa and numbers of species representing them in the 1972 and 1973 isolations are listed in Table 7. The species representing fungal taxa are listed in Appendix 8. Thirty six species have not been reported previously in

TABLE 5. Comparative levels of general microbial populations in soils along the Mauna Loa Transect, as determined by the use of relatively non-selective media.* Populations are expressed as propagules per gram oven-dry soil.

Soil Site No.	IBP Focal Site (No.)	Actinomycetes	Bacteria	Fungi
1	--	4,200,000	11,000,000	108,000
2	(1)	800,000	28,400,000	56,000
3	(2)	2,400,000	18,200,000	104,000
4	(3)	1,400,000	12,600,000	44,000
5	(4)	5,800,000	21,400,000	196,000
6	(4)	9,100,000	11,300,000	272,000
7	(5)	3,000,000	5,100,000	76,000
8	(5)	5,400,000	13,400,000	288,000
9	(6)	4,400,000	16,600,000	236,000
10	(7)	7,800,000	9,000,000	296,000
11	(8)	2,700,000	5,900,000	49,500
12	(9)	3,550,000	13,350,000	288,000
13	(10)	1,400,000	3,000,000	13,000
14	(11)	5,600,000	11,600,000	248,000
15	(12)	1,800,000	1,400,000	206,000
16	(13)	800,000	8,801,000	35,200
17	(14)	240,000	1,100,000	4,820

* Fungi counted on DFA, bacteria and actinomycetes on SCA; see Appendix 2 for contents of media.

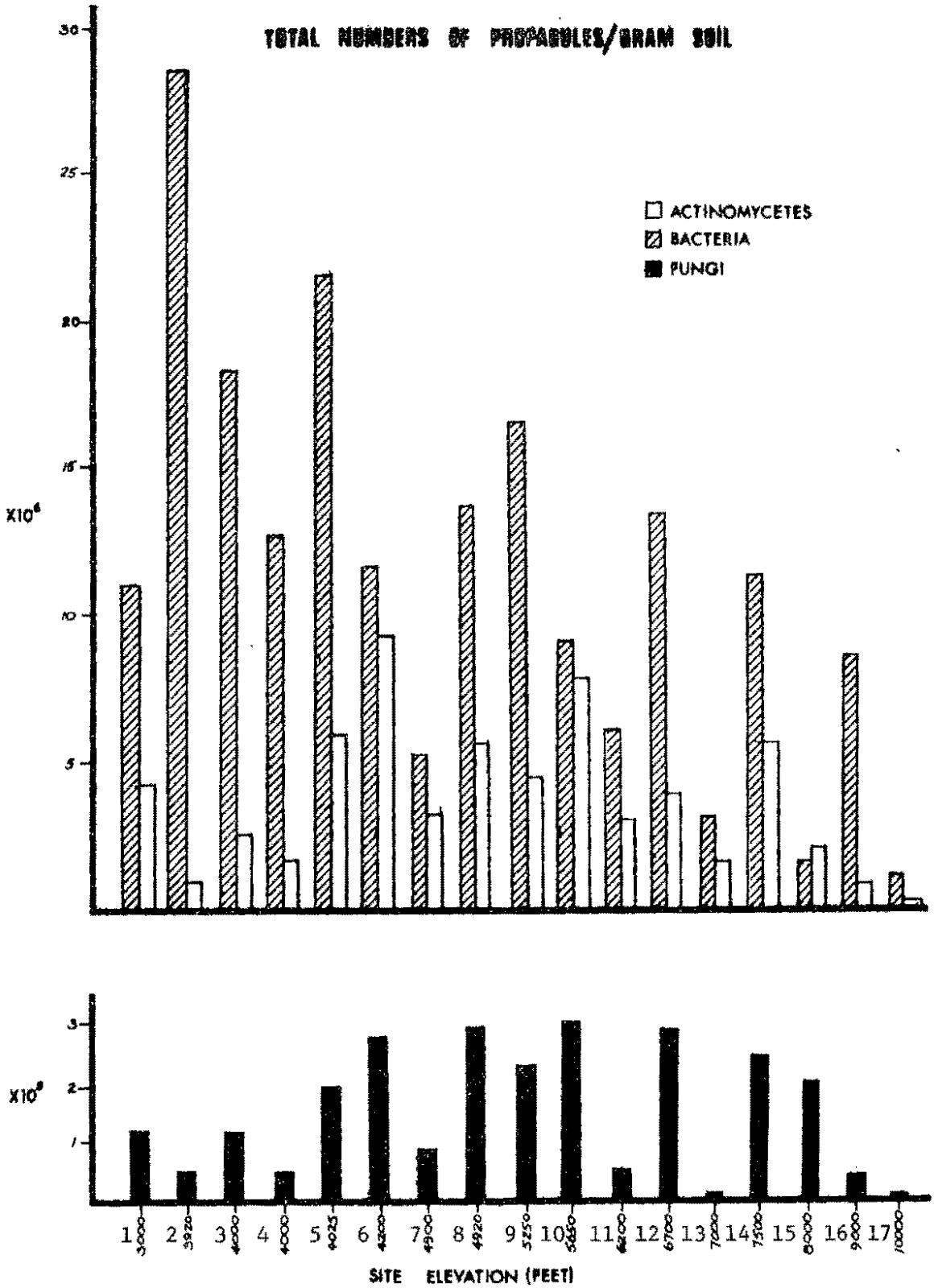


FIG. 5. Total numbers of propagules per gram dry soil of actinomycetes, bacteria, and fungi in soils along the Mauna Loa Transect.

TABLE 6. Complete list of soil-borne fungi found at sites along the Mauna Loa Transect. Site numbers in parentheses represent IBP Focal Sites.

Site 1 (Not on transect)

Absidia spinosa
Cladosporium cladosporioides
Fusarium solani
Gliocladium vermoeseni
Gliomastix murorum var. felina
Mucor strictus
Penicillium frequentans
P. ochro-chloron
Pythium irregulare
Trichoderma viride
T. viride (T. koningi type)
Verticillium cephalosporum

Site 2 (1)

Cylindrocarpon didymum
C. magnusianum
Gliocladium catenulatum
Mortierella ramanniana
Pythium irregulare
Staphylotrichum coccosporium
sterile isolate #77
Trichoderma viride
Verticillium cephalosporum

Site 3 (2)

Aureobasidium pullulans
Cylindrocarpon didymum
Gliocladium catenulatum
Gliomastix murorum var. felina
Mammaria echinobotryoides
Mortierella ramanniana
sterile isolate #77
sterile isolate #228
Trichoderma viride (T. koningi type)

Site 4 (3)

Aphanocladium sp.
Cylindrocarpon didymum
Fusarium oxysporum
Gliocladium catenulatum
G. deliquescens
G. vermoeseni
Gliomastix murorum var. felina
Mortierella ramanniana
Mucor lausannensis
Paecilomyces carneus
Papulospora irregularis
Penicillium lilacinum
P. ochro-chloron
P. rubrum
Pythium irregulare
sterile isolate #77
Trichoderma viride

Site 5 (4)

+Absidia spinosa (K,M)
+Anixiopsis sp. (M)
Aspergillus flavus
+Cephalosporium acremonium (K,M)
+Chalaropsis sp. (M)
+Chloridium chlamydosporis (K)
+Coniothyrium sp. (M)
+Cordana pauciseptata (K)
+Cylindrocarpon candidum (M)
+C. destructans (K)
+C. ianthothele (M)
+C. lucidum (K,M)
+C. obtusisporum (K)
+Doratomyces microsporum (K)
+Fusarium oxysporum (K,M)
F. rigidiusculum
(+)F. solani (K,M)
(+)Gliocladium deliquescens (K,M)
(+)G. roseum (K,M)
+G. vermoeseni (M)
+Gliomastix murorum var. felina (K,M)

+ = 1972 isolations; (+) = found in both 1972 and 1973; all others represent only 1973 isolations from all 17 sites

K = Acacia koa relevé; M = Metrosideros relevé (refer to 1972 isolates only)

TABLE 6 Continued.

Site 5 continued

+Humicola fuscoatra (K,M)
+Mortierella isabellina (M)
+M. ramanniana (K,M)
+Mucor globosus (K,M)
Mucor strictus
+Myrothecium verrucaria (M)
+Paecilomyces carneus (K,M)
Penicillium atramentosum
P. clavigerum
+P. diversum (K)
+P. implicatum (K)
+P. janthinellum (K,M)
+P. lanosum (K)
+P. lilacinum (K)
+P. nigricans (K,M)
P. ochro-chloron
+P. rugulosum (K,M)
+P. variabile (K,M)
+Phialophora sp. (K)
Pycnidial isolate #1
+Pyrenochaeta decipiens (K,M)
+Pythium sp. (K,M)
P. irregulare
+P. spinosum (K)
+Sphaerosporium sp. (M)
+Spicaria violacea (K,M)
sterile isolate #147
+Stilbella bulbicola (K)
Torula herbarum
(+)Trichoderma viride (K,M)
T. viride (T. koningi type)
Verticillium cephalosporum
(+)V. chlamydosporium (K)
V. lateritium

Site 6 (4)

Absidia spinosa
Cylindrocarpon lucidum
Fusarium oxysporum
F. solani
Gliocladium deliquescens
G. roseum
G. vermoeseni
Mortierella ramanniana
Mucor strictus
Paecilomyces carneus

Site 6 continued

Penicillium atramentosum
P. frequentans
P. ochro-chloron
Trichoderma viride (T. koningi type)
Verticillium cephalosporum

Site 7 (5)

Absidia glauca
Cylindrocarpon didymum
Fusarium oxysporum
Gliocladium catenulatum
Gliomastix murorum var. felina
Mortierella isabellina
M. ramanniana
Papulospora irregularis
Penicillium atramentosum
P. aurantio-candidum
P. nigricans

Site 8 (5)

Absidia spinosa
Cylindrocarpon didymum
Fusarium oxysporum
Gliocladium deliquescens
Gliomastix murorum var. felina
Mortierella ramanniana
Paecilomyces carneus
Penicillium nigricans
P. ochro-chloron
P. verruculosum
Rhizopus microsporus
Spicaria violacea
sterile isolate #19
Trichoderma viride

Site 9 (6)

Absidia glauca
A. spinosa
Aureobasidium pullulans
Fusarium oxysporum
Gliocladium deliquescens
Penicillium lanosum

TABLE 6 Continued.

Site 9 continued

Penicillium ochro-chloron
Pythium irregulare
Spicaria violacea
Trichoderma viride
T. viride (T. koningi type)

Site 10 (7)

Absidia glauca
A. spinosa
Fusarium oxysporum
Gliocladium deliquescens
Mortierella ramanniana
Penicillium atramentosum
P. nigricans
Pythium irregulare
sterile isolate #137
Trichoderma viride
T. viride (T. koningi type)

Site 11 (8)

Absidia spinosa
Curvularia harveyi
Fusarium oxysporum
Gliocladium deliquescens
G. roseum
Mortierella ramanniana
Papulospora irregularis
Penicillium nigricans
P. ochro-chloron
Pycnidial isolate #1

Site 12 (9)

(+)Absidia glauca (K)
(+)A. spinosa (K,M)
+Aspergillus sydowi (K)
+Cephalosporium acremonium (K,M)
+C. curtipes (M)
+Chaetomium fusisporale (M)
+Cladosporium cladosporioides (M)
+C. oxysporum (M)
+Colletotrichum sp. (K)
+Curvularia verruculosa (M)

Site 12 continued

+Cylindrocarpon destructans (K)
+C. obtusisporum (K)
+Fusarium sp. (M)
+F. oxysporum (K)
+F. solani (K)
(+)Gliocladium deliquescens (K)
+G. roseum (K,M)
+Gliomastix murorum var. felina (K)
+Humicola fuscoatra (M)
+Mortierella ramanniana (K,M)
+Mucor hiemalis (K)
+M. jansseni (K)
+Myrothecium verrucaria (M)
(+)Paecilomyces carneus (K,M)
+Papulospora irregularis (M)
+Penicillium aurantio-virens (K)
+P. chermesinum (K)
+P. citrinum (K)
+P. clavigerum (M)
+P. commune (M)
+P. corylophilum (K)
+P. frequentans (K)
+P. funiculosum (M)
+P. janthinellum (M)
+P. kapuscinski (K)
+P. lanosum (M)
(+)P. nigricans (K,M)
+P. psittacinum
+P. variabile (M)
+Pestalotia planimi (K,M)
Pycnidial isolate #1
+Pythium sp. (K)
P. irregulare
(+)Trichoderma viride (K)
T. viride (T. koningi type)
+Verticillium chlamydosporium (M)
+V. lecanii (M)

Site 13 (10)

Absidia glauca
Curvularia harveyi
Fusarium lateritium
Gliocladium catenulatum
Mortierella hygrophila var. minuta
M. ramanniana
Mucor hiemalis

TABLE 7. Total numbers of fungi, according to major taxa, isolated from soils along the Mauna Loa Transect.

Fungi	1972*	1973	Total both years
Phycomycetes	9	11	15
Ascomycetes	3	0	3
Fungi Imperfecti	54	41	75
Moniliales	50	39	70
Moniliaceae	30	25	41
Dematiaceae	9	7	14
Stilbaceae	1	0	1
Tuberculariaceae	10	7	14
Melanconiales	1	0	1
Sphaeropsidales	2	1	3
Mycelia Sterilia	1	1	1
Non-sporulating mycelium	--	9	9
Total number of species	66	61	102

* Phase 1 Preliminary Study

Hawaii (Table 8); 42 species constitute new records from soil in Hawaii (Table 9). No new species were found among the identified fungi.

The occurrence of Aspergillus in soils along the transect is apparently very limited. Only two, isolated records exist--A. flavus at site 5 and A. sydowi at site 12.

The largest populations (Appendix 6) of identified fungi (propagules/g dry soil at site) determined belonged to Trichoderma viride (140,000; site 9), Gliocladium deliquescens (112,000; 10), and Penicillium nigricans (112,000; 10). The smallest populations belonged to Absidia glauca (20, site 13), Curvularia harveyi (20, 11), Fusarium oxysporum (40, 3), Mortierella ramanniana (< 20, 11), Papulospora irregularis (< 20, 4), and Pythium irregulare (< 20, 4).

Appendix 6 is useful in discerning the distributional patterns of individual genera or species.

Spatial Distribution of Fungi and Transect Zones Based on the Mycoflora

The zonation of the Mauna Loa Transect according to the spatial distribution of soil-borne fungal communities was based on both objective and subjective analyses. A complete list of reference species is given in Table 10. A summary of the characteristic as well as total species composition of soil-fungus zones of the Mauna Loa Transect, including qualifying information on determinants, is presented in Appendix 9. Proving that a fungus is truly absent from a soil is difficult. Therefore, absence as discussed here means not detected, which is interpreted to imply, at most, a very small population.

Two related sets of soil-fungus zones (Fig. 6) were determined according to different levels of interpretation based on strong indications in the dendrograph (Fig. 7) and two-way table (Table 11), and on a conservative, subjective evaluation of all information. Although different rules or limitations were imposed in the two-way table technique, the 50/10 rule produced what was considered as the most meaningful information. Population levels of fungi at the intraspecific level were evaluated subjectively. Complete information on populations is given in Appendix 6, and a graphic display of characteristic populations of reference species is presented in Figure 8.

Soil-fungus zone set 1 (Zones A, B, C) includes relatively broad areas of fungal distribution that reflect more general environmental influences related to soil, vegetation, and climate. Set 2 (Zones I-VI) includes relatively narrow

TABLE 8. Fungi not reported previously in Hawaii.

Absidia glauca Hagem
Anixiopsis Hansen
Aphanocladium Gams
Chaetomium fusisporale Rai and Mukerjee
Cordana pauciseptata Preuss
Curvularia harveyi Shipton
Curvularia verruculosa Herb.
Cylindrocarpon destructans (Zins) Scholten
Cylindrocarpon ianthothele Wollenw. var. majus Wollenw.
Cylindrocarpon magnusianum Wollenw.
Cylindrocarpon obtusisporum (Cooke & Harkness) Wollenw.
Doratomyces microsporum (Sacc.) Morton & Smith
Fusarium lateritium emend. Synder et Hansen
Fusarium rigidiusculum emend. Synder et Hansen
Gliocladium vermoeseni (Biourge) Thom
Mammaria echinobotryoides Ces.
Mortierella hygrophila Linnemann var. minuta Linnemann
Mucor jansseni Lendner
Mucor lausannensis Lendner
Mucor strictus Hagem
Paecilomyces carneus (Duche' et Heim) Brown et G. Smith
Papulospora irregularis Hotson
Penicillium atramentosum Thom
Penicillium aurantio-candidum Dierckx
Penicillium aurantio-virens Biourge
Penicillium clavigerum Demelius
Penicillium implicatum Biourge
Penicillium kapuscinskii Zaleski
Penicillium psittacinum Thom
Pestalotia planimi Vize
Pythium spinosum Sawada apud Sawada & Chem
Rhizopus microsporum van Teighem
Sphaerosporium Schw.
Trichocladium opacum (Corda) Hughes
Verticillium cephalosporum W. Gams
Verticillium chlamydosporium Goddard

TABLE 9. Soil-borne fungi of Hawaii not previously reported. All records pertain to soils along the Mauna Loa Transect.

Absidia glauca
Anixiopsis sp.
Aphanocladium sp.
Chaetomium fusiporale
Chloridium chlamydosporus
Collectotrichum sp.
Cordana pauciseptata
Curvularia harveyi
Curvularia verruculosa
Cylindrocarpon destructans
Cylindrocarpon ianthothele
Cylindrocarpon magnusianum
Cylindrocarpon obtusisporum
Doratomyces microsporum
Fusarium lateritium emend. Synder et Hansen
Fusarium rigidiusculum emend. Synder et Hansen
Gliocladium vermoeseni
Humicola fuscoatra
Mammaria echinobotryoides
Mortierella hygrophila var. minuta
Mucor jansseni
Mucor lausannensis
Mucor strictus
Paecilomyces carneus
Papulospora irregularis
Penicillium aurantio-candidum
Penicillium aurantio-virens
Penicillium atramentosum
Penicillium clavigerum
Penicillium implicatum
Penicillium kapuscinskii
Penicillium psittacinum
Pestolatia planimi
Pythium irregulare
Pythium spinosum
Rhizopus microsporum
Sphaerosporium sp.
Torula herbarum
Trichocladium opacum
Verticillium cephalosporum
Verticillium chlamydosporium
Verticillium lecanii

TABLE 10. Reference species employed in statistical analyses by computer. The distribution of these species along the transect is tabulated in Appendix 6.

Absidia glauca
A. spinosa
Cylindrocarpon didymum
C. lucidum
C. magnusianum
Fusarium lateritium
F. oxysporum
R. rigidiusculum
F. solani
Gliocladium catenulatum
G. deliquescens
G. roseum
G. vermoeseni
Gliomastix murorum var. felina
Mortierella hygrophila var. minuta
M. isabellina
M. ramanniana
Mucor fragilis
M. hiemalis
M. lausannensis
M. strictus
Paecilomyces carneus
Penicillium atramentosum
P. aurantio-candidum
P. clavigerum
P. diversum
P. frequentans
P. funiculosum
P. lanosum
P. lilacinum
P. nigricans
P. ochro-chloron
P. rubrum
P. verruculosum
Pythium irregulare
Rhizopus microsporus
Trichoderma viride
Verticillium cephalosporum
V. chlamydosporium
V. lateritium

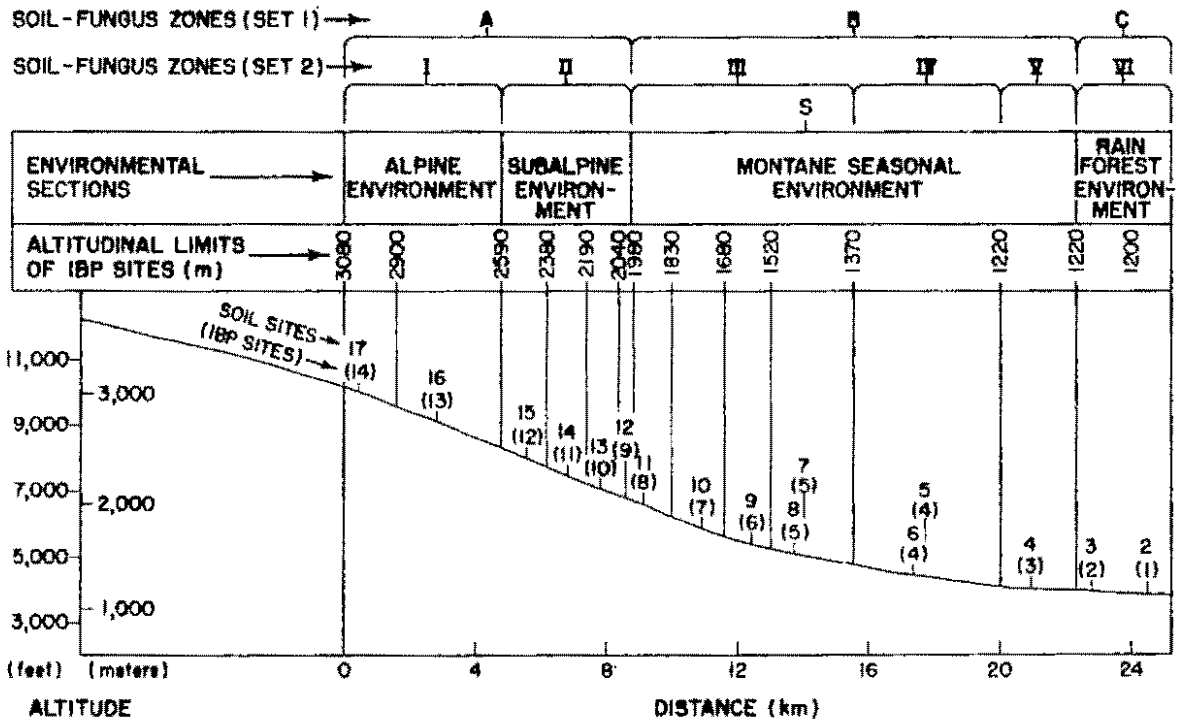


FIG. 6. Profile diagram of Mauna Loa Transect relating soil-fungus zones to general environmental sections.
A = Dry, Cool High Altitude Scrub, B = Mesic Montane, C = Metrosideros Rain Forest; I = Alpine Scrub, II = Sub-alpine Scrub, III = Mountain Parkland, IV = Montane Kipuka, V = Open Metrosideros Dry Forest, VI = Metrosideros Rain Forest; S = Styphelia Scrub Component Community

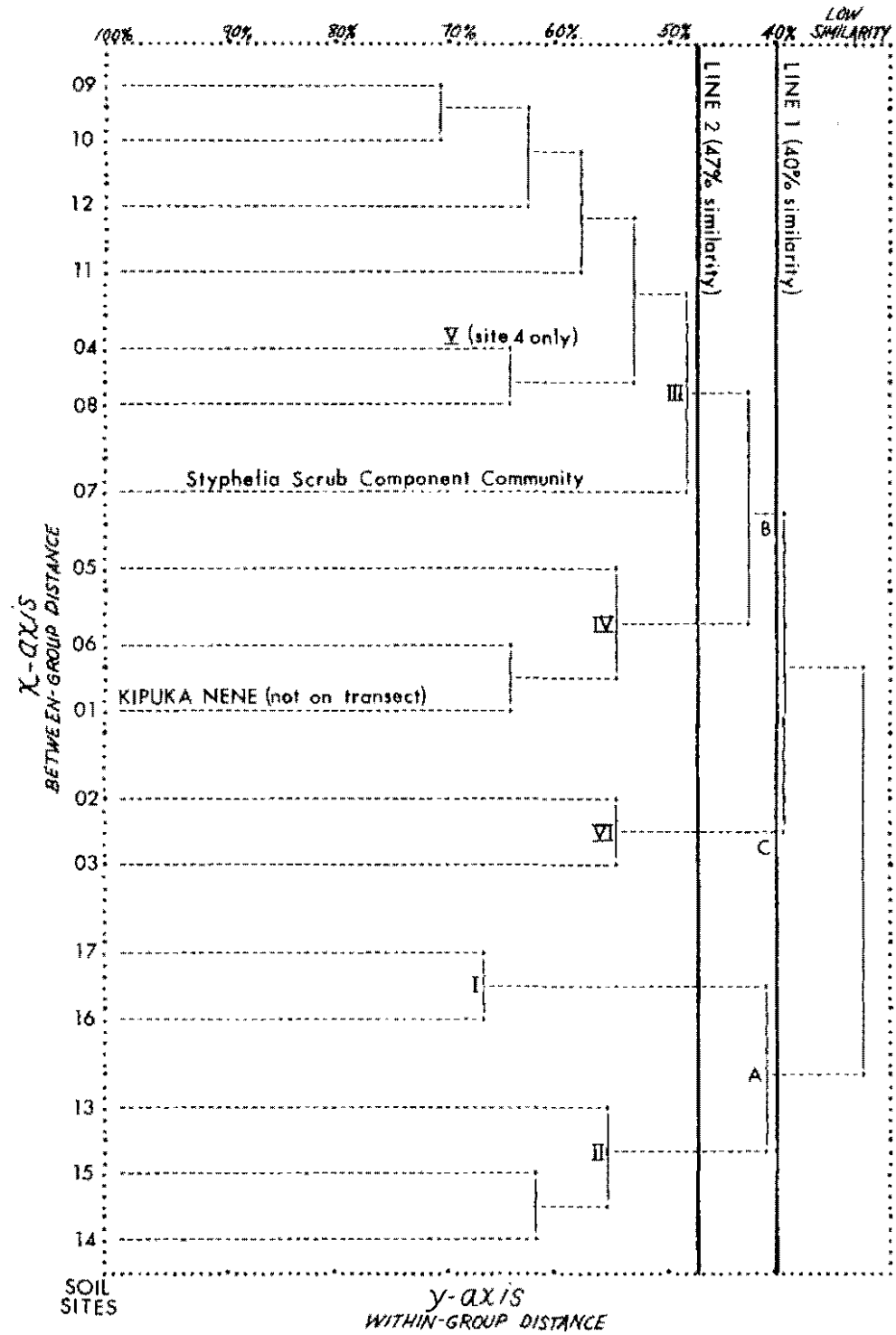
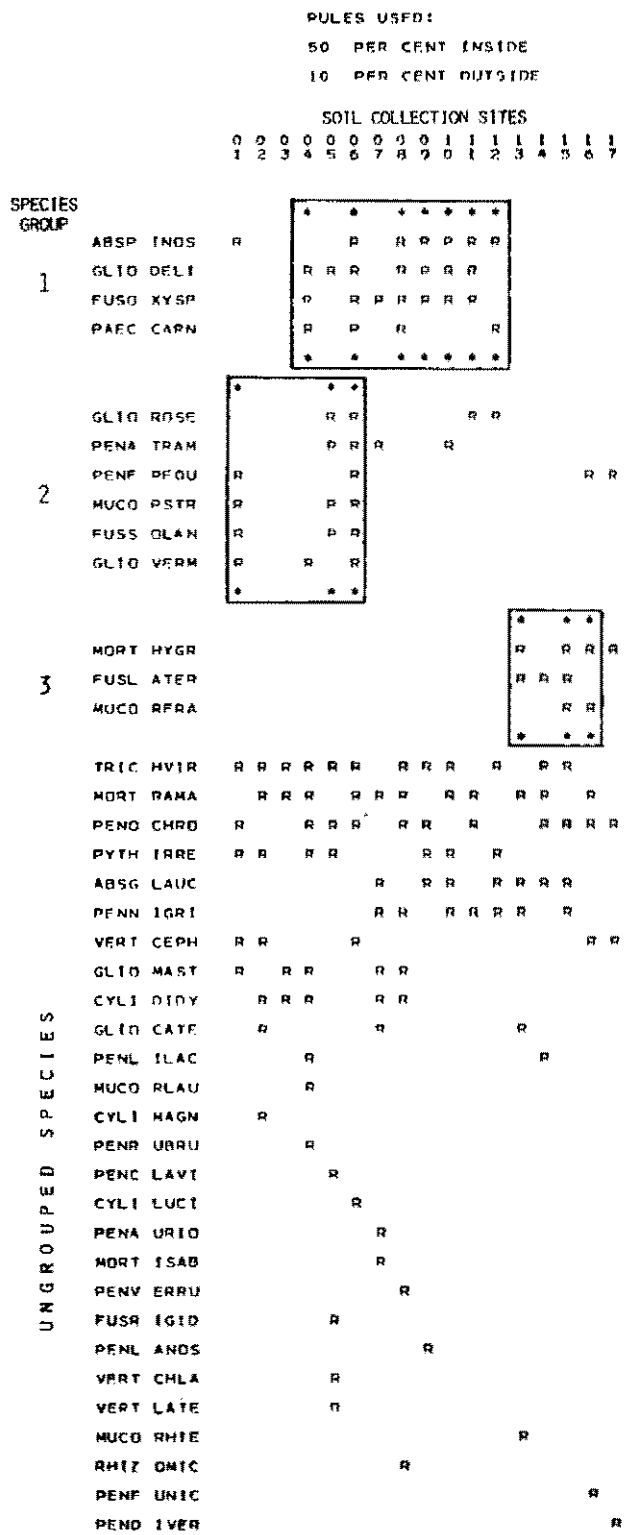
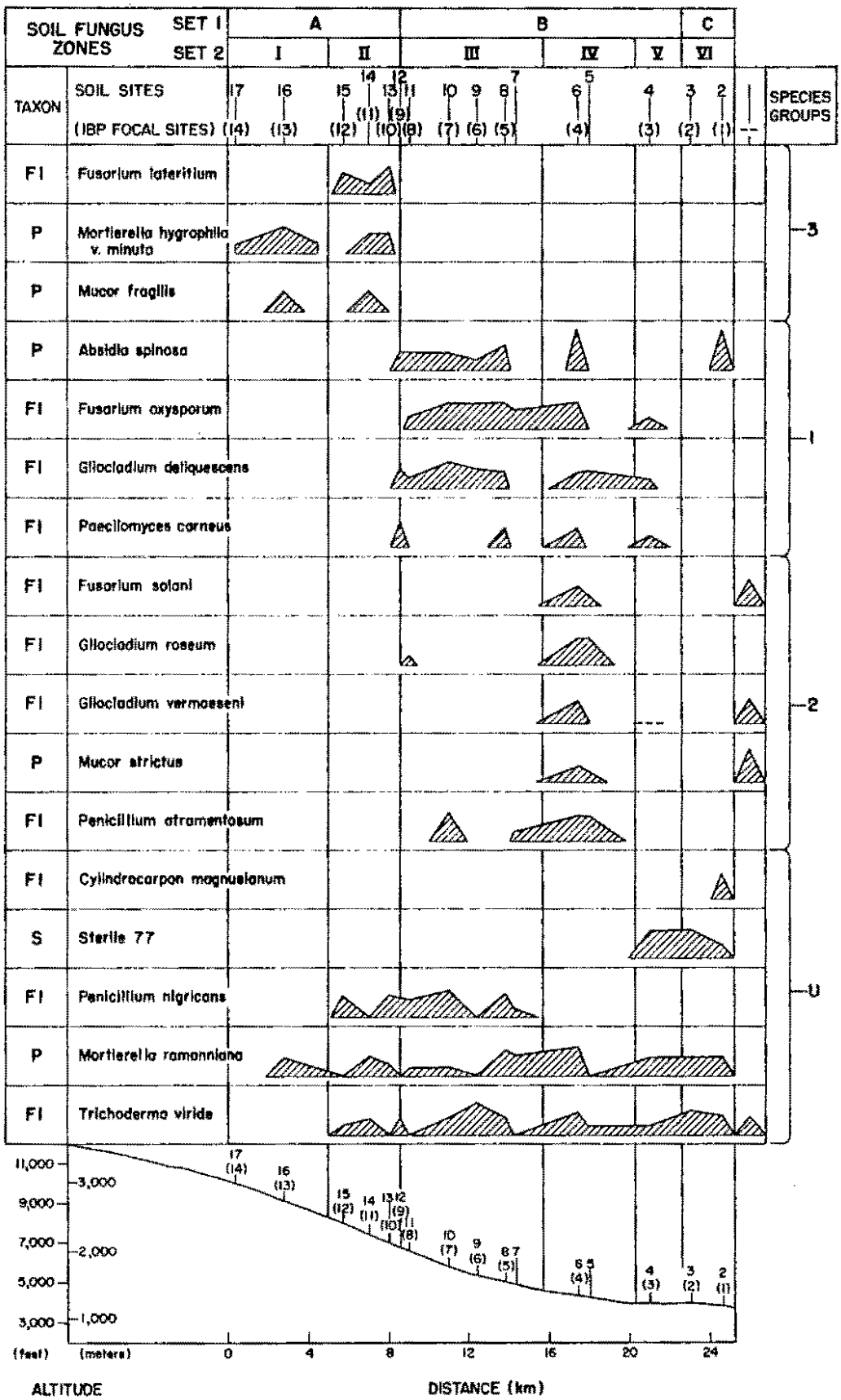


FIG. 7. Dendrograph based on 17 soil collection sites (fungal communities) compared by the qualitative Sørensen index of similarity. The designated soil-fungus zones (see Fig. 6) are: A = Dry, Cool High Altitude Scrub, B = Mesic Montane, C = Metrosideros Rain Forest; I = Alpine Scrub, II = Sub-alpine Scrub, III = Mountain Parkland, IV = Montane Kipuka, V = Open Metrosideros Dry Forest, VI = Metrosideros Rain Forest; S = Styphelia Scrub Component Community.

TABLE 11. Two-way table based on 50/10 rule. Blocked areas represent fungal groups used in the determination of transect zones. Complete names of fungal species listed below are given in Table 10.




SOIL FUNGUS ZONES
SET 1
SET 2
A
B
C
I
II
III
IV
V
VI
TAXON
SOIL SITES
(IBP FOCAL SITES)
SPECIES GROUPS
Fl Fusarium lateritium
P Mortierella hygrophila v. minuta
P Mucor fragilis
P Absidia spinosa
Fl Fusarium oxysporum
Fl Gliocladium deliquescens
Fl Paecilomyces carneus
Fl Fusarium solani
Fl Gliocladium roseum
Fl Gliocladium vermoeseni
P Mucor strictus
Fl Penicillium atramentosum
Fl Cylindrocarpon magnusianum
S Sterile 77
Fl Penicillium nigricans
P Mortierella ramanniana
Fl Trichoderma viride
3
1
2
4
11,000
9,000
7,000
5,000
3,000
3,000
2,000
1,000
(feet)
(meters)
0
4
8
12
16
20
24
ALTITUDE
DISTANCE (km)
Vertical scale for each species
relative population level within species

zones of distribution that reflect more localized environmental influences which tend to align fungal groups with specific soil-plant-climatic complexes.

With one exception, the broad zones in set 1 extend across the more restricted zones in set 2 (Fig. 6). Zone A of set 1 (dry, cool, high altitude scrub soil-fungus zone) includes zones I and II of set 2 (alpine and sub-alpine scrub soil-fungus zones). Zone B of set 1 (mesic montane soil-fungus zone) encompasses zones III, IV, and V of set 2 (mountain parkland, montane kipuka and open Metrosideros dry forest soil-fungus zones, respectively). Zone C of set 1 is identical with zone VI of set 2 (Metrosideros rain forest soil-fungus zone).

The characteristic species composition of soil-fungus zones is discussed below. It should be kept in mind that the importance of characteristic species was, in general, evaluated on the basis of group-occurrence, rather than peculiarities of individual species. Additional information regarding the relative importance of determinants is presented in Appendix 9. The dendrograph (Fig. 7) and two-way table (Table 11) should be consulted for illustrations of site and fungus groups relating to zones. The positions of soil collection sites within soil-fungus zones are shown in Figure 6.

Soil-Fungus Zone Set 1

Zone A--Dry, Cool High Altitude Scrub Zone (Sites 13-17)

Fusarium lateritium, Mortierella hygrophila v. minuta, and M. ramanniana identify this zone. Gliocladium catenulatum, Mucor fragilis, Penicillium frequentans, and P. ochro-chloron are additional evidence for the integrity of the zone. Mortierella hygrophila v. minuta is an especially important indicator of this zone.

This zone, which covers high altitudes, is characterized by relatively cool, dry conditions; shallow and topographically discontinuous soils; and alpine to sub-alpine scrub vegetation. Ground frost can occur at anytime of the year in this zone (Mueller-Dombois 1967).

Zone B--Mesic Montane Soil-Fungus Zone (Sites 4-12)

Absidia spinosa, Fusarium oxysporum, Gliocladium deliquescens, and Paecilomyces carneus are key representatives of this zone. Papulospora irregularis, Penicillium atramentosum, and Pycnidial isolate #1 (with its highest populations in the zone) further define the zone. The zone is indicated strongly by Group 1 on the two-way table (Table 11), and is supported by clusters on the

dendrograph (Fig. 7).

This broad zone covers three zones of set 2: mountain parkland, montane kipuka, and Metrosideros dry forest. While these sub-zones are distinct as treated under set 2, they show important fungal interrelationships that contribute to the integral nature of the Mesic Montane Soil-Fungus Zone. These common bonds are partly illustrated in Figure 8; Fusarium oxysporum, Gliocladium deliquescens, and Paecilomyces carneus are three example links.

This broad zone of intermediate elevations on the transect is characterized by seasonal, mesic conditions; moderately deep to deep soils; and a variety of plant communities including scrub, grassland, savanna, and forest.

Zone C--Metrosideros Rain Forest Soil Fungus Zone (Sites 2-3)

Although this zone does not have a particularly unique group of characteristic species, it lacks several important reference genera that contributed to the delineation of other zones throughout the Mauna Loa Transect. These genera are Absidia, Fusarium, Mucor, and Penicillium. While Gliocladium was not completely absent, the important species G. deliquescens and G. roseum were not detected. The presence of Cylindrocarpon magnusianum and Sterile isolate #77 strengthens the identity of this zone.

This zone covering the lowest elevations on the transect is characterized by relatively high rainfall, muck soils, and rain forest vegetation.

Soil-Fungus Zone Set 2

Zone I--Alpine Scrub Soil-Fungus Zone (Sites 16-17)

This zone is distinguished importantly from adjacent Zone II (sub-alpine scrub) by its combined lack of Absidia glauca, Fusarium lateritium, and Trichoderma viride. The presence of Penicillium frequentans and P. funiculosum is considered important. The individuality of this zone is evident in the dendrograph (Fig. 7).

Zone I is characterized by elevations of over 2440 m (8000 ft); daily ground frost (Mueller-Dombois and Krajina 1968); the discontinuous distribution of soil in shallow pockets and sparse scrub vegetation.

Zone II--Sub-alpine Scrub Soil-Fungus Zone (Sites 13-15)

Fusarium lateritium is a key indicator of this zone. Other indicative species are Absidia glauca, Curvularia harveyi, Gliocladium catenulatum, Penicillium nigricans, and Trichoderma viride. This zone is indicated strongly

by the dendrograph (Fig. 7) and by Group 3 on the two-way table (Table 11).

This zone is characterized by relatively cool, dry conditions; shallow soils; and scrub vegetation ranging downslope from tree line. The scrub vegetation is much more dense on the whole than in Zone I.

Zone III--Mountain Parkland Soil-Fungus Zone (Sites 7-12)

Zone III possesses a wide array of fungi, including 20 reference species. The range of Fusarium oxysporum is primarily in this zone. The nearly complete absence of Gliocladium catenulatum is noteworthy since this fungus is generally distributed above and below this zone on the transect. The general occurrence within the zone of Absidia spinosa and Penicillium nigricans is significant also. Populations of Absidia glauca and Gliocladium deliquescens are generally strong in this zone. Overlap with the lower, adjacent site 6 (savanna) of Zone IV (Montane Kipuka Zone) is evident in the two-way table (Table 11).

Site 7, a Styphelia scrub area within this zone, is of special interest and will be discussed separately.

Zone III is characterized by the upper montane elevations on the transect; seasonal, mesic conditions; moderately deep, well developed soils; and mountain parkland vegetation (Mueller-Dombois and Krajina 1968).

Zone IV--Montane Kipuka Soil-Fungus Zone (Sites 5, 6)

Fusarium solani, Gliocladium roseum, G. vermoeseni, and Mucor strictus are strongly indicative of this zone. The zone is further characterized by the presence of Penicillium atramentosum, P. frequentans, and the relatively high population of Gliocladium roseum. The uniqueness of this zone is shown well both by the dendrograph (Fig. 7) and the two-way table (Table 11; see Group 2).

Zone IV is in a kipuka area with lower montane elevations on the transect; very deep, well developed soils; and both savanna and closed forest communities. The nature and history of soils in this zone are different than those of surrounding areas (Mueller-Dombois and Lamoureux 1967). Soil samples representing this zone were taken from a closed forest area (site 5, Kipuka Puaulu) and a savanna area (site 6, Kipuka Ki).

Of special interest here is the similarity of site 1 (Kipuka Nene), which was not on the transect, to montane kipuka sites 5 and 6 of Zone IV (Table 11, Group 2; Fig. 7; Appendix 9). The similarity of these three sites, in spite of their differences in location, specific vegetation, soil, and perhaps age (Mueller-Dombois and Lamoureux 1967), suggests that a complex of interrelated

environmental factors that we might refer to here as "kipuka influence" could serve to modify or nullify the effects of the altitudinally related factors (and perhaps other forces) that partly determine fungal distribution. This speculation is based in part on the otherwise apparent altitudinal distribution of fungal zones on the transect.

A complex "kipuka influence," particularly with respect to soil fungi, could be defined in part as involving a diversity of organic substrates, including an array of woody and herbaceous plants. This factor, in turn, would be supported and augmented by the older, deeper, and generally richer soils that allow more room for root development. The soil characteristics together with abundant and varied quality of litter and humus would appear to form an optimal basis for decomposition and nutrient cycling, and extensive niches relating to these processes. The activity of wood rotting fungi such as Ganoderma applanatum, Polyporus sulphureus, and P. versicolor is particularly evident in the kipukas (Stoner, unpublished data). The formative isolation of the kipuka could contribute importantly to the overall development of this unique physical and biological unit.

While all kipuka sites show a strong similarity, the 1973 reference group data suggest a clear difference in fungi between sites 5 (Kipuka Puaulu) and 6 (Kipuka Ki). Both of these sites are at nearly the same elevation and share certain geological and vegetational similarities (Mueller-Dombois and Lamoureux 1967). The reason for the evident difference based on this study is attributed to the collection of soil samples from two different soil-vegetation areas. The sample from site 5 represented a closed forest; sample 6, a savanna. Mueller-Dombois and Lamoureux pointed out the physical dissimilarity of the forest and savanna soils; results reported here would appear to signify a biological difference. It is interesting to note, however, that if a broader sampling base is taken into account in site comparisons by considering the fungal species isolated for site 5 in both 1972 and 1973 (Table 6), a greater degree of similarity between Kipuka Puaulu and Kipuka Ki is evident. Since both the 1972 and 1973 collections at site 5 (Kipuka Puaulu) were from closed forest areas, the overall results tend to diminish--but not by any means eliminate--the apparent biotic differences between savanna and forest soils of the kipuka zone. It is possible that with additional sampling and mycological comparisons, the kipuka zone could be shown to have component fungal communities separately representing the savanna and forest areas.

The additional similarities between sites 5 and 6 revealed by the combined 1972-73 data further demonstrate the integral structure of the Montane Kipuka Soil-Fungus Zone as well as the Mesic Montane Zone.

Fusarium rigidiusculum, a fungus usually reported as a pathogen on Theobroma cacao, was found on site 5. This is a new record of occurrence in Hawaii. Whether it exists in Hawaii as a parasite or pathogen remains to be seen.

Zone V--Open Metrosideros Dry Forest Soil-Fungus Zone (Site 4)

The absence of Absidia spinosa distinguishes this zone from others within the Mesic Montane Zone (B). The very low populations of Fusarium oxysporum and Gliocladium are considered significant. Additional indicators include Mucor lausannensis, Penicillium lilacinum, P. rubrum, and Sterile isolate #77, a species shared with the lower rain forest sites. Penicillium lilacinum is associated with only one other site, 14, which supports an open ohia scrub forest. Zone V has a relatively low population of fungi.

Zone V is located in the lower portion of the transect at the same general elevation (1220 m; 4000 ft) of sites 2 and 3 (rain forest, below Zone V) and 5, 6 (kipuka forest and savanna, above). The area is characterized by mesic conditions; a very sandy soil (Inceptisol) with only 3% organic matter, the lowest amount noted at any site; and an open scrub forest. The sandy, well drained soil, together with a relatively high atmospheric evaporation rate (Clark, Austring and Juvik 1975) may explain partly the low fungal populations and scrub nature of vegetation at this site.

Zone VI--Metrosideros Rain Forest Soil-Fungus Zone (Sites 2, 3)

This zone is identical with, and has been described under, Zone C of set 1. It was noted that the major reference genera Absidia, Fusarium, Mucor, and Penicillium were not detected at this site, and that two major Gliocladium species, G. deliquescens and G. roseum, also were absent.

All of the Penicillium and Gliocladium isolated elsewhere in this research have been determined to be cellulolytic (Table 12); and G. deliquescens particularly is a very common decomposer at several sites. Fusarium species were shown also to utilize cellulose. The absence of some of these otherwise common, potentially cellulolytic fungi from sites 2 and 3 does not necessarily mean that cellulose degradation is restricted at sites 2 and 3 as compared to other sites. Cellulose degradation could be carried out by other species of fungi or by bacteria and actinomycetes. Nevertheless, it is conceivable that the muck

TABLE 12. Cellulose-degrading[1] fungi isolated from soils along the Mauna Loa Transect in 1972 and 1973.[2]

Absidia glauca (weak growth, S)
A. spinosa (weak growth, S)
Aureobasidium pullulans (slow growth, S)
Aphanocladium sp. (I)
+Chaetomium fusisporale (I)
Cladosporium cladosporioides (I)
C. oxysporum (weak growth, S)
Curvularia verruculosa (I)
Cylindrocarpon didymum (I,S)
+C. lucidum (I)
Fusarium lateritium (moderate growth, S)
+F. oxysporum (weak growth, I)
F. rigidiusculum (slow but with heavy sporulation, S)
(+)F. solani (slow-moderate growth with heavy sporulation, I,S)
Gliocladium catenulatum (coremia formed, I,S)
(+)G. deliquescens (I,S)
(+)G. roseum (I)
(+)G. vermoeseni (I,S)
Gliomastix murorum v. felina (I,S)
+Humicola fuscoatra (I)
Mammaria echinobotryoides (I)
Mortierella ramanniana (heavy sporulation, S)
Mucor fragilis (moderate growth, S)
M. lausannensis (moderate growth, S)
Papulospora sp. (moderate growth, S)
Paecilomyces carneus (I)
Penicillium atramentosum (S)
P. aurantio-candidum (I,S)
(+)P. citrinum (S)
(+)P. clavigerum (S)
(+)P. diversum (I)
(+)P. frequentans (I,S)
(+)P. janthinellum (I,S)
+P. lanosum (I)
P. lilacinum (S)
(+)P. nigricans (I)
P. ochro-chloron (I,S)
P. rubrum (I)
P. verruculosum (I)
Staphylotrichum coccosporium (I)
sterile isolate #147 (I)
sterile isolate #247 (I)
sterile isolate #256 (I)
(+)Trichoderma viride (I)
T. viride (T. koningi type) (I)
Verticillium cephalosporum (I)
V. chlamydosporium (I)

[1] Determined by original isolation on alpha-cellulose antibiotic medium (I) and/or by growth resulting from spore-inoculations (S) of previously isolated fungi onto alpha-cellulose medium

[2] + = 1972; (+) = 1972 and 1973; all others 1973 only; only part of 1972 isolates was tested

character of soils in Zone VI is the result, in part, of organic matter decomposition carried out by a different regime of microorganisms. This hypothesis would be an interesting one to explore, since many biologists studying nutrient cycling phenomena today operate under the questionable belief that the microbial species composition in a soil has little importance in decomposition; the services that might be rendered by one species that is absent will be equally taken care of by a substitute in that niche (personal communications, IBP Interbiome Decomposition and Nutrient Cycling Committee meeting, San Francisco, 1973). This may be true in cases where there are a few substitutions; however, we question the validity of this concept in cases where the soil environment excludes a broad spectrum of decomposers that are generally associated with many soils. If broad species differences do affect the quality and quantity of decomposition, particularly of major materials such as cellulose, then there could be far-ranging ecological impacts affecting soil structure, drainage, root development, the composition and condition of plant communities, etc. The basic question here deserves additional attention.

Soil-Fungus Component Communities in Zone III

Within Zone III (Mountain Parkland Soil-Fungus Zone), site 7 in a Styphelia scrub community possesses a relatively unique mycoflora. This site differs clearly even from another mountain parkland site, 8, that is only about 100 m away. Although site 7 has strong links to the Mountain Parkland Zone (Absidia glauca, Fusarium oxysporum, and Penicillium nigricans), it is distinguished by the lack of Absidia spinosa, Gliocladium deliquescens, Paecilomyces carneus, and Trichoderma viride. The fungi that characterize site 7 are Fusarium oxysporum (in this case because of low population), Gliocladium catenulatum, Mortierella isabellina, and Penicillium aurantio-candidum. At nearby site 8, in an Acacia koa colony, the soil-fungal community showed strong similarity to other mountain parkland sites except 7 (Table 11; Fig. 7). All mountain parkland sites with the exception of 7 were in the vicinity of koa rhizosphere. On the basis of these facts, it is concluded that the fungi from site 7 represent a special group within the Mountain Parkland Zone, the Styphelia Scrub Soil-Fungus Component Community (Appendix 9). Nearby site 8 is considered to be representative of the contrasting Acacia koa Soil-Fungus Component Community of the Mountain Parkland Zone. Acacia koa-related fungal communities of the mountain parkland are indicated by Absidia spinosa, Fusarium oxysporum, Gliocladium deliquescens,

Paecilomyces carneus, and Penicillium nigricans (population); and by the absence of Gliocladium catenulatum.

Overall Significance of Soil-Fungus Zones in Set 2

Set 2 of soil-fungus zones coincides very closely with the transect zonation pattern based on vascular plants, determined independently by Mueller-Dombois and Bridges (1975). While Zones I to V match exactly, the mycological data were interpreted to justify only one additional zone (VI) which included both the open and closed areas of Metrosideros rain forest. The distribution of vascular plants justified two rain forest zones (VI and VII). This difference in the two zonation patterns is a small one that could be explained by the somewhat greater latitude of environmental tolerance in the fungi, combined with a microbial-distributional "buffering" effect of similar soil conditions throughout the studied rain forest area.

Factors Determining Fungal Distribution

The results suggest the involvement of various biotic and physical factors as determinants of fungal distribution. Previous studies and this research indicate that distribution generally is governed by interacting factors. Individual factors are secondary in overall importance to the combined forces of soils, vascular plant associates, and climate. The former two factors seem especially influential. Some examples are discussed here to clarify possible environmental parameters of fungal distribution.

Interrelated Factors

The basic, heterotrophic nature of fungi naturally relates them directly or indirectly to other organisms such as vascular plants through parasitism, commensalism, decomposition of organic substrata, or other relationships. Factors which govern the distribution of vital organic substrates would therefore be expected to influence the distribution of fungi. This overall consideration points to the most basic complex determining fungal distribution.

Many studies have been performed to determine the affects of individual factors on the growth and survival of fungi; and although some reasonably simple relationships have been demonstrated, the combined influences of factors have been cited often (Griffin 1972; Parkinson and Waid 1960; Sewell 1965).

A good example of the involvement of complex factors was revealed by this research in regard to the genus Fusarium (Stoner 1974a and unpublished data).

The species of Fusarium show a very definite altitudinal distribution along the transect (Fig. 9); however, this distribution is not correlated clearly with any specifically identified factors such as soil pH or organic matter content. Instead, results indicate broader correlations with soils, plants, and climatic conditions. There appear to be three centers of Fusarium distribution: the kipuka, mountain parkland, and sub-alpine zones.

Overall fungal populations were determined to be quantitatively and qualitatively greatest in the Mesic Montane Soil-Fungus Zone (B, Fig. 6), indicating a general suitability of this area.

The similarity of fungal communities in the kipuka areas of sites 1, 5, and 6 (Appendix 9) is another illustration of the involvement of complex determinants.

A few fungi are relatively ubiquitous along the transect: Mortierella ramanniana, Penicillium ochro-chloron, and Trichoderma viride. Other fungi which seem to bridge the zones include Cylindrocarpon didymum, Gliocladium catenulatum, and Verticillium cephalosporum. A number of fungi were found at only one site (Appendix 6).

General Climatic Factors

The general area of the transect has a tropical, insular climate (Mueller-Dombois and Bridges 1975). The transect represents an altitudinal gradient of temperature and rainfall (Fig. 2, 10), ranging from a mild rain forest at the lowest elevation to a cool, dry sparse-scrub alpine area at the highest. The relationship of the established soil-fungus zones to the climatic gradient can be seen by comparing Figure 2 and 6.

The influence of general climatic factors (vs. soils or plants) on fungal distribution is suggested by the fact that, while certain vascular plant associates (e.g. Metrosideros, Holcus) have relatively wide ranges or widely spaced occurrences on the transect, certain fungi (e.g. certain Fusarium and Penicillium species) are more limited. The overall results, however, indicate that general climatic conditions probably are interacting in a secondary sense with the stronger forces of soil and vegetation.

The restriction of some fungi to certain regions of the transect is considered an indication of climatic effects. For example, Mucor strictus is found only in the lower, warmer third of the transect (sites 1-6, Zones VI-IV, Fig. 6); Absidia spinosa, Fusarium oxysporum, and Paecilomyces carneus, in the intermediate climatic range (sites 7-12, Zones IV-III); and Mortierella hygrophila

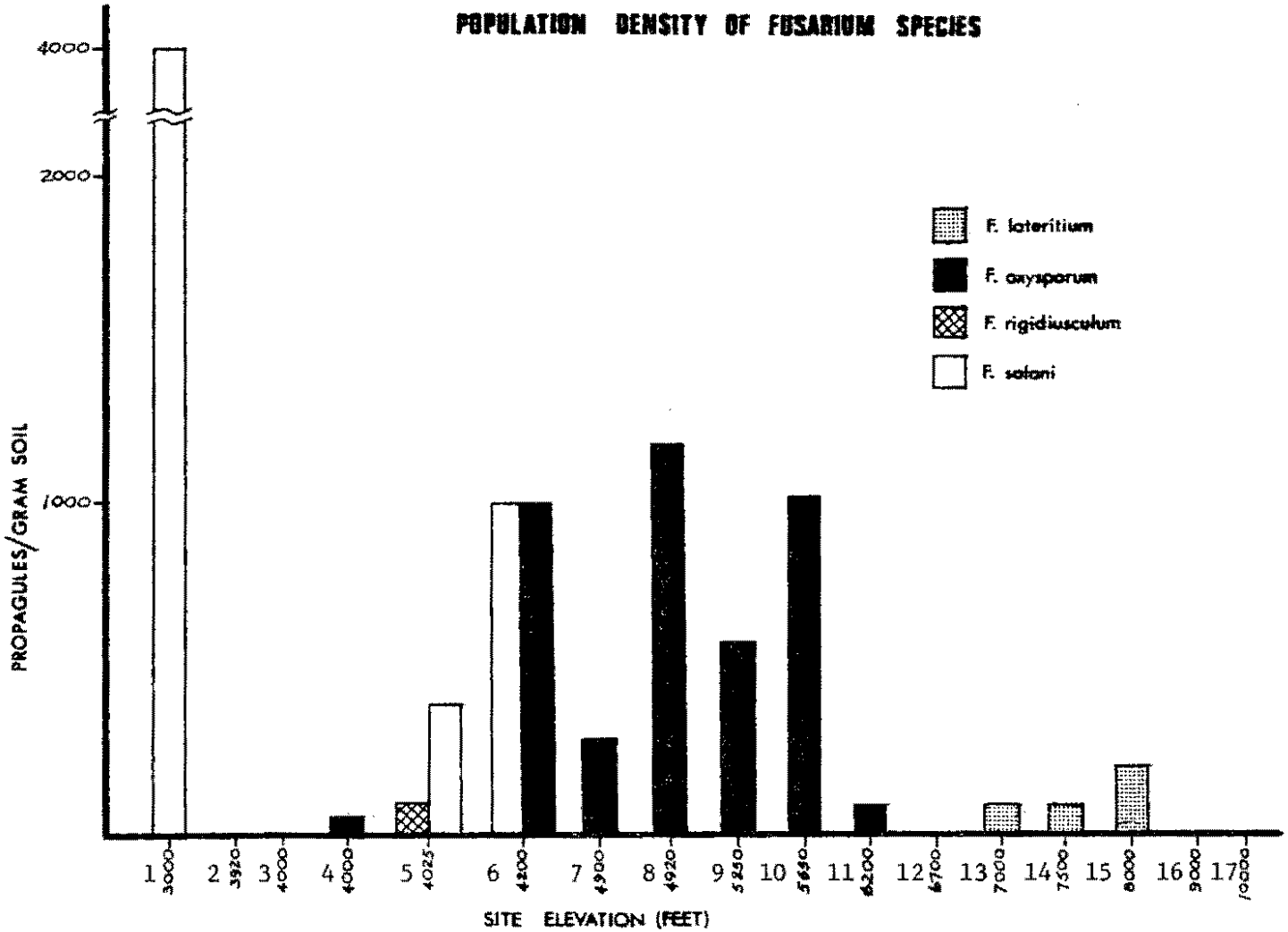


FIG. 9. Distribution and populations of Fusarium species in soils along the Mauna Loa Transect.

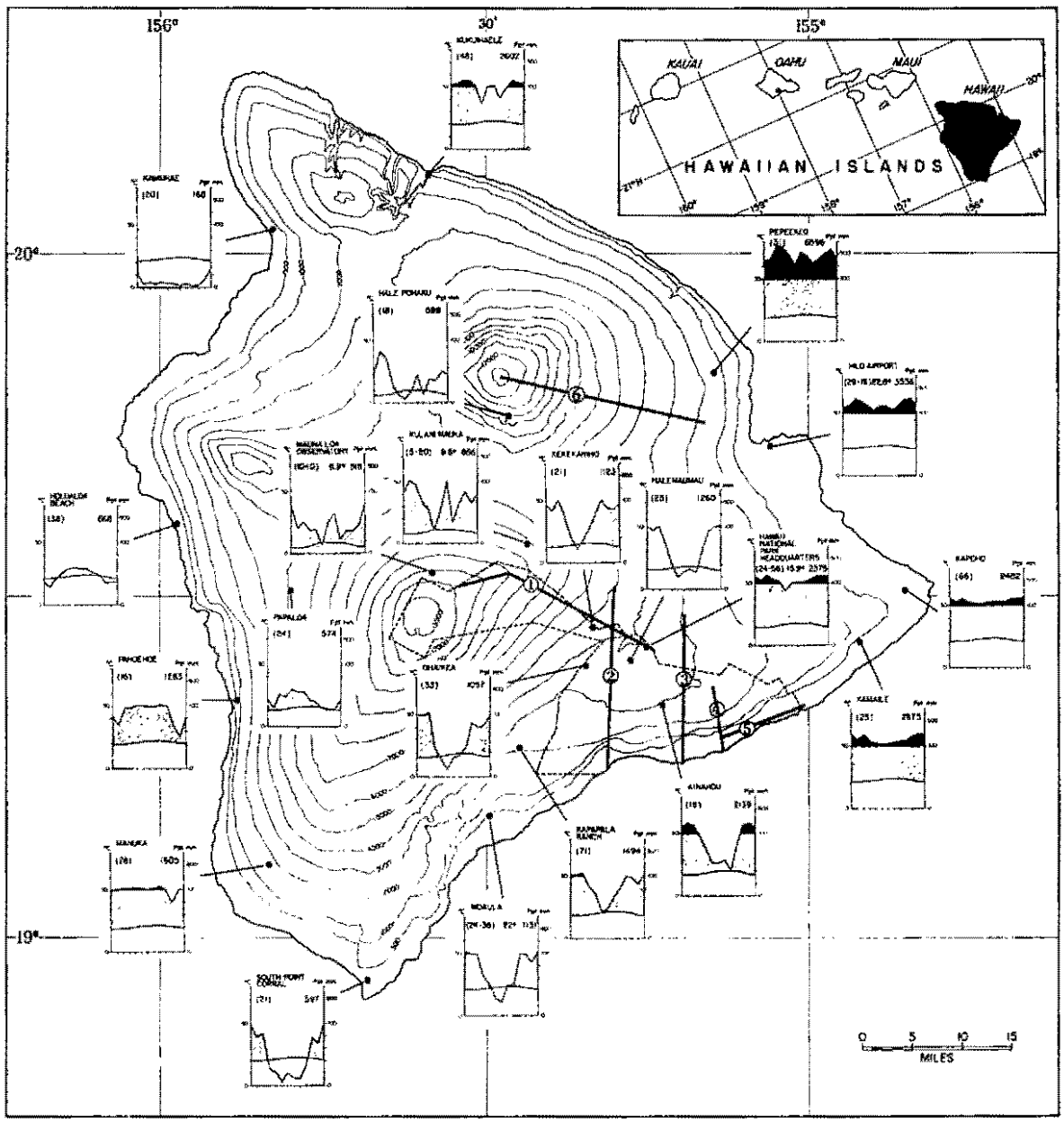


FIG. 10. Location and climate of IBP transects 1-6. The Kilauea rain forest site is at the north end of T-2. Dashed lines indicate the limits of Hawaii Volcanoes National Park. Mean monthly rainfall (mm), temperature curves (0°C) and mean annual rainfall at 21 weather stations are also indicated. (From Mueller-Dombois, Berger and Gressitt 1972)

v. minuta, Mucor fragilis and Sterile isolate #91 in the drier, cooler upper third of the transect (sites 13-17; Zones II-I). Absidia glauca occurs only in the upper half of the transect, in the seasonal, mesic-dry areas (sites 9-17; Zones III-I); whereas Cylindrocarpon didymum and Gliomastix murorum are limited to the lower half of the transect (sites 1-8; Zones VI-III). Gliocladium deliquescens, Paecilomyces carneus and Penicillium nigricans appear to be good representatives of the intermediate, mesic range of the transect.

Vascular Plant Influences

The strong similarity of transect zones determined separately on the basis of vascular plant (Mueller-Dombois and Bridges 1975) and fungal components (reported herein) is a strong indication of the interrelated distribution of the two groups.

Broad influences of vascular plant communities have been reported, and thus provide for interesting comparisons with this research. For example, Aspergillus has been reported as uncommon in forest soils (Tresner, Backus and Curtis 1954; Wright and Bollen 1961). Aspergillus is uncommon along the Mauna Loa Transect.

Thorton (1960) associated Fusarium more with grassland than forest soils. On the Mauna Loa Transect, Fusarium species on the whole are more plentiful in more open areas where grasses occur, although F. rigidiusculum and F. solani (smallest population) were found in a closed forest with apparently no grasses in the sampling area. It should be noted that none of the Fusarium isolates from the Mauna Loa Transect produced Ascomycete stages in vitro. According to Drs. W. C. Snyder and R. J. Cook (Univ. California, Berkeley; U.S.D.A., A.R.S., Pullman, Wash., personal communication), many, if not most, of the parasitic fusaria are heterothallic and therefore unable to produce the sexual stage when isolated from single spores. Homothallic fusaria are usually saprophytes. While it is unlikely that all of our isolates were parasitic, the lack of perfect stages in vitro indicates indirectly that parasites could have been well represented among the fusaria recorded. This possibility, considered together with distribution, suggests that grasses could be serving as major, but not sole, hosts for fusaria along the transect.

Mortierella ramanniana is considered a common component of forest soils (Jensen 1931; Wright and Bollen 1961). This fungus was ubiquitous on the transect and was not limited to forested sites.

Jensen observed that there were fewer species of Penicillium in wet, heavy

soils in temperate forests. The absence of Penicillium from the muck soils of the rain forest zone extends the range of this observation.

Soil Factors

Properties of soils within the soil-fungus zones are summarized in Table 13; more specific data are given in Table 4.

Soil Temperature

The temperature of soil relates in general to the climatic region. Localized temperature effects, however, can be attributed to different trends in soil temperature fluctuation because of water content. Sites such as 4 (Tree Molds), with open vegetation, well drained soil, and relatively high atmospheric evaporation rates (Clark, Austring and Juvik 1975), could be more susceptible to daily soil temperature fluctuations. Lack of plant cover, therefore, could mean generally higher soil temperatures or the daily occurrence of relatively high temperatures. Either factor could affect the growth and reproduction of fungi. Gliomastix murorum v. felina was most abundant, and occurred almost exclusively, in soils of sites 1, 4, 7, and 8. All of these sites have relatively open vegetation and higher soil temperatures. It is possible that soil pH could affect the temperature optima of fungi (Sewell 1965).

The higher population of Fusarium solani at Kipuka Nene than at Kipuka Puaulu and Kipuka Ki may be explained by the warmer soil as well as the abundant grasses at the former site (Fig. 9).

Aspergillus, a genus frequently associated with warmer tropical soils (Domsch and Gams 1972; Warcup 1951), apparently is uncommon along the Mauna Loa Transect; whereas Penicillium, a characteristic genus of relatively cooler latitudes, is well represented along the transect.

Distributional patterns indicate that temperature may be a major determining factor also in the ranges of Absidia glauca, Fusarium lateritium, and Mortierella hygrophila v. minuta.

Soil Moisture

The overall populations of fungi were greatest in the mesic, central portion of the transect, indicating a positive, general correlation with moderate levels of moisture as well as with organic matter content (compare Fig. 3 and 5). In view of this general trend, populations were noticeably low on the wet rain forest soils. The impact of wet soils on fungal distribution along the transect is

TABLE 13. Ranges of edaphic characteristics among specific sites within transect zones[1] based on the distribution of soil-borne fungi.

Transect Zone (Soil Site Numbers)	Elevation Range (m)	pH	% Organic Matter	% Water	Temperature[2] (°C)
Soil-Fungus Zone Set 1					
A Dry, Cool, High Altitude Scrub Zone (13-17)	3080-2040	5.2-6.5	12-20	10-23	12-20
B Mesic Montane Zone (4-12)	2040-1120	5.0-5.9	3-23	14-27	17-22
C Metrosideros Rain Forest Zone (2, 3)	1220-1195	5.3-5.4	11-15	46-47	16-17
Soil-Fungus Zone Set 2					
I Alpine Scrub (16, 17)	3080-2590	5.2-6.5	12-14	10-13	12-14
II Sub-alpine Scrub (13-15)	2590-2040	5.2-5.5	13-20	19-23	13-20
III Mountain Parkland (7-12)	2040-1370	5.0-5.4	14-23	18-27	17-22
IV Montane Kipuka (5-6)	1370-1220	5.7-5.9	16-17	22-24	17-19
V Open Metrosideros dry forest (4)	1220	5.2	3	14	20
VI Metrosideros rain forest (2, 3)	1220-1195	5.3-5.4	11-15	46-47	16-17

[1] See Figure 6 for a graphic display of transect zones.

[2] Although these temperature ranges represent the soils only at the time of collection, the values are useful for relative comparisons of sites and zones.

indicated by the lack of Absidia, Mucor, Fusarium and Penicillium from the rain forest soils at sites 2 and 3. Jensen (1931) also observed the absence of penicillia from very wet soils.

Water competes with air for space in soil (Sewell 1965). Fungi are mostly aerobic and are generally discouraged by low oxygen tensions (Griffin 1972) and heavy, wet soil (Jensen 1931). Plant or litter cover delays moisture fluctuation in soil (Wright and Bollen 1961). Sites 2 and 3, with their plant and litter cover, relatively high rainfall, and muck soils, are poorly suited for many fungi.

Organic Matter

The overall populations of fungi show a general, positive correlation with the organic matter content of soil (compare Fig. 3 and 5). Exceptions to this rule at sites 2, 3, 7, and 13 might be explained by either high water content (sites 2, 3) or by soil heating. No explanation is apparent for the exception at site 11.

The absence of cellulolytic fungi such as the penicillia from muck soils of the Metrosideros rain forest could result in qualitative as well as quantitative differences in organic matter breakdown.

Hydrogen Ion Concentration

All sampled soils of the Mauna Loa Transect are acidic; most are in the range pH 5.0-5.9. No clear correlation of pH and fungal distribution was determined. The diverse fungal communities in most of these soils support the often mentioned rule that acid soils generally have a richer mycoflora (Griffin 1972). This research also confirms earlier reports (Jensen 1931; Warcup 1951) on the abundance of Penicillium and Trichoderma species in acid soils.

Soil Mineral Abundance

Soils of the Mauna Loa Transect have only low to moderate levels of many available minerals (Fig. 4, Appendix 5). However, considering the well established vegetation on many of the sites, mineral abundance probably does not act directly as a strong determinant of species distribution; however, it probably is partly responsible for the stature and vigor of the vegetation. Endemic plants and many of the adventive species probably are adapted to lower mineral concentrations than are commonly considered optimal for agricultural soils. The data on mineral abundance (Appendix 5), while very limited for speculative purposes do suggest possibilities for research. For example, those sites (3, 4, 7, 13-17)

that have the lowest available soil nitrogen levels are characterized by short or scrub vegetation. Climate is understandably limiting on sites 13-17; but the strong action of soil factors seem particularly plausible on 3, 4, and 7. Interestingly, sites 7 and 8, which are within about 100 m of each other, but which have unlike plant communities, differ primarily in available nitrogen. These examples are not intended to suggest simple or direct relationships but to point to the possibility that the influences of soil mineral availability may be more pronounced than might be suggested by a cursory view of the data.

Animal Factors

Undoubtedly, propagules of soil-borne fungi have been and are disseminated over transect areas by animals. The grazing of cattle in the areas above 1220 m (4000 ft) elevation continued until 1948 (Mueller-Dombois and Bridges 1975). Foraging and other activities of feral pigs, goats and other wild animals, including arthropods, continues at present. The overlap of some fungal species between sites such as the savanna of site 6 and adjoining mountain parkland could be attributed in part to feral pig or other animal activity. The impact of animal-assisted dissemination on fungal communities is not clear. This factor is considered further in the following discussion.

Stability of Fungal Communities

Surely the movement of fungi across zonal borders of the Mauna Loa Transect has occurred by various agents such as feral animals, cattle, man, and wind-blown soil. Baker (1966) demonstrated man's capacity for inadvertent distribution of fungi through travel. The foraging habits of feral pigs should support widespread movement of fungi. In spite of all these possibilities for fungal movement, the results of this study demonstrate that distinct fungal zones exist along the transect. The existence of these zones demonstrates that the nature of fungal communities at this time in evolution of the island is determned more strongly by complex environmental parameters than simply by the distributional range of propagules, and that the established soil-fungus systems are not, in general, susceptible to major alteration by isolated invasions or disturbances by extra-zonal elements. The exception to this, of course, might involve very widespread, major disturbances. Even in the more extreme cases, it is suspected that changes in the overall structure of fungal communities would necessitate and follow major alteration of the soil-plant-climate complexes governing distribution and

survival. Although the individual roles of fungi in these soils are not well understood, the zonal patterns indicate also that the mycoflora has undergone considerable niche differentiation. The entire situation implies a reasonably high level of stability in fungal communities along the transect.

Comparisons with Other Ecosystems

The ecological significance of the soil-borne fungi which exist along the Mauna Loa Transect is not in their individual identities but in the structure and spatial distribution of the communities they form and in their associations with other elements of the ecosystems.

None of the morphological genera and species of fungi identified from soils of the Mauna Loa Transect in this research are unique to Hawaii. All of the species have been reported from various habitats in other island and/or continental ecosystems, and many are considered to be cosmopolitan (Barron 1968; Domsch and Gams 1972; Gilman 1957). This does not exclude the possibility that physiologic (non-morphological) endemism could exist in the otherwise morphologically nondistinct species of fungi in soils along the transect. Physiological specialization to habitat and substrate has been shown to be common in certain groups of fungi. Although the question of endemism is not resolved, this research has demonstrated that the fungi present in soils along the transect do occur in communities which characterize ecologically significant zones. It should be kept in mind that even cosmopolitan species can have clearly limited distributions within a given geographic area and, therefore, can serve as important indicators of ecological zones or factors when studied carefully within the context of a certain region.

In view of the cosmopolitan nature of many fungi reported herein, it would not be particularly productive to make detailed, species-by-species mycological comparisons between Hawaiian soils and those of other ecosystems. However, the peculiar distribution of certain fungi and the presence or absence of specific genera and species in the Hawaiian soils do support some meaningful, broad comparisons with other insular and continental ecosystems. With the possible exception of groups in the muck soils of the Metrosideros-tree fern rain forests, the fungal communities identified along the Mauna Loa Transect are not particularly unusual or unique when compared to the mycoflora of soils in other islands or in continental ecosystems. However, the spatial distribution and attendant ecological relationships of fungal groups along the transect follow some

ecological patterns observed previously in other ecosystems.

Many fungal species that are known to occur in wildlands and agricultural areas of both temperate and tropical insular and continental areas around the world were found in soils along the Mauna Loa Transect. Examples include Absidia glauca (Christensen 1969; Domsch and Gams 1972; Farrow 1954), Fusarium oxysporum (Kubikova 1968; Mueller-Dombois and Perera 1971), Gliocladium roseum (Farrow 1954; Jorgensen and Hodges 1962), Penicillium lilacinum (Mueller-Dombois and Perera 1971; Warcup 1951), Spicaria violacea (Farrow 1954; Tresner, Backus and Curtis 1954), and Trichoderma viride (Jorgensen and Hodges 1970; Stotsky, Goos and Timonin 1962; Thorton 1960). Soils of the Mauna Loa Transect possess fungal species in common with various wildlands including montane grasslands of Ceylon (Mueller-Dombois and Perera 1971); grasslands in England (Warcup 1951); hardwood forests in Honduras (Stotsky, Goos and Timonin 1962); forest nurseries in Czechoslovakia (Kubikova 1968); conifer forests in Oregon, U. S. A. (Wright and Bollen 1961); grasslands and forests of New Zealand (Thorton 1960); and numerous other locations. While some of the fungi are cosmopolitan, certain species, e.g. Penicillium lilacinum and Spicaria violacea, had limited distribution along the transect, thus reflecting regional influences.

When fungi with more limited geographic ranges are considered, the soil-borne mycoflora of the Mauna Loa Transect possesses more similarities to temperate and subtropical forests and grasslands than to ecosystems in warmer, tropical regions. For example, Mortierella ramanniana, a zygomycete frequently associated with temperate forests (Christensen 1969; Hendrix, Campbell and Chien 1971; Jensen 1931; Tresner, Backus and Curtis 1954; Wright and Bollen 1961), was collected at most levels on the transect. Penicillium nigricans, another fungus reported from temperate forests (Christensen 1969; Jorgensen and Hodges 1970) and grasslands (Warcup 1951), is common in the montane zones of the Mauna Loa Transect. Species such as Cylindrocarpon didymum (Domsch and Gams 1972), Mucor hiemalis and Paecilomyces carneus (Christensen 1969) also indicate the mycological similarity between these particular Hawaiian soils and those of temperate and subtropical regions. Species of Penicillium generally are more common in, and frequently representative of, various wildland and agricultural soils of cooler (temperate and subtropical) latitudes (Domsch and Gams 1972; Stoner, unpublished data; Warcup 1951). This genus was well represented in most soils along the Mauna Loa Transect (Appendix 6).

The similarity of soils along the transect to those of subtropical and

temperate latitudes is indicated strongly also by the apparent paucity of Aspergillus species. In both phases of this research, only two Aspergillus species, A. flavus (Kipuka Puaulu, 1220 m elevation, 1973) and A. sydowi (End of Strip Road, 2040 m, 1972) were detected, and these had very restricted distributions (Appendices 3, 6). Aspergillus generally is well represented in warm, tropical soils where it is believed to have a niche similar to Penicillium which predominates in temperate regions (Domsch and Gams 1972; Farrow 1954).

Although Absidia glauca has been found in both temperate and tropical areas, it is particularly associated with the former. Interestingly, this fungus was common along the transect, but only above 1280 m (4200 ft) elevation.

Fusarium solani, which was detected in kipuka soils below 1485 m (4900 ft) elevation indicates the tropical influences of the Mauna Loa Transect region. While this fungus is not limited to the tropics, it is associated most frequently with warmer soils and plant hosts of subtropical and tropical latitudes (Domsch and Gams 1972; Mueller-Dombois and Perera 1971; Stotsky, Goos and Timonin 1962). Interestingly, the largest populations of Fusarium solani encountered in this research were at Kipuka Nene, the lowest-elevation and warmest site.

The fungal communities along the Mauna Loa Transect, based on species content per se, do not represent unique insular groups. However, the apparently strong subtropical-temperate nature of the fungal communities along the transect, in spite of the latitude of Hawaii, could indicate a peculiar, selective influence of this particular insular environment. Considered foremost among the determinants of this selective environment are the east-flank orientation and the 1195 m (3920 ft) to 3050 m (10,000 ft) elevations that contribute to the relatively mild climate along the transect, and the edaphic factors.

Some reported correlations between certain fungi and specific environmental factors in other insular and continental ecosystems apparently apply also to the Mauna Loa Transect areas. Examples include the common association of certain Fusarium species (e.g. F. oxysporum) with grasslands or grass-containing ecosystems (Domsch and Gams 1972; Mueller-Dombois and Perera 1971; Thorton 1960); Papulospora spp. with tree communities (Thorton 1960); Mortierella ramanniana (= Mucor ramannianus) with hardwood forests and scrub wildlands (Christensen 1969; Hendrix, Campbell and Chien 1971; Thorton 1960); Trichoderma viride with acid soils, particularly in forests (Jensen 1931; Warcup 1951); and Absidia spp. with cooler soils (Christensen 1969; Domsch and Gams 1972; Thorton 1960).

More research is needed to determine if the muck soils of the Metrosideros-

tree fern rain forests (sites 2, 3; Table 3, Fig. 6) possess unique fungal communities not found commonly in similar ecosystems elsewhere. Still, the relative paucity of fungal species and, especially, the apparent absence or extremely limited populations of otherwise common and important soil-borne genera such as Absidia, Fusarium, Mucor, and Penicillium in these soils is decidedly unusual. The stony muck soils of the rain forest sites together with the subtending volcanic strata and other contributing environmental factors of the region could indeed comprise one of the most unique edaphic systems in the Hawaiian Islands. It is possible that these soils, based on their structure, unusual microflora and developmental nature, may contribute a degree of fragility to the Metrosideros-tree fern ecosystems.

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APPENDIX 1. Locations and descriptions of 1972 Soil Collection Sites (IBP Focal Site numbers) along the Mauna Loa Transect, at the time of sampling. All soil information pertains to the A_1 horizon.

Site	Location and Description	Plant Community	Soil* and Litter	Roots in A_1 Soil
1 (4) Kipuka Puaulu *Acacia koa* relevé	"Giant Koa" area in Kipuka Puaulu (Bird Park); 1-2% grade; 4025 ft (1224 m) elev.; forest floor heavily shaded. Kipuka Puaulu is fenced and, therefore, usually protected from feral goats and pigs	Closed kipuka forest, koa colony; "giant" koa surrounded by smaller trees; scattered *Pipturus*	deep, fine, dark brown forest soil; litter 50-60 mm deep, over 12-mm thick fermentation (F) layer and thin (6-mm) humus layer; litter almost pure koa; soil collected under koa litter in undisturbed areas; 6 July 1972	dense in A_1 and extending well into lower horizons
2 (4) Kipuka Puaulu *Metrosideros* relevé	Area of large *Metrosideros* trees 39 m southeast (downhill) on trail from giant koa path junction, 5 m east of path; forest floor heavily shaded; 4015 ft (1216 m) elev.	Closed kipuka forest; area of large *Metrosideros* trees	deep, fine, dark brown forest soil; litter 25-50 mm deep, primarily of ohia leaves; soil collected under ohia litter in undisturbed areas; 6 July 1972	moderately dense in A_1 and extending into lower horizons
3 (9) End of Strip Rd. *Acacia koa* relevé	Colony of mature koa trees near the intersection of the Strip Road and the Mauna Loa summit trail head; 6700 ft (2040 m) elev.	*Acacia koa* colony with closed canopy but sparse understory of scattered *Styphelia* and mixed ground cover of *Holcus* and *Brassica*	dark brown soil interrupted in some areas by shallow or surface rock; litter 12 m deep; thin (3-mm) humus layer; soil collected under koa; 6 July 1972	very dense, primarily koa; roots extend well into lower horizons
4 (9) End of Strip Rd. *Metrosideros* relevé	*Metrosideros* scrub area about 180 m up the summit trail from end of Strip Road; collection area 10 m uphill from trail	Open *Metrosideros* scrub forest with scattered clumps of *Styphelia*	fine light brown soil in rock land; litter 6-12 mm deep, mostly of ohia leaves; soil collected under ohia litter; 6 July 1972	moderately dense

* A_1 or first mineral horizon of soil with incorporated humus.

APPENDIX 2. Composition, preparation, and applications of culture media and additives employed in the identification of soil-borne fungi, bacteria, or actinomycetes. The formulae are for 1-liter volumes of media. Items designated by * are added after media have been autoclaved.

ACA +

Alpha-cellulose agar. Used for the isolation of cellulose-degrading fungi; also useful (without antibiotics or NPX) as a culture medium for stimulating sporulation in pure cultures of cellulolytic species; regularly supports coremium formation in Gliocladium catenulatum; some Trichoderma sporulates the 7th day after plating; many other fungi sporulate after 8-9 days; this medium gives relatively high counts.

Alphacel[1]	20 g
Agar (DIFCO)[2]	20 g
Bacto yeast nitrogen base	6.7 g
Water, demineralized	970 ml
*Tergitol NPX[3] 10% stock	10 ml
*Penicillin-Streptomycin stock	20 ml

CMA

Corn meal agar (DIFCO[2]), prepared according to the label.

CMA +

Corn meal agar with antibiotics and surfactant; prepared same as PDA+ except DIFCO CMA used instead of PDA, and no yeast extract added; for general isolation of fungi; medium does not support good differentiation of colonies, thereby hindering initial counting and isolation purposes.

CZA

Czapek solution agar (DIFCO[2]), prepared according to the label; a standard medium for the identification of Aspergillus, Penicillium, Gliocladium, and allied genera.

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[1] Alphacel--an alpha cellulose produced by Nutritional Biochemicals Corp., Cleveland, Ohio.

[2] DIFCO Laboratories, Detroit, Michigan.

[3] Tergitol--sold by J. T. Baker Chemical Co., Phillipsburg, New Jersey.

SGA +

Soil-grass extract agar with antibiotics and surfactant; for the general isolation of soil-borne fungi;

Soil extract (see below)	100 ml
Grass extract (see below)	100 ml
Dextrose	1 g
Yeast extract (DIFCO[2])	1 g
Agar (DIFCO[2] Bacto)	20 g
Water, demineralized	770 ml
*Tergitol NPX[3] 10% stock final conc. in medium = 0.1% (1000 ppm)	10 ml
*Penicillin-Streptomycin stock	20 ml

Soil extract: Mix 500 g moist soil with 900 ml demin. water; autoclave 30 min. at 121 C; cool to 50 C, then add 0.5 $CaCO_3$ and swirl; filter solution through double filter papers twice or as needed to clarify reasonably; reconstitute to 1000 ml with demin. water, dispense in 100 ml amounts to containers; autoclave for 20 min. at 121 C; store at 4 C.

Grass extract: Mix 100 g turfgrass clippings with 1000 ml; autoclave 30 min. at 121 C; filter; reconstitute to 1000 ml with demin. water; dispense in 100-ml portions to containers; autoclave 20 min. at 121 C; store at 4 C.

*Tergitol NPX[3] Stock Solutions

Stock solutions are prepared by mixing NPX and demineralized water (v/v). NPX solution can be added before or after autoclaving; in this study NPX was always added after autoclaving. Media should be swirled gently during and after the addition of NPX to facilitate uniform distribution. NPX retards the mycelial growth of many fungi, including Trichoderma, thereby facilitating colony counts and isolation (Lee 1970; Steiner and Watson 1965).

V-8A

V-8 vegetable juice[8] agar; prepared same as V-8A+ but without antibiotics, surfactant, and yeast extract; used for general culture of various fungi (Diener 1952; Miller 1955)

V-8A +

V-8 vegetable juice agar with selective antibiotics and surfactant; employed primarily in the selective isolation of Zygomycetes; many colonies develop well in 2-5 days.

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[8]V-8 juice cocktail--Campbell Soup Co., Camden, New Jersey.

V-8 vegetable juice cocktail[8]	200 ml	
$CaCO_3$	3 g	
Yeast extract (DIFCO[2])	2 g	
Agar (DIFCO[2] Bacto)	20 g	
Water, demineralized	720 ml	
*Penicillin-Streptomycin Stock Solution	20 ml	
*Benlate[9] 60% wettable powder; final conc. in medium = 150 ppm	0.16 g	in 10 ml sterile H_2O; rinse in with 40 ml H_2O
*Tergitol NPX[3] 1% stock solution; final conc. in medium = 0.01% (100 ppm)	10 ml	

[9]Benlate (benomyl)--a product of E. I. DuPont de Nemours and Co.

APPENDIX 3. Alphabetical list of fungi isolated from soil collected at the Kipuka Puaulu and End of Strip Road sites on the Mauna Loa Transect, July 1972. Numerical values indicate propagules per gram dry soil estimated for selected relevés.

Fungi	Kipuka Puaulu (Site 5*; 1220 m)		End of Strip Road (Site 12*; 2040 m)	
	K	M	K	M
Absidia glauca Hagem			>600 (WA)	
Absidia spinosa Lendner	1800	6000	800	very low
Anixiopsis Hansen		very low		
Aspergillus sydowi (Bain & Sart.) Thom & Church			4000	
Cephalosporium acremonium Corda	>4000 (SW)	recorded (no count)	recorded (no count)	recorded (no count)
Cephalosporium curtipes Saccardo				very low (SW)
Chaetomium fusisporale Rai & Mukerjee				2000
Chalaropsis Peyronel		very low		
Chloridium chlamydosporum (van Beyma) Hughes	very low			
Cladosporium cladosporioides (Fresen.) de Vries				>40 (SW)
Cladosporium oxysporum Berk. & Curt.				4000
Colletotrichum Corda			2000	
Coniothyrium Corda		>40 (SW)		
Cordana pauciseptata Preuss	very low			

* Number indicates Stoner's soil collection sites which are described in Table 3 and Appendix 1.
K = Acacia koa relevé
M = Metrosideros relevé
SW = Soil wash technique only
WA = Warcup soil-plate technique only

APPENDIX 3 Continued.

Fungi	Kipuka Puaulu (Site 5 ; 1220 m)		End of Strip Road (Site 12 ; 2040 m)	
	K	M	K	M
Curvularia verruculosa Tandon & Bilgrami ex M. B. Ellis				200
Cylindrocarpon candidum (Link) Wollenw.		very low		
Cylindrocarpon destructans (Zins.) Scholten	2000		very low	
Cylindrocarpon ianthothele Wollenw. var. majus Wollenw.		4000		
Cylindrocarpon lucidum C. Booth	18,000	4000		
Cylindrocarpon obtusisporum (Cooke & Harkness) Wollenw.	very low (SW)		8000	
Doratomyces microsporum (Sacc.) Morton & Smith	very low			
Fusarium Link ex Fr.				very low (WA)
Fusarium oxysporum emend. Synder et Hansen	200	very low		
Fusarium solani emend. Snyder et Hansen	600	800		
Gliocladium deliquescens Sopp	22,000	20,000	130,000	
Gliocladium roseum (Link) Thom	42,000	2000	4000	>4000 (WA)
Gliocladium vermoeseni (Biourge) Thom		very low (WA)		
Gliomastix murorum (Corda) Hughes var. felina (Marchal) H.	14,000	2000	60,000	
Humicola fuscoatra Traaen	14,000	10,000		200
Mortierella isabellina (Oudemans) Zycha		very low		

APPENDIX 3 Continued.

Fungi	Kipuka Puaulu (Site 5; 1220 m)		End of Strip Road (Site 12; 2040 m)	
	K	M	K	M
Mortierella ramanniana (Moeller) Linnemann	600	600	6000	40
Mucor globosus Fischer	200	>80 (SW)		
Mucor hiemalis Wehmer			200	
Mucor jansseni Lendner			>140 (SW)	
Myrothecium verrucaria (Alb. & Schw.) Ditm. ex Fr.		very low		very low (WA)
Paecilomyces carneus (Duché et Heim) Brown et G. Smith	4000	2000	46,000	200
Papulospora irregularis Hotson				200
Penicillium aurantio-virens Biourge			very low	
Penicillium chermesinum Biourge			>40 (WA)	
Penicillium citrinum Thom			4000	
Penicillium clavigerum Demelius				>4000 (SW)
Penicillium commune Thom				2000
Penicillium corylophilum Dierckx.		very low	20,000	
Penicillium diversum Raper & Fennell	18,000			
Penicillium frequentans Westling		2000	>400 (SW)	
Penicillium funiculosum Thom				48,000
Penicillium implicatum Biourge	12,000			
Penicillium janthinellum Biourge	recorded (no count)	4000		2000
Penicillium kapuscinski Zaleski			4000	

APPENDIX 3 Continued.

Fungi	Kipuka Puaulu (Site 5; 1200 m)		End of Strip Road (Site 12; 2040 m)	
	K	M	K	M
Penicillium lanosum Westling	1200			2000
Penicillium lilacinum Thom	very low			
Penicillium nigricans (Bainier) Thom	6000	2000	120,000	2000
Penicillium psittacinum Thom				2000
Penicillium rugulosum Thom	4000	4000		
Penicillium variabile Sopp	20,000	6000		4000
Pestalotia planimi Vize			very low	>8000 (WA)
Phialophora Medlar	very low			
Pyrenochaeta decipiens Marchal	very low	very low		
Pythium irregulare Buis emend. Vaartaja	4000 >400 (SW)	600	4000	
Sphaerosporium Schw.		>1200 (SW)		
Spicaria violacea Abbott [Paecilomyces marquandii (Masse) Hughes]	14,000	2000		
Stilbella bulbicola P. Hennings	very low (WA)			
Trichoderma viride Pers.	12,000	6000	>400	
Verticillium chlamydosporium Goddard	>1200 (SW)			very low
Verticillium lecanii (Zimm.) Viegas.				>40 (SW)

APPENDIX 4. Locations and descriptions of 1973 Soil Collection Sites (IBP Focal Site numbers) along Mauna Loa Transect and at Kipuka Nene at the time of sampling. Soil temperatures were taken at 7-10 cm deep. All soil information pertains to the A_1 horizon*.

Site	Location and Description	Plant Community	Soil* and Litter	Roots in A_1 Soil
1 Kipuka Nene	4.7 miles in on Hilina Pali Rd. from Chain of Craters Rd.; 100 ft (3 m) e. of H.P. Rd.; level to gently rolling terrain; kipuka with savanna-like features; 2850 ft (864 m) elevation	Open Metrosideros (ohia) forest; ohia ave. 0.3 m d.b.h.; mamane ave. 13 cm d.b.h.; scattered mamane, guava; dense, mixed understory of Pteridium, Andropogon, Cynodon, and Rubus	fine, brown, sandy soil, well developed and generally distributed in area; 24.5 C soil temperature at 7-10 cm; 20 mm-deep, mixed litter of ohia, grass, fern, etc., light in color; humus layer not well developed; soil collected under ohia canopy; 6 July 1973	roots moderately dense; ohia, mamane, grasses, etc.; roots ave. 2-5 mm diameter
2 (1) Thurston Lava Tube	10 m north of service road gate located to east of main entrance area to Thurston lava tube walk; near IBP weather station and Radovsky arthropod pit fall site; 3920 ft (1195 m) elevation	Closed Metrosideros-Cibotium (tree fern) rain forest; limited understory of mosses near tree ferns, and scattered ferns	gravelly, dark muck soil, well developed and uniformly distributed, wet; earthworms noted; 16 C soil temp.; 25-mm-deep litter, primarily of ohia and fern, grading to dark humus layer with many fungal rhizomorphs in lower layer; all layers clearly moist; soil collected under ohia-tree fern canopy; 7 July 1973	roots dense, highly branched; ohia roots 2-13 mm diameter
3 (2) Sulphur Bank	0.8 miles south of HVNP park entrance on main highway; 23 m southeast of highway; 2% grade; 4000 ft (1220 m) elevation	Open Metrosideros-Gleichenia (matted fern) forest; ohia 2-4 m apart; understory of Lycopodium, Sadleria, etc.	sandy (upper)-gravelly, dark brown muck soil; upper 6-8 cm more clay-like; 17 C soil temp.; 16-mm-thick litter, grading to thin humus; soil collected in vicinity of ohia and ferns; 7 July 1973	roots moderately dense
4 (3) Tree Molds area	About 50 m from Strip Road on paved Tree Molds road, 41 m west on gravel road from Tree Molds road, 23 m south of gravel road near Radovsky arthropod pit fall site; flat area surrounded by low mounds; 4000 ft (1220 m) elevation	Open Metrosideros-native shrub forest; small ohia 1-1.5 m apart, 12-15 m high	light brown, sandy soil with thin (5-8 cm) A_1 horizon, discontinuous distribution; breaking of soil surface yielded mushroom odor; 20 C soil temp.; litter scattered and thin to 12 mm, very dry, mostly of ohia and shrub leaves; little or no humus layer; some lichen ground cover in open areas; soil collected in vicinity of ohia roots; 7 July 1973	moderately dense; roots primarily in A_1

* A_1 or first mineral horizon of soil with incorporated humus.

APPENDIX 4 (Continued).

Site	Location and Description	Plant Community	Soil and Litter	Roots in A_1 Soil
5 (4) Kipuka Puaulu (Bird Park)	25 m northwest of Pritchardia near main gate to Bird Park trail; on slope between two very large Sapindus trees; about 3% grade; near Radovsky arthropod pit fall site; kipuka area; 4000 ft (1220 m) elevation	Closed mixed kipuka forest, with Sapindus, Psychotria, Coprosma; dense, with some very large Sapindus and many small-trunked trees	fine, brown forest soil, deep, uniformly distributed; 17 C soil temp.; litter 50-75 mm thick; thin, poorly developed humus layer; 7 July 1973	moderately dense; roots extending into lower horizons
6 (4) Kipuka Ki	1.3 miles on Strip Road, above Bird Park; 18 m northwest of IBP climatic station; 3% grade; near arthropod pit fall site; 4220 ft (1279 m) elevation	Acacia koa-Sapindus savanna; some ohia trees; understory of Holcus, with scattered Veronica and Solanum	deep fine-granular, brown forest soil, well developed and uniformly distributed; soil in places has many decomposing roots; 19 C soil temp.; 50-75-mm deep litter of koa and ohia; 6-mm humus layer; soil collected under koa canopy; 7 July 1973	moderately dense; many fine (1-2 mm) roots; a few larger (up to 13 mm) roots of koa, grass
7 (5) Power Line Trail (Styphelia)	Close to site 8; 18 m northeast from junction of paved Strip Road and unpaved Power Line Rd.; Mt. Parkland, Styphelia-grass-fern zone; much evidence of widespread feral pig rooting; 4900 ft (1485 m) elevation	Mt. Parkland ecosystem; Styphelia-Pteridium (fern)-Deschampsia (grass) zone; relatively open area with little shade	light, rust-brown, granular soil (some granularity may be due to slowly decomposing root material); soil generally uniform and well developed, with numerous small a'a rocks throughout; some evidence of mycelial activity; 19.5 C soil temp.; litter layer 6-12 mm thick; soil collected under edges of Styphelia canopies; 8 July 1973	dense, fine root mass in upper 5-7 cm
8 (5) Power Line Trail (Koa colony)	About 2.8 miles up-road from Kipuka Ki site; 120 m east of junction of Strip Road and Power Line Road; koa colony on knoll; near arthropod pit fall site; 2-3 % grade; rocky; 4920 ft (1500 m) elevation	Mt. Parkland ecosystem, Acacia koa colony with Deschampsia and Anthoxanthum grasses, and scattered Pteridium	light brown, granular-fine soil, well developed and generally distributed with many small a'a fragments; 22 C soil temp.; litter layer 25-mm thick, of koa leaves and grass; very thin humus layer; soil collected under koa canopy; 7 July 1973	moderately dense; generally small roots (2-4 mm diameter) of koa and grasses

APPENDIX 4 (Continued).

Site	Location and Description	Plant Community	Soil and Litter	Roots in A_1 Soil
9 (6) IBP Climatic Station	In vicinity of IBP Climatic Station; 1-2% grade; 5250 ft (1600 m) elevation	Mt. Parkland ecosystem, *Acacia koa* colony with *Deschampsia* and scattered *Carex*	light brown to rusty brown fine soil, uniformly distributed; soil in some areas slightly granular or with small pebbles; 18 C soil temp.; litter layer 25-50 mm thick, of koa and grass materials; very thin humus layer (1 mm); soil collected under koa; 8 July 1973	very dense root mat; large and small koa roots in A_1 and deeper
10 (7) Keamoku Flow	1.1 mile up on Strip Road from Site 9; 18 m southeast of road; 20-40% grade; well shaded, rocky; 5650 ft (1720 m) elevation	Mt. Parkland ecosystem, *Acacia koa* colony with some *Dodonea viscosa*; few, scattered *Styphelia* and mamane	fine, granular brown soil, well developed; 18.5 C soil temp.; litter layer 75-100 mm thick; thin (1-2 mm) humus layer; soil collected under koa-*Dodonea* canopy; 8 July 1973	moderately dense; koa and *Dodonea* roots
11 (8) Above Goat Exclosure	About 1.5 mile up on Strip Road from Site 10, 1.3 miles from end of Strip Road; 20 m south of road in koa colony; 2-3% grade; 6200 ft (1890 m) elev.	Mt. Parkland ecosystem, *Acacia koa* colony; somewhat open area with *Styphelia*, *Deschampsia*, and a few *Vaccinium*	fine, rusty brown soil, well developed, with rock outcroppings; 19.5 C soil temp.; litter layer 25-50 mm deep; slight or no humus layer; soil collected under koa canopy; 8 July 1973	moderately dense
12 (9) End of Strip Road	31 m southwest of beginning of trail to summit; near arthropod pit fall site; 6700 ft (2040 m) elevation	Mt. Parkland ecosystem, koa colony; partially open koa-*Styphelia* area; koa trees about 6 m apart; *Styphelia* in clusters about 3 m apart	fine, brown, shallow soil over pahoehoe; 17 C soil temp.; litter layer 25-75 mm deep; scattered rock outcroppings; soil collected in koa-*Styphelia* area; 8 July 1973	moderately dense
13 (10) 7000-ft level	15 m southwest of summit trail; slightly rolling a'a rockland; 7000 ft (2130 m) elevation	Open *Metrosideros*-scrub forest with scattered trees; *Styphelia*, *Dodonea*, *Vaccinium*, and *Gahnia*	fine, light brown, well developed, shallow soil with numerous rock outcroppings; 20 C soil temp.; litter 12 mm deep, primarily of ohia, *Styphelia*; no detectable humus layer; soil collected near ohia trees; 11 July 1973	moderately dense, very close to surface as well as deeper

APPENDIX 4 (Continued).

Site	Location and Description	Plant Community	Soil and Litter	Roots in A_1 Soil
14 (11) 7500-ft level	15 m northwest of summit trail; slightly rolling a'a rockland; 7500 ft (2290 m) elevation	Open Metrosideros scrub-forest; ohia very widely spaced, ohia tend toward tree-line habit; Styphelia Dodonea, Vaccinium; scattered Deschampsia	fine, light brown, well developed but shallow soil generally distributed among rock outcroppings; 16 C soil temp.; litter 25-38 mm deep; 1-3-mm, thin, dry humus layer; soil collected in the vicinity of ohia; 11 July 1973	dense, well developed
15 (12) 8000-ft level	20 m southwest of summit trail; 8000 ft (2440 m) elevation	Metrosideros tree line ecosystem; open scrub with scattered trees; Styphelia, Vaccinium, Dodonea	fine, light rusty brown soil, widely distributed in large area and mixed with a'a and pahoehoe outcroppings; 13 C soil temp.; litter 6-12 mm deep, somewhat compacted to form a dry cover on ground; in some areas the humus layer 4 mm thick and compact; soil collected under ohia canopy with scattered Styphelia; 11 July 1973	dense, well developed
16 (13) 9000-ft level	10-20 m south of summit trail; rolling a'a rockland; 9000 ft (2745 m) elevation	Vaccinium-Styphelia low-scrub desert; very sparse scrub; shrubs 0.3-6 m apart; stems of many plants extend from between lava layers; root zones of many plants not accessible; Styphelia growth appears limited	fine, light brown soil in pockets separated by areas of a'a and pahoehoe; 12 C soil temp.; litter 6-13 mm deep, immediately around accessible plant bases; soil collected from accessible bases of different shrub clusters; 11 July 1973	moderately dense
17 (14) 10000-ft level Puu Ulaula area	On slope of Red Hill northeast of junction of summit trail and path to cabin area; 10000 ft (3050 m) elev.	Vaccinium-Styphelia low-scrub desert; shrubs very sparse; scattered grass	rusty red to brown sandy to gravelly ash soil covered by 25-100 mm layer of 50-100 mm-rocks; 14 C soil temp.; no litter; soil collected after removal of rock cover; 10 July 1973	sparse

APPENDIX 5. Mineral abundances[1] and electrical conductivity of A_1 soils at soil collection sites (IBP Focal Sites) along the Mauna Loa Transect. Numerical values indicate concentrations in parts per million.

Element	Soil Collection Sites																
	1 —	2 (1)	3 (2)	4 (3)	5 (4)	6 (4)	7 (5)	8 (5)	9 (6)	10 (7)	11 (8)	12 (9)	13 (10)	14 (11)	15 (12)	16 (13)	17 (14)
N	M 17	H 44	L 3	L 3	H 60	H 36	L 3	H 48	H 58	H 60	M 6	H 68	L 3	L 5	L 5	L 4	L 4
P	T <15.6	T <15.6	VL-L 21.9	M 46.8	L 31.3	VL 15.6	VL 15.6	T <15.6	T <15.6	T <15.6	T <15.6	T <15.6	T <15.6	VL 15.6	VL 15.6	M 46.9	T –
K	M 150	L 50	L-M 75	L-M 75	M-H 200	M-H 200	L-M 75	L-M 75	L-M 75	M 100	VL 25	M-H 125	VL-L 37.5	M 150	L-M 75	M 100	VL 25
S	M 120	M 30	M 60	M 30	M 90	M 90	M 50	M 30	M 30	M 60	M 30	M 50	M 30	M 100	M 50	M 50	Z 0
Fe	M 19.6	M 14	M 14.8	M 80	M 20.4	M 20.4	M 15.6	M 17	M 16.4	M 18.4	M 11	M 17	M 14	M 19.2	M 15.4	M 19	L-M 5.2
Mg	L 312.5	L 312.5	L-M 468.5	T <156.3	L 312.5	L 312.5	VL-L 218.8	VL 156.3	T <156.3	VL-L 218.8	T <156.3	VL 156.3	T <156.3	VL-L 218.8	VL-L 218.8	T <156.3	T <156.3
Ca	M-H 3125	L-M 937.5	M-H 2500	L 625	M-H 3125	M-H 3125	M 1250	M-H 3125	L 625	M-H 3125	L 625	M-H 3125	L-M 937.5	H 3750	M-H 1875	M-H 3125	T <312.5
Cu	M 2.2	M 2.8	M 14	M 1.4	M 3.4	M 1.6	M 2	M 1.8	M 1.8	M 1.6	M 1.2	M 1.6	M 2.6	M 2.2	M 3.6	M 2.2	M 1
Mo[2]	Z 0	Z 0	Z 0	Z 0	Z 0	Z 0	Z 0	Z 0	Z 0	Z 0	Z 0	Z 0	Z 0	Z 0	Z 0	Z 0	Z 0
Mn	L 0.6	M 10	M 1.6	L 0.4	M 1.6	M 1.2	L 0.6	L 0.8	M 1.2	M 1.8	L 0.6	M 2	L 1	M 4	L 0.8	M 3	VL 0.2
Zn	M 1.2	M 1.2	M 1.4	L 0.4	M 1.8	H 7.4	H 4.4	M 1.6	H 4.8	H 5.2	L 0.4	M 1	L 0.6	M 1.8	L 0.8	M 1	VL 0.2
Na	L 20	M 28	L 16	M 24	L 24	L 20	L 16	L 18	L 24	L 20	L 18	L 20	VL 6	VL 7	VL 7	VL 7	VL 6
B	M 0.2	M 0.2	M 0.3	M 0.1	M 0.1	M 0.2	M 0.1	M 0.2	M 0.1	M 0.1	M 0.1	M 0.1	M 0.1	M 0.2	M 0.1	M 0.2	M 0.1
Cl	M 44	M 44	M 44	M 44	M 27	M 27	M 27	M 36	M 53	M 113	M 44	M 71	M 36	M 62	M 53	M 36	M 27
Electrical conductance (EC x 10^3)	0.9	1.1	0.3	0.3	1	0.5	0.2	0.6	0.5	0.7	0.2	0.8	0.1	0.05	0.04	0.04	0.2

[1] Z = zero, T = trace, VL = very low, L = low, M = medium, H = high (relative agricultural levels for optimal plant growth)

[2] It is difficult to measure Molybdenum; therefore, Z is interpreted as at least a trace amount.

APPENDIX 6. Alphabetical list of fungi isolated from A_1 soil collected at 17 sites along the Mauna Loa Transect, July 1973. Numerical values indicate propagules per gram dry soil estimated for the sites. Fungi selected as reference species for statistical analysis programs are designated by an asterisk.

Fungi	Soil Collection Sites[1] (IBP Focal Sites)																
	1	2 (1)	3 (2)	4 (3)	5 (4)	6 (4)	7 (5)	8 (5)	9 (6)	10 (7)	11 (8)	12 (9)	13 (10)	14 (11)	15 (12)	16 (13)	17 (14)
*[2]Absidia glauca Hagem							<200		160	140		40	20	80	60		
*Absidia spinosa Lendner	7600					6000		1200	60	500	360	240					
Aphanocladium Gams				2400													
Aspergillus flavus Link					40,000												
Aureobasidium pullulans (de Bary) Arn.			40,000						30,000								
Cladosporium cladosporioides (Fresen.) de Vries	600																160
Curvularia harveyi Shipton											20		60				
*Cylindrocarpon didymum (Hartig) Wollenw.		8000	12,000	2000			800	8000									
*Cylindrocarpon lucidum C. Booth						500											
*Cylindrocarpon magnusianum Wollenw.		4000															
*Fusarium lateritium emend. Snyder et Hansen													400	100	220		
*Fusarium oxysporum emend. Snyder et Hansen				40		<2000	300	1200	760	1000	100						
*Fusarium rigidiusculum emend. Snyder et Hansen					200												
*Fusarium solani emend. Snyder et Hansen	4000				800	2000											
*Gliocladium catenulatum Gilman & Abbott		500	2000	200			2000						200	200	200		<20
*Gliocladium deliquescens Sopp				1000	18,000	12,000		24,000	50,000	112,000	9000	46,000					

[1] See Appendix 4 or Table 3 for site names and descriptions

[2] Reference species used in statistical analysis programs

APPENDIX 6 (Continued).

Fungi	Soil Collection Sites (IBP Focal Sites)																
	1	2 (1)	3 (2)	4 (3)	5 (4)	6 (4)	7 (5)	8 (5)	9 (6)	10 (7)	11 (8)	12 (9)	13 (10)	14 (11)	15 (12)	16 (13)	17 (14)
*Gliocladium roseum (Link) Bainier					8000	10,000					<2000						
*Gliocladium vermoeseni (Biourge) Thom	12,000			100		12,000											
*Gliomastix murorum (Corda) Hughes var. felina (Marchal) H.	10,000		2000	6000			39,000	56,000									
Mammaria echinobotryoides Ces.			30,000														
*Mortierella hygrophila Linnemann var. minuta Linnemann													1000	1000		4000	600
*Mortierella isabellina (Oudemans) Zycha							600										
*Mortierella ramanniana (Moeller) Linnemann		200	400	600		1000	600	1000		100	<20		120	600		500	
*Mucor fragilis Bainier														100		80	
*Mucor hiemalis Wehmer													120				
*Mucor lausannensis Lendner				<20													
*Mucor strictus Hagem	3000				200	600											
*Paecilomyces carneus (Duché et Heim) Brown et G. Smith				800		20,000		20,000				42,000					
Papulospora irregularis Hotson				<20			40				100						
*Penicillium atramentosum Thom					6000	4000	600			10,000							
*Penicillium aurantio-candidum Dierckx							16,000										
*Penicillium clavigerum Demelius					14,000												
*Penicillium diversum Raper & Fennell																	800
*Penicillium frequentans Westling	8000					8000										6000	300
*Penicillium funiculosum Thom																1200	

APPENDIX 6 (Continued).

	1	2 (1)	3 (2)	4 (3)	5 (4)	6 (4)	7 (5)	8 (5)	9 (6)	10 (7)	11 (8)	12 (9)	13 (10)	14 (11)	15 (12)	16 (13)	17 (14)
*Penicillium lanosum Westling									12,000								
*Penicillium lilacinum Thom				1000										14,000			
*Penicillium nigricans Bainier							1000	90,000		60,000	8000	20,000	6000		20,000		
*Penicillium ochro-chloron Biourge	12,000			1000	4000	20,000		6000	10,000		6000			24,000	58,000	14,000	1200
*Penicillium rubrum Stoll				200													
*Penicillium verruculosum Peyronel								400									
Pycnidial isolate #1					4000						1000	4000			<200		
*Pythium irregulare Buis. emend. Vaartaja	600	260		<20	1600				18,000	2000		40					
*Rhizopus microsporus van Tieghem								1800									
Spicaria violacea Abbott [=Paecilomyces marquandii (Masse) Hughes]								30,000	60,000								
Staphylotrichum coccosporium Meyer & Nicot		400															
Sterile isolate #19								1000									
Sterile isolate #77		800	4000	4000													
Sterile isolate #91														800	140		
Sterile isolate #96															20,000		
Sterile isolate #137										60,000							
Sterile isolate #147					400												
Sterile isolate #228			200														
Sterile isolate #247													<200				
Sterile isolate #256																	198,000

APPENDIX 6 (Continued).

Fungi	Soil Collection Sites (IBP Focal Sites)																
	1	2 (1)	3 (2)	4 (3)	5 (4)	6 (4)	7 (5)	8 (5)	9 (6)	10 (7)	11 (8)	12 (9)	13 (10)	14 (11)	15 (12)	16 (13)	17 (14)
Torula herbarum (Pers.) Link ex S. F. Gray					200												
Trichocladium opacum (Corda) Hughes													400				
*Trichoderma viride Pers.	2600	1000	20,000	100	400	10,000		2000	140,000	1000		6000		4000	200		
*Verticillium cephalosporum W. Gams	10,000	1000			4000	20,000										800	5000
*Verticillium chlamydosporium Goddard					<2000												
*Verticillium lateritium Berkeley					1 only												

APPENDIX 7. Selectivity of isolation media. Numerical values indicate population levels detected (propagules/g dry soil). Media are described in Appendix 2.

Fungi	DFA+	ACA+	PCNB	V-8A+
*[1]Absidia glauca				<200, 160, 140, 40, 240, 20, 80, 60
*Absidia spinosa				7600, 6000, 1200, 60, 500, 360
Aphanocladium	2400	6000		
Aspergillus flavus	40,000			
Aureobasidium pullulans	40,000, 30,000			
Cladosporium cladosporioides	160	600		
Curvularia harveyi				20, 60
*Cylindrocarpon didymum	8000, 4000, 2000	1400, 12,000, 800, 8000	2000, 4000	
*Cylindrocarpon lucidum			500	
*Cylindrocarpon magnusianum	4000			
*Fusarium lateritium	400		100, 100, 220	
*Fusarium oxysporum	6000		40, <2000, 300, 1200, 760, 4000, 100	
*Fusarium rigidiusculum			200	
*Fusarium solani	6000		4000, 800, 2000	
*Gliocladium catenulatum	500, 2000	2000, 200, 1000, 200, 200, 200, <20		
*Gliocladium deliquescens	18,000, 12,000, 24,000, 28,000, 112,000, 9000, 40,000	10,000, 10,000, 40,000, 8000, 24,000	6000, 50,000, 14,000, 2000, 46,000	
*Gliocladium roseum	10,000, 1000	4000, <2000	8000	
*Gliocladium vermoeseni	12,000	10,000, 12,000	6000, 100, 4000	
*Gliomastix murorum var. felina	8000, 2000, 6000, 39,000, 56,000	10,000	6000, 24,000	

[1] Reference species used in statistical analysis

APPENDIX 7 (Continued).

Fungi	DFA+	ACA+	PCNB	V-8A+
Mammaria echinobotryoides		30,000		
*Mortierella hygrophila var. minuta			1000, 1000, 4000, 600	
*Mortierella isabellina				600
*Mortierella ramanniana				200, 400, 600, 1000, 600, 1000, 100, <20, 120, 600, 500
*Mucor fragilis				100, 80
*Mucor hiemalis				120
*Mucor lausannensis				<20
*Mucor strictus				3000, 200, 600
*Paecilomyces carneus	20,000, 20,000, 42,000	800		
Papulospora irregularis				<20, 40, 100
*Penicillium atramentosum	6000, 4000, 600, 10,000			
*Penicillium aurantio-candidum	16,000	8000		
*Penicillium clavigerum	14,000			
*Penicillium diversum		800		
*Penicillium frequentans	8000, 8000, 6000, 300	6000		
*Penicillium funiculosum	1200			
*Penicillium lanosum	12,000			
*Penicillium lilacinum	1000, 14,000			
*Penicillium nigricans	1000, 40,000, 3000, 10,000, 5000	1000, 90,000, 60,000, 8000, 20,000, 6000, 20,000		
*Penicillium ochro-chloron	12,000, 1000, 4000, 20,000, 6000, 10,000, 2400, 24,000, 58,000, 4400, 1000	8000, 400, 4000, 10,000, 6000, 10,000, 12,000, 14,000, 1200		
*Penicillium rubrum		200		

APPENDIX 7 (Continued).

Fungi	DFA+	ACA+	PCNB	V-8A+
*Penicillium verruculosum		400		
Pycnidial isolate #1	4000, 1000, 4000, <200			
*Pythium irregulare			6000, 1200	600, 260, 20, 1600 18,000, 2000, 40
*Rhizopus microsporus				1800
Spicaria violacea	30,000, 60,000			
Staphylotrichum coccosporium		400		
Sterile isolate #19				
Sterile isolate #77				
Sterile isolate #91				
Sterile isolate #96				
Sterile isolate #137				
Sterile isolate #147				
Sterile isolate #228				
Sterile isolate #247				
Sterile isolate #256				
Torula herbarum	200			
Trichocladium opacum	400			
*Trichoderma viride	2000, 1000, 4000, 10,000, 2000, 140,000, 400, <200, 2000	2600, 400, 20,000, 100, 400, 10,000, 2000, 56,000, 1000, 6000, 4000, 200	2800	
*Verticillium cephalosporum	5000	6000, 1000, 20,000		10,000, 4000, 16,000, 800
*Verticillium chlamydosporium		<2000		
*Verticillium lateritium	1 only			

APPENDIX 8. Fungal taxa isolated from soils along the Mauna Loa Transect in 1972[1] and 1973.

PHYCOMYCETES (Oomycetes, Zygomycetes)

(+)[2]Absidia glauca (K)[3]
(+)Absidia spinosa (K,M)
Mortierella hygrophila v. minuta
(+)Mortierella isabellina (M)
(+)Mortierella ramanniana (K,M)
Mucor fragilis
+Mucor globosus (K,M)
(+)Mucor hiemalis (K)
+Mucor janssenii (K)
Mucor lausannensis
Mucor strictus
+Pythium (K,M)
Pythium irregulare
+Pythium spinosum (K)
Rhizopus microsporus

ASCOMYCETES

+Anixiopsis (M)
+Chaetomium fusisporale (M)
+Colletotrichum

FUNGI IMPERFECTI

Moniliales

Moniliaceae

Aphanocladium
Aspergillus flavus
+Aspergillus sydowi (K)
+Cephalosporium acremonium (K,M)
+Cephalosporium curtipes (M)
+Doratomyces microsporum (K)
Gliocladium catenulatum
(+)Gliocladium deliquescens (K,M)
(+)Gliocladium roseum (K,M)
(+)Gliocladium vermoeseni (M)
(+)Paecilomyces carneus (K,M)
Penicillium atramentosum
Penicillium aurantio-candidum
+Penicillium aurantio-virens (K)
+Penicillium chermesinum (K)
+Penicillium citrinum (K)
(+)Penicillium clavigerum (M)
+Penicillium commune (M)
+Penicillium corylophilum (K,M)

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[1] Preliminary Study

[2] + = 1972 isolates; (+) = 1972 and 1973; all other isolated in 1973 only

[3] K = Acacia koa area; M = Metrosideros area; pertains to soil sites 5, 12 only; see Table 6 for specific locations.

(+)Penicillium diversum (K)
(+)Penicillium frequentans (K,M)
(+)Penicillium funiculosum (M)
+Penicillium implicatum (K)
+Penicillium janthinellum (K,M)
+Penicillium kapuscinski (K)
(+)Penicillium lanosum (K,M)
(+)Penicillium lilacinum (K)
(+)Penicillium nigricans (K,M)
Penicillium ochro-chloron
+Penicillium psittacinum (M)
Penicillium rubrum
+Penicillium rugulosum (K,M)
+Penicillium variabile (K,M)
Penicillium verruculosum
(+)Spicaria violacea (K,M)
Staphylotrichum coccosporium
(+)Trichoderma viride (K,M)
Verticillium cephlosporum
(+)Verticillium chlamydosporium (K,M)
Verticillium lateritium
+Verticillium lecanii

Dematiaceae

Aureobasidium pullulans
+Chalaropsis (M)
+Chloridium chlamydosporis (K)
(+)Cladosporium cladosporioides (M)
+Cladosporium oxysporum (M)
+Cordana pauciseptata (K)
Curvularia harveyi
+Curvularia verruculosa (M)
(+)Gliomastix murorum var. felina (K,M)
+Humicola fuscoatra (K,M)
Mammaria echinobotryoides
+Phialophora (K)
Torula herbarum
Trichocladium opacum

Stilbaceae

+Stilbella bulbicola (K)

Tuberculariaceae

+Cylindrocarpon candidum (M)
+Cylindrocarpon destructans (K)
Cylindrocarpon didymum
+Cylindrocarpon ianthothele (M)
(+)Cylindrocarpon lucidum (K,M)
Cylindrocarpon magnusianum
+Cylindrocarpon obtusisporum (K)
+Fusarium (M)
Fusarium lateritium
(+)Fusarium oxysporum (K,M)
Fusarium rigidiusculum

(+)Fusarium solani (K,M)
+Myrothecium verrucaria (M)
+Sphaerosporium (M)

Melanconiales

+Pestalotia planimi (K,M)

Sphaeropsidales

+Coniothyrium (M)
Pycnidial isolate #1
+Pyrenochaeta decipiens (K,M)

Mycelia Sterilia

(+)Papulospora irregularis (M)

Non-sporulating mycelium

Sterile isolate #19
Sterile isolate #77
Sterile isolate #91
Sterile isolate #96
Sterile isolate #137
Sterile isolate #147
Sterile isolate #228
Sterile isolate #247
Sterile isolate #256

APPENDIX 9. Characteristic and total species composition of soil-fungus zones, based on 1973 soil collection sites.

Soil-Fungus Zone Set 1

Zone A. Dry, Cool, High-Altitude Scrub Zone
(sites 13-17; IBP Focal 10-14)

+ Absidia glauca
Cladosporium cladosporioides
Curvularia harveyi
*+ Fusarium lateritium
(s)+ Gliocladium catenulatum
s*+ Mortierella hygrophila var. minuta
(s)+ M. ramanniana
s*+ Mucor fragilis
+ M. hiemalis
+ Penicillium diversum
(s)+ P. frequentans
+ P. funiculosum
+ P. lilacinum
+ P. nigricans
(s)+ P. ochro-chloron
Pycnidial isolate #1
Sterile isolate #91
Sterile isolate #96
Sterile isolate #247
Sterile isolate #256
Trichocladium opacum
+ Trichoderma viride
+ Verticillium cephalosporum

Note: Absence of Fusarium oxysporum
Gliocladium deliquescens

+ = all reference species used in computer analyses.

* = reference species forming groups that are especially representative of a particular soil-fungus zone, as determined by the two-way table technique (50/10 rule), a relatively objective method.

s = species that were determined by subjective evaluation to be especially significant in the delimitation of a particular zone. (s) = noteworthy but considered of secondary significance; or important especially when considered together with other features.

p = population level (propagules/gram dry soil) was particularly noteworthy for site differentiation (see Appendix 6).

All other species listed are of lesser individual importance in zone differentiation.

Zone B. Mesic Montane Soil-Fungus Zone
(sites 4-12; IBP 3-9)

+ Absidia glauca
s*+ A. spinosa
Aphanocladium sp.
Aspergillus flavus
Aureobasidium pullulans
Curvularia harveyi
+ Cylindrocarpon didymum
+ C. lucidum
s*+ Fusarium oxysporum
+ F. rigidiusculum
+ F. solani
+ Gliocladium catenulatum
s*+ G. deliquescens
+ G. roseum
+ G. vermoeseni
+ Gliomastix murorum var. felina
+ Mortierella isabellina
+ M. ramanniana
+ Mucor lausannensis
+ M. strictus
s*+ Paecilomyces carneus
(s) Papulospora irregularis
(s)+ Penicillium atramentosum
+ P. aurantio-candidum
+ P. clavigerum
+ P. frequentans
+ P. lanosum
+ P. lilacinum
+ P. nigricans
+ P. ochro-chloron
+ P. rubrum
+ P. verruculosum
p Pycnidial isolate #1
+ Pythium irregulare
+ Rhizopus microsporus
Spicaria violacea
Sterile isolate #19
Sterile isolate #77
Sterile isolate #137
Sterile isolate #147
Torula herbarum
+ Trichoderma viride
+ Verticillium cephalosporum
+ V. chlamydosporium
+ V. lateritium

Zone C. Metrosideros Rain Forest Soil-Fungus Zone
(sites 2, 3; IBP 1, 2)

Aureobasidium pullulans
+ Cylindrocarpon didymum
(s)+ C. magnusianum
+ Gliocladium catenulatum
+ Gliomastix murorum var. felina
Mammaria echinobotyroides
+ Mortierella ramanniana
+ Pythium irregulare
Staphylotrichum coccosporium
(s) Sterile isolate #77
Sterile isolate #228
+ Trichoderma viride
+ Verticillium cephalosporum

Note: Although this zone does not have a particularly unique group of characteristic species, it lacks several very important reference genera that contribute to the delimitation of zones throughout the Mauna Loa Transect.
ABSENT GENERA: Absidia
Fusarium
Gliocladium deliquescens, G. roseum
Mucor
Penicillium

Soil-Fungus Zone Set 2

Zone I. Alpine Scrub Soil-Fungus Zone
(sites 16-17; IBP 13, 14)

Cladosporium cladosporioides
+ Gliocladium catenulatum
+ Mortierella hygrophila var. minuta
+ M. ramanniana
+ Mucor fragilis
(s)+ Penicillium diversum
(s)+ P. frequentans
+ P. funiculosum
+ P. ochro-chloron
Sterile isolate #256
(s)+ Verticillium cephalosporum

Note: This zone is distinguished importantly from Zone II by its lack of:
Absidia glauca
Fusarium lateritium
Trichoderma viride

Zone II. Subalpine Scrub Soil-Fungus Zone
(sites 13-15; IBP 10-12)

(s)+ Absidia glauca
(s)p Curvularia harveyi
s*+ Fusarium lateritium
(s)p+ Gliocladium catenulatum
+ Mortierella hygrophila var. minuta
+ M. ramanniana
+ Mucor fragilis
+ M. hiemalis
+ Penicillium lilacinum
s+ P. nigricans
+ P. ochro-chloron
Pycnidial isolate #1
Sterile isolate #91
Sterile isolate #96
Sterile isolate #247
Trichocladium opacum
s+ Trichoderma viride

Zone III. Mountain Parkland Soil-Fungus Zone
(sites 7-12; IBP 5-9)

p+ Absidia glauca
(s)+ A. spinosa
Aureobasidium pullulans
Curvularia harveyi
+ Cylindrocarpon didymum
s+ Fusarium oxysporum
+ Gliocladium catenulatum
p+ G. deliquescens
+ G. roseum
+ Gliomastix murorum var. felina
+ Mortierella isabellina
+ M. ramanniana
+ Paecilomyces carneus
Papulospora irregularis
+ Penicillium atramentosum
+ P. aurantio-candidum
+ P. lanosum
(s)+ P. nigricans
+ P. ochro-chloron
+ P. verruculosum
Pycnidial isolate #1
+ Pythium irregulare
+ Rhizopus microsporus
(s) Spicaria violacea
Sterile isolate #19
Sterile isolate #137
+ Trichoderma viride

Note: Almost complete absence of Gliocladium catenulatum.

Zone IV. Montane Kipuka Soil-Fungus Zone
(sites 5, 6; IBP focal site 4)

+ Absidia spinosa
Aspergillus flavus
+ Cylindrocarpon lucidum
+ Fusarium oxysporum
+ F. rigidiusculum
s*+ F. solani
+ Gliocladium deliquescens
p*+ G. roseum
s*+ G. vermoeseni
+ Mortierella ramanniana
s*+ Mucor strictus
+ Paecilomyces carneus
(s)*+ Penicillium atramentosum
+ P. clavigerum
(s)*+ P. frequentans
+ P. ochro-chloron
Pycnidial isolate #1
+ Pythium irregulare
Sterile isolate #147
Torula herbarum
+ Trichoderma viride
+ Verticillium cephalosporum
+ V. chlamydosporium
+ V. lateritium

Kipuka Nene
(site 1; not on IBP transect)

+ Absidia spinosa
Cladosporium cladosporioides
s*+ Fusarium solani
s*+ Gliocladium vermoeseni
+ Gliomastix murorum var. felina
s*+ Mucor strictus
(s)*+ Penicillium frequentans
+ P. ochro-chloron
+ Pythium irregulare
+ Trichoderma viride
+ Verticillium cephalosporum

Zone V. Open Metrosideros Dry Forest Soil-Fungus Zone
(site 4; IBP 3)

Aphanocladium sp.
+ Cylindrocarpon didymum
p+ Fusarium oxysporum
+ Gliocladium catenulatum
p+ G. deliquescens
+ G. vermoeseni
+ Gliomastix murorum var. felina
+ Mortierella ramanniana
(s)+ Mucor lausannensis
+ Paecilomyces carneus
Papulospora irregularis
(s)+ Penicillium lilacinum
+ P. ochro-chloron
(s)+ P. rubrum
+ Pythium irregulare
(s) Sterile isolate #77
+ Trichoderma viride

Note: The absence of Absidia spinosa distinguishes this zone (site) from others in the Mesic Montane Zone (B).

Zone VI. Metrosideros Rain Forest Soil-Fungus Zone
(sites 2, 3; IBP 1, 2)

Aureobasidium pullulans
+ Cylindrocarpon didymum
(s)+ C. magnusianum
+ Gliocladium catenulatum
+ Gliomastix murorum var. felina
Mammaria echinobotyroides
+ Mortierella ramanniana
+ Pythium irregulare
Staphylotrichum coccosporium
(s) Sterile isolate #77
Sterile isolate #228
+ Trichoderma viride
+ Verticillium cephalosporum

Note: Although this zone does not have a particularly unique group of characteristic species, it lacks several very important reference genera that contribute to the delimitation of zones throughout the Mauna Loa Transect.
ABSENT GENERA: Absidia
Fusarium
Gliocladium deliquescens, G. roseum
Mucor
Penicillium

Soil-Fungus Zone Component Communities
(Zone III only)

Component S. Styphelia Scrub Component Community of Zone III
(site 7; IBP 5)

+ Absidia glauca
+ Cylindrocarpon didymum
p+ Fusarium oxysporum
s+ Gliocladium catenulatum
+ Gliomastix murorum var. felina
s+ Mortierella isabellina
+ M. ramanniana
Papulospora irregularis
+ Penicillium atramentosum
s+ P. aurantio-candidum
+ P. nigricans

Note: Although this community has strong links to the Mountain Parkland Zone, it is distinguished by the lack of significant species present in other sites of Zone III.

s*+ Absidia spinosa
s*+ Gliocladium deliquescens
s*+ Paecilomyces carneus
s+ Trichoderma viride

Component K. Acacia koa Component Communities of Zone III
(sites 8-12; IBP 5-9)

+ Absidia glauca
s*+ A. spinosa
Aureobasidium pullulans
Curvularia harveyi
+ Cylindrocarpon didymum
*+ Fusarium oxysporum
s*+ Gliocladium deliquescens
+ G. roseum
+ Gliomastix murorum var. felina
+ Mortierella ramanniana
p*+ Paecilomyces carneus
Papulospora irregularis
+ Penicillium atramentosum
+ P. lanosum
p+ P. nigricans
+ P. ochro-chloron
+ P. verruculosum
Pycnidial isolate #1
+ Pythium irregulare
+ Rhizopus microsporus
(s) Spicaria violacea
Sterile isolate #19
Sterile isolate #137
+ Trichoderma viride

Note: Absence of Gliocladium catenulatum

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