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DISTRIBUTIONAL PATTERNS OF MESOPHILOUS AND THERMOPHILOUS MICROFUNGI IN TWO BAHAMIAN SOILS

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Abstract

This study focuses on the characteristics displayed by mesophilous and thermophilous microfungal populations occurring in two tropical monodominant plant communities, a *Cocos nucifera* grove and a *Casuarina equisetifolia* forest, that provide distinctly different edaphic conditions. The mesophilous population sampled at 25°C by the dilution plate method and the thermophilous population that developed on soil plates incubated at 45°C consisted of 1693 isolates representing 60 species and 29 genera and 8887 isolates representing 20 species and 10 genera, respectively. The mesophilous propagules averaged 9,990 per gram dry soil in the coconut grove that lacks a litter layer, is low in moisture and organic matter and is subjected to high solar irradiation. The population was characterized by the prevalence of aspergilli and dematiaceous-sphaeropsidaceous forms and the near absence of mucoraceous isolates. Ascomycetes were common. The only widespread taxa were the three species, *Aspergillus niger, Penicillium chrysogenum,* and *Cladosporium cladosporioides*. Species diversity was high and 73% of the isolates were cellulolytic. In the casuarina forest, adequate moisture and organic matter and a protecting litter layer provide a mesic environment. The mean number of mesophilous fungi per gram dry soil was 32,800. This figure is considerably lower than ones reported for mesic temperate communities and may be due to more rapid propagule removal through accelerated microfaunal and microbial activity. An abundance of mucoraceous and moniliaceous isolates and penicillia, and the rarity of aspergilli, dematiaceous-sphaeropsidaceous forms and ascomycetes characterize the population. The infrequency of aspergilli is thought to be due to their poor competitive ability. Eight species, *Absidia cylindrospora, Penicillium notatum, Pestalotia cocculi*?, *Cylindrocarpon heteronema, Gliocladium roseum, Trichoderma viride, Paecilomyces marquandii*, and *Penicillium funiculosum* were widespread in the area. Species diversity equaled that observed in mesic temperate communities. Less than one third of the isolates were cellulolytic. Phytopathogens were common, a feature characteristic of tropical populations. Thermophilous fungi averaged 33 per gram dry soil in the casuarina forest and increased to 943 per gram in the insolated soil of the coconut grove. Thermotolerant forms (94% of the isolates) were abundant and were principally species of *Aspergillus* and *Chaetomium*. Thermophilic fungi were rare and of the six species isolated only *Chaetomiun britannicum* was widespread. Four species, *Ch. osmaniae, Ch. medusarum, Ch. sulphureum*, and *Thielavia arenaria*, appear to be new records for western hemisphere soils.

Introduction

A field trip to New Providence Island, The Bahamas, accompanying a class of upper level biology students, provided the opportunity to investigate tropical populations of soil fungi and compare them with those from temperate areas. Two monodominant plant communities, a casuarina forest and a coconut grove that provide very different edaphic conditions but have developed on soils derived from the same parent material, were selected for study. The former has a stable mesic environment characterized by adequate moisture and organic matter; the latter is an arid environment subjected to high solar irradiation. My principal interests were how the shift from mesic to xeric conditions affected the soil microfungal community with regards to number of propagules, important species, and selected groups including cellulolytic forms and whether these warm tropical soils harbor a thermophilous population.

Materials and methods

Study Areas

The Bahama archepeligo comprises 29 islands and numerous

cays and rocks and occupies an area over 975 km long. The islands, composed of dead coral weathered into limestone sand, support a woody 'scrub-lands' vegetation of shrubs and low trees. In addition, forests of caribbean pine and small stands of hardwoods exist (7). Extensive naturalized plantings of *Casuarina equisetifolia* Forest, a native of Australia, occur especially along the beaches and cultivated groves of coconut palms, *Cocos nucifera* L., are common. The mesic stand is located at the east end of New Providence Island about 165 m back from the ocean. The casuarina trees planted many years ago, now average about 20 m in height and produce a homogeneous forest of several hectares. Their extensive root system spreads through soil only 5-10 cm in depth. Above the soil is a thin layer of branchlets 2-3 cm deep. The lower cm is partially decomposed. Understory and herbaceous layers are absent. The xeric stand, a small coconut grove of 30 mature trees, is on the east end of Rose Island located about 6.5 km northeast of New Providence. No other higher vegetation occurs in the grove although the area is ringed by a dense scrub growth. The tree canopy is quite sparse and a litter layer is absent so the ground receives considerable solar irradiation.

Collection of Samples

Ten soil samples were collected at 3 m intervals at randomly selected sites on April 8 in the coconut grove and on April 10, 1971 in the casuarina forest. Time was too short to do preliminary analyses but the number of samples is considered adequate based upon information obtained during previous investigations of areas that support comparable or larger microfungal populations (16, 17, 18). Approximately 100 g of soil was collected at each site after first scraping away the upper 2-3 mm of surface soil, placed in a plastic bag, secured with a rubber band, and refrigerated (7°C) approximately 2 hours after collection for up to 4 days before being transported by air back to New York. In the laboratory, each sample was passed through a sterile 2 mm sieve and a portion refrigerated until analyzed for its mesophilous and thermophilous fungi on April 17 and 19, 1971, respectively. In addition a small amount of each sample was used for determination of the amount of moisture present and the pH. The soil that remained was air dried and used for edaphic analysis.

Microfungal Analyses

For analysis of the mesophilous populations, dilutions of 1 : 500, 1 : 2000 and 1 : 300, 1 : 600 were prepared from a portion of each of the casuarina and cocos samples, respectively. Four plates containing Gochenaur's Rose Bengal Agar (14) modified so that it contained 100 units of penicillin per ml and 30 ppm rose bengal were prepared for each dilution, dried at 60°C for 15 min, then surface inoculated with 1.0 ml of a soil-water suspension, and incubated for 7 days at 25°C (± 0.5°). After incubation, the number of propagules per gram dry soil was calculated for the dilution that yielded 20 to 60 colonies per plate and this figure adjusted according to the per cent moisture in the sample.

In this study, the term 'thermophilous' is applied to the fungal populations obtained from isolation plates incubated at 45°C. For analysis of the thermophilous populations, 1.000 g of soil was dispensed among 20 sterile petri dishes, each containing 1.0 ml sterile water. The sample was thoroughly mixed with the water, 30 ml of Rose Bengal Agar was added, and the soil-water sample well dispersed through the agar before it solidified. The isolation plates were incubated at 45°C (± 0.5°) for up to 5 days. After incubation, the number of propagules per gram dry soil was determined by counting the total number of colonies occurring in the 20 plates and adjusting this figure on the basis of the per cent moisture in the sample.

Table I. Soil characteristics and numbers of fungi per gram dry soil in two Bahamian ecosystems.

	Casuarina forest	Coconut grove
Water-retaining capacity (% at pF O)	164.7±6.3	41.2±0.1
Moisture content (g water/100 g dry soil)	35.8±8.5	1.4±0.4
pH	7.3–7.5	8.4–8.6
Organic matter content (%)	8.3±2.6	1.1±0.2
Chlorides (%)	0.24±0.03	0.022±0.008
Total soluble salts (%)	1.06±0.11	0.36±0.04
Carbonates (%)	72.9±3.0	80.1±2.6
Temperature (°C)		
0,5 cm depth – shaded area	28	32
– unshaded area	.	49
Numbers of fungi		
Mesophilous fungi		
Mean	32,800	9,900
Range	17,500–39,600	3,500–16,900
Thermophilous Fungi		
Mean	33	943
Range	6–160	432–1,564

A minimum of 50 sequentially-selected mesophilous and all thermophilous colonies that developed on the isolation plates prepared per soil sample were examined. A pure culture was established for each visually different isolate and the number of colonies represented by this pure culture was recorded. Relative density (% of total mesophilous or thermophilous isolates) and frequency (% of sites of occurrence) were calculated for each entity. An estimate of the average number of viable propagules per gram dry soil was calculated (16).

Identifications were based upon morphological and cultural characteristics. Isolates were plated on a minimum of three media and incubated for up to 30 days before being considered sterile. Plant pathogens isolated from soil are often impossible to identify because a knowledge of their apperance on host tissue is required. Guba's monograph (20) was used for *Pestalotia* and *Hyalopsis* isolates. It was assumed that in the monodominant plant communities sampled that either *Cocos nucifera* or *Casuarina equisetifolia* had served as their host. In addition, the morphology of spores produced in culture or on plant tissue was considered identical although this is not always the case.

Cellulolytic Activity

Eighty-three, 33 from the casuarina and 50 from the cocos populations (representing 94% of the mesophilous isolates) were tested for their ability to hydrolyze cellulose. The agar-diffusion method of Rautela and Cowling (34) employing acid-swollen powdered cellulose (Nutritional Biochemical Corp., Cleveland, Ohio) prepared according to Walseth's directions (43) was used. A cellulose agar preparation containing 0.25% (W/V) acid-swollen cellulose and 0.85% Ion Agar 2 (Baltimore Biological Laboratory, Md.) suspended in 0.02 M phosphate buffer at pH 5.4 was heated to dissolve the agar, dispensed into test tubes (18 × 150 mm) in 9 ml amounts, capped with stainless steel closures, sterilized at 121°C for 10 min, and then cooled to 48°C in a water bath. One ml of filter-sterilized (pore size, 0.45 μm) 10X strength basal medium (2.0 g vitamin-free casein hydrolysate, 0.2 g $MgSO_4 \cdot 7H_2O$, 0.2 mg Fe+++ as $FeCl_3 \cdot 6H_2O$, 0.1 mg Mn++ as $MnCl_2 \cdot 7H_2O$, 0.2 mg Zn++ as $ZnSO_4 \cdot 7H_2O$, 5 μg biotin, 100 μg thiamin, 100 μg pyridoxine, 5 mg inositol, 200 μg nicotinamide, and 5 mg cellobiose per liter of 0.02 M phosphate buffer at pH 5.4) was added aseptically to each tube, the mixture gently vortexed to evenly suspend the cellulose particles, and then rapidly gelled by cooling in crushed ice before the particles settled out. A second set of tubes containing the above medium in 0.02 M phosphate buffer at pH 7.4 also was prepared. Each culture was tested in triplicate at pH 5.4 and pH 7.4. The inocula were single germinating spores or hyphal tips cut from young colonies of ascomycetes, pycnidial, and sterile fungi. Cultures were incubated for 21 days at 26°C (± 0.5°). Cellulose hydrolysis was considered positive if any degree of clearing of the agar medium was observed.

Growth and Temperature Study

The temperature relationships of all the thermophilous species isolated were studied. Plates of glucose-yeast extract agar (1.5% glucose, 0.3% yeast extract, 0.2% K_2HPO_4, and 1.5% agar) were inoculated with 3 mm plugs removed from the margin of actively growing colonies. Triplicate cultures of each species were incubated at 18, 25, 30, 35, 40, 45, and 50°C. Temperature variation did not exceed ± 0.5°C. After 4 days incubation colony diameters were recorded. Plates showing no growth were held for an additional 3 days and then examined microscopically before being recorded as negative.

Edaphic Analysis

The % moisture (water lost after drying to constant weight at 105°C) and pH (measured with a glass electrode on a 1 : 2 (W/V) soil-water slurry) for each fresh sample were determined. In addition, air-dried samples from each stand were sorted into three groups and the members of each thoroughly mixed before portions were removed for analysis of calcium carbonate content by the rapid titration method (30), water-retaining capacity (30), organic matter by Walkley & Black's rapid titration method modified so that the H_2SO_4 contained 1.25% $AgSO_4$ to precipitate the chlorides (30), total soluble salts by the gravimetric method (30), and chloride content by the chromate titration method (30). The limits shown for all measurements are a standard deviation of the mean.

Results

Eight per cent of the 1693 isolates that comprised the mesophilous population were sterile or could not be identified. The remaining isolates were reduced to 60 species (Table II) belonging to 29 genera. Six pycnidial forms (cultures of *Phoma, Phomopsis, Botryodiplodia, Diploidia,* and *Pyrenochaeta*) could be identified only to genus. The distribution of the isolates among selected groups and the average number of propagules per gram dry soil for each group is given in Table IV.

Table II. Frequency (%) of occurrence of mesophilous microfungi in two Bahamian ecosystems, species diversity and cellulolytic activity of selected isolates. The mean number of propagules for some of the species per gram dry soil is given in parentheses.

Name	Casuarina forest	Coconut grove	Cellulolytic activity
High frequency			
1. Absidia cylindrospora Hagem	100 (2530)	.	–
2. Penicillium notatum Westling	100 (4240)	.	–
3. Pestalotia cocculi Guba?	80 (1510)	.	+
4. Cylindrocarpon heteronema (Berk & Br.) Wollenw.	80 (4610)	.	–
5. Gliocladium roseum Bainier	80 (810)	.	+
6. Trichoderma viride Persoon	90 (1410)	10 (10)	+
7. Paecilomyces marquandii (Massee) Hughes	90 (2200)	50 (385)	–
8. Penicillium funiculosum Thom	90 (6470)	20 (25)	+
9. Cladosporium cladosporioides (Fres.) deVries	10 (85)	90 (975)	±[1]
10. Penicillium chrysogenum Thom	.	90 (695)	+
11. Aspergillus niger van Tieghem	.	90 (1865)	+
Moderate frequency			
12. Fusarium solani (Martius) (Appel & Wollenw.) Snyder & Hansen	60 (460)	30 (130)	+
13. Pestalotia palmarum Cooke	.	70 (225)	+
14. Hyalotia lateripes (Ell. & Ev.) Guba	.	70 (215)	+
15. Chaetomium osmaniae Rao & Reddy?	. .	70 (315)	+
16. Penicillium purpurogenum Stoll	.	70 (560)	±
17. Pestalotia versicolor Speg.	.	60 (240)	+
18. Metarrhizum anisopliae (Metsch.) Sorok.	.	60 (815)	–
19. Aspergillus japonicus Saito	.	60 (425)	+
20. Penicillium verruculosum Peyronel	50	.	±
21. Stachybotrys atra Corda	.	50	+
22. Chaetomium sulphureum Sörgel ex Seth	.	50	+
23. Verticillium psalliotae Treschow	40	10	.
24. Penicillium frequentans Westling	10	40	–
Low frequency			
25. Penicillium waksmani Zaleski	30	30	–
26. Acremonium roseo-griseum (Saksena) Gams	30	.	.
27. Penicillium piscarium Westling	30	.	–
28. Penicillium stoloniferum Thom	30	.	–
29. Aureobasidium pullulans (deBary) Arnaud	.	30	–
30. Aspergillus pulvinus Kwon & Fennell?	.	30	–
31. Cryptococcus laurentii (Kufferath) Skinner var. laurentii Phaff & Fell	.	30	–
32. Monocillium mucidum Gams	.	30	.
33. Chaetomium seminudum Ames	20	10	+
34. Penicillium sclerotiorum van Beyma ?	20	.	–
35. Scopulariopsis brumptii Salvanet-Duval	20	.	+
36. Aspergillus tamarii Kita	.	20	.
37. Penicillium avellaneum Thom & Turesson	.	20	–
38. Myrothecium verrucaria (Alber. & Schwein.) Ditmar	.	20	.
39. Neosartorya fischeri (Wehmer) Malloch & Cain	.	20	+
40. Aspergillus flavipes (Bain. & Sart.) Thom & Church	10	10	±
41. Acrostalagmus albus Preuss	10	10	–
42. Absidia spinosa Lendner	10	.	.
43. Acremonium charticola (Lindau) Gams	10	.	.

Name	Casuarina forest	Coconut grove	Cellulolytic activity
44. Acremonium polychromum (van Beyma) Gams	10	.	+
45. Aspergillus terreus Thom	10	.	+
46. Beauveria bassiana (Bals.) Vuill.	10	.	–
47. Penicillium multicolor Grig.-Manoil. & Porad	10	.	+
48. Penicillium nigricans (Bainier) Thom	10	.	+
49. Verticillium chlamydosporium Goddard	10	.	+
50. Aspergillus ochraceus Wilhelm	.	10	–
51. Aspergillus sulphureus (Fres.) Thom & Church	.	10	+
52. Aspergillus wentii Wehmer	.	10	+
53. Cunninghamella echinulata Thaxter	.	10	–
54. Curvularia geniculata (Tracy & Earle) Boedijn	.	10	–
55. Emericella rugulosa (Thom & Raper) Benjamin	.	10	–
56. Eurotium cristatum (Raper & Fannell) Malloch & Cain	.	10	–
57. Fusarium lateritium Ness emend. Snyder & Hansen	.	10	.
58. Humicola grisea Traaen	.	10	–
59. Penicillium rugulosum Thom	.	10	+
60. Scolecobasidium variabile	.	10	–
Total number of isolates	868	825	
Species diversity – Mean number of species per 100-isolate sample	16	27	

1) Not all strains tested were positive.

The 3 species of phycomycetes, belonging to the genera *Absidia* and *Cunninghamella*, represent but a minor fraction of the total population and were of importance only in the mesic casuarina stand. Members of the ascomycetes (5 genera, 12 species) also were rare, accounting for 6% of the total isolates. *Chaetomium* with 9 species (6 of which were unidentified) was the only abundant taxon. The number of ascomycetes was highest in the cocos population.

The majority of the isolates (83%) were members of the Deuteromycetes. *Penicillium* with 14 species and 33% of the isolates and *Aspergillus* with 9 species and 14% of the isolates were the most important genera. Only 5 yeasts belonging to a single species, *Cryptococcus laurentii* var. *laurentii*, were found.

The thermophilous population consisted of 8887 isolates; 36 were sterile and 76 representing 4 taxa could not be identified. The remaining isolates were reduced to 20 species belonging to 10 genera (Table III).

The population was predominately ascomyceteous (82% of the isolates) with the chaetomia accounting for 46% of the total isolates. Among the deuteromycetes (18% of the isolates) only *Aspergillus* was important. The members of the population can be separated on the basis of their minimum temperature requirements into two groups: the thermophiles with a minimum at or above 20°C and the thermotolerant species with a minimum below 20°C (9). Most of the isolates (81%) were cellulolytic and thermotolerant (96%). The latter exhibited optimum growth and conidiation at 40°C or higher but their sexual reproduction was restricted to temperatures below 35°C with the exception of *T. arenaria* and *T. sepedonium*. Over one half of the species (Table III 1, 2, 5, 6, and 11) that displayed a moderate or high frequency of occurrence also were found on the 'mesophilous' plates. True thermophiles were rare, accounting for only 6% of the isolates. None of thesa taxa (Table III 7, 13, 15, 17, 18, and 19) with the exception of *Ch. britannicum* (93% of the thermophile isolates) was widespread in these ecosystems.

Identification of many of the chaetomia was complicated by their failure to form fertile ascocarps on standard mycological media supplimented with Ca++ and cellulose and incubated under various environmental conditions and in their sensitivity to refrigerated storage resulting in the death of several of the isolates before they could be completely characterized. The latter was a feature also exhibited by many of the other thermophilous and mesophilous isolates.

Among the chaetomia studied, several deserve comment. *Chaetomium osmaniae*? was the most abundant species with 2002 isolates. The size and morphology of the perithecia, the nature of the terminal hairs and the fusoid shape of the ascospores matches exactly the type description (33). It differs bij producing much longer ascospores, (18-20 μm) 19 × 6.5 μm (6-7.5 μm) not 10.8-14 × 6.2-7.8 μm. Four species, *Ch. osmaniae, Ch. medusarum, Ch. sulphureum*, and also *T. arenaria*, appear to be new records for western hemisphere soils. All were isolated originally from tropical regions - Hyderabad, India, Lumbumbashi, Congo, the

Table III. Frequency (%) of occurrence of thermophilous microfungi in two Bahamian ecosystems, growth in vitro at 18 °C and cellulolytic ability of selected isolates. The mean number of propagules for some of the species per gram dry soil is given in parentheses.

Name	Casuarina forest	Coconut grove	Growth at 18 °C	Cellulolytic activity
High frequency				
1. Aspergillus terreus Thom	100 (12)	.	+	–
2. Neosartorya fischeri (Wehmer) Malloch & Cain	90 (3)	100 (186)	+	+
3. Aspergillus fumigatus Fresenius	90 (10)	.	+	.
4. Sepedonium sp. TSF 17	80 (2)	.	+	+
5. Aspergillus niger van Tieghem	70 (1)	90 (159)	+	+
6. Chaetomium osmaniae Rao & Reddy ?	40 (<1)	90 (228)	+	+
7. Chaetomium britannicum Ames ?	10	100 (106)	–	+
8. Chaetomium sulphureum Sörgel ex Seth	.	100 (117)	±[1]	+
moderate frequency				
9. Thielavia species TSF 8	70 (1)	40 (8)	+	+
10. Kernia nitida (Sacc.) Nieuwland	40 (1)	.	+	+
11. Emericella rugulosa (Thom & Raper) Benjamin	.	50 (25)	+	–
Low frequency				
12. Thielavia arenaria Mouchacca	30	.	±	+
13. Chaetomium thermophile LaTouche var. thermophile Cooney & Emerson	20	.	–	+
14. Chaetomium species ? TSF 22	20	10	+	–
15. Dactylomyces crustaceus Apinis & Chesters	10	30	–	–
16. Chaetomium medusarum Meyer & Lanneau	10	20	+	+
17. Chaetomium species TSF 12	10	30	–	+
18. Malbranchea pulchella Sacc. & Penzig var. sulfurea (Miehe) Cooney & Emer.	10	10	–	–
19. Chrysosporium thermophilum (Apinis) von Klopotek	10	.	–	+
20. Thielavia sepedonium Emmons	10	20	±	–
Total number of isolates	327	8, 560		

[1] Growth very weak.

Canary Islands, and Egypt, respectively. Finally, *Chaetomium* sp. (TSF 12) seems to be identical in morphology to *Chaetomium* sp. A described by Evans (12) from coal spoil tips in England. The 4 Bahamian isolates of this species differ in being unable to grow at 18°C.

Discussion

Although the soils in both areas are basically limestone sand, their edaphic environments differ in three fundamental ways (Table I). First, the pH showed a 10-fold increase in the coconut grove over the slightly alkaline readings obtained for the casuarina forest. Second, organic matter which affects positively soil texture and water retaining capacity and serves in part as a potential food source, was eight times greater in the casuarina samples. Third, and possibly the most important difference was in the temperature-moisture regime. The mesic environment in the casuarina forest provides adequate moisture and warm but not extreme temperatures. The litter layer and extensive canopy greatly retard evaporation, shield the ground from breezes and irradiation, and provide a relatively stable environment. In contrast, the coconut grove is almost perpetually under xeric stress exacerbated by oceanic winds passing over a small hot land mass whose unprotected soil is subject to rapid evaporation and prolonged periods of insolation. This arid habitat is characterized by little available moisture and organic matter, alkaline conditions, and fluctuating soil temperatures. These stresses result in a reduction of viable

propagules to approximately one third the level found in the casuarina forest (Table I). In addition, the percentage of thermophilous forms increased 100-fold from 0.1% of the mesophilous population in the casuarina stand to almost 10% in the coconut grove. The number of fungi per gram dry soil in the mesic forest was less than one quarter the number recorded for mesic temperate soils (willow-cottonwood stand 5 (16), Irradiated Forest control zone (18), mesic prairies (27), & mesic forests (8, 38)), and may be due to the soluble salts or alkaline conditions encountered. It is more likely that the rapid cycling of the litter and the greater rate of decomposition observed in tropical plant communities (21) also operates at the microfungal level. Old (26) found death of *Cochliobolus* conidia in natural soils was increased at incubation temperatures of 25°C and apparently was due to some component of the microflora. In the casuarina soil, it is conceivable that moist alkaline conditions and warm temperatures probably accelerate microbial metabolism and the activity of the microfauna so that the longevity of hyphae and dormant structures is considerably shortened. Consequently, the total number of propagules at any sampling period will be low.

Several characteristics of the microfungal populations are influenced by the shift from mesic to xeric conditions. First, the widespread taxa are common in the mesic forest but are infrequent in the xeric coconut grove. In addition, species diversity and rare (low frequency) forms are highest in the latter area and decrease in the former (Table II). These trends may be due to the intrinsic features of the sampling method and the environmental conditions encountered. The relatively stable and uniform mesic habitat permits environmentally-selected forms to establish themselves throughout the area and consequently when sampled by the dilution plate method, their high numbers mask most of the low density taxa that may occur. In the xeric area, the propagule level is low because the harsh and variable edaphic conditions prevent any form from assuming dominance, minimize reproduction, and create conditions where spore removal is retarded and foreign spore survival increased. Consequently, the number of rare forms developing on dilution plates will be high and the richness of species increased. Although the basic causes underlying these results are probably different, it is interesting that high diversity with the species represented by only a few individuals also has been recorded for tropical plant communities developing on poor soil (40). The number of widespread forms recorded for the coconut and casuarina populations are identical to those observed in previous studies. Pioneer or disturbed areas typically yield between 2 to 4 taxa (willow-cottonwood forests 1-4 (16), sandbar willow stands (17), Irradiated Forest 15 m zone (18)), but when conditions ameliorate, these forms increase to around 8 (Irradiated Forest control zone and monodominant carex zone (18), willow-cottonwood stand 5 (16)).

Second, the abundance of mucoraceous and moniliaceous isolates, the preponderance of penicillia, and the extreme rarity of aspergilli, dematiaceous-sphaeropsidaceous forms and ascomycetes characterize the mesic population. The distribution of isolates among these groups shifts under xeric conditions to populations rich in fungi with 'protective' or 'resistant' features but poor in forms with hyaline delicate thin-walled hyphae, as shown by the near disappearance of members of the mucorales and the decrease in such moniliaceous genera as *Trichoderma, Gliocladium, Fusarium, Verticillium* and *Acremonium* (Table II). The numerous ascomycetes with their multi-layered spore coats and/or protective ascocarps and the increase in dark-pigmented forms with relatively thick-walled hyphae and conidia is a trend that is now well established for xeric soil populations (15, 17, 24, 29).

Third, cellulolysis is a feature that is common among the xeric stand isolates but much less so among those of the mesic forest (Table IV). Cellulose constitutes a major fraction of the organic matter component of terrestrial ecosystems (25). It is degraded by a large variety of terrestrial ascomycetes and imperfect fungi (10, 25, 37) and to a much lesser extent by bacteria and actinomycetes (35, 41). Why three-fourths of the members of the xeric population should be cellulolytic while less than one third of the forest species possess this ability is difficult to explain. It does not appear to be due to the abundance of cellulolytic ascomycetes in the population for their numbers are not sufficiently large to account for the difference. Cellulolytic activity is often coupled with an ability to use starch, xylan, pectin, and other plant constituents (10). Fungi with these capabilities should be better able to exploit all available organic matter and would possess a distinct advantage in an arid soil with its low amount of carbon-containing compounds. Accordingly, those features in xeric habitats that select for fungi showing morphological adaptations and broad ecological tolerances may also be operating to select for forms exhibiting nutritional versatility and a low level of nutrient specialization while the abundance and variety of organic matter in mesic soils enables forms with more restrictive nutritional patterns to survive.

Penicillium and *Aspergillus* with 47% of the isolates constitute the two most important genera in the population. *P. notatum, P. chrysogenum, P. purpurogenum*, and *P.*

Table IV. Prevalence (% of total isolates) of certain groups in the mesophilous populations isolated from two Bahamian ecosystems. The figures in parentheses are an estimate of the average number of propagules per gram dry soil.

	Casuarina forest	Coconut grove	Total population
Mucorales	13 (4275)	<1 (10)	7
Moniliaceae (excluding Penicillium & Aspergillus)	33 (10,925)	20 (1975)	27
Penicillium species	46 (15,175)	20 (1925)	33
Aspergillus species[1)]	<1 (75)	28 (2750)	14
Dematiaceous-sphaeropsidaceous isolates[1)]	2 (500)	32 (3150)	17
Ascomycetes	<1 (75)	11 (1050)	6
Sterile isolates	<1 (225)	4 (425)	2
potential phytopathogens	23 (7550)	10 (1025)	17
Cellulolytic isolates	31 (10,300)	73 (7225)	52
High frequency species (see table II)	78 (25,575)	27 (2675)	53

[1)] Includes members of the Aspergillus niger series.

funiculosum were the dominant penicillia and were also the major species in Egyptian soils (22, 23). Among the aspergilli, *A. niger* was the leading species followed by *A. japonicus*. The latter is not common in soil but the former is often recorded (1, 22, 36). In the arid coconut grove, the density and diversity of the penicillia are reduced but their propagules still form a significant part of the population. The aspergilli, however, are important only under xeric conditions. The latter appears related to their tolerance to both high temperatures and low water potentials and their intolerance to competition by mesic forms. This assumption is strongly supported by results obtained from *in vitro* experiments. Borut (6), who determined the optimal temperature for growth of 15 common fungi from arid soils of the Northern Negev, found species of *Aspergillus* grew and sporulated well at 36°C while 26°C was best for most of the other fungi including 5 penicillia. Griffin and his associates (19) showed that species of both *Aspergillus* and *Penicillium* could colonize hair baits at lower water potentials than other fungi but the aspergilli were the more tolerant of drought conditions and are considered more xerothermic than the penicillia. Ecological data reveals the aspergilli to be typically absent or at best rare in wet to mesic forest and prairie soils (8, 16, 27, 38) but definitely more prevalent in dry prairies (27) and common in other arid ecosystems (6, 15, 28, 29, 32). These distributional patterns are most likely the result of a poor competitive ability not the lack of capacity for development under improved environmental conditions.

These ecosystems possess soils with a moderate concentration of soluble salts (Table I), generally below the amounts recorded for saline areas (1, 23). However, under conditions of low moisture, the concentration of the solute phase probably reaches a level that is intolerable to many fungi. The patterns of distribution recorded for certain species shows strong correlation with the results of an *in vitro* study conducted by Tresner & Hayes (39), who surveyed the NaCl tolerance of 975 species of terrestrial fungi. They found the 469 strains of *Penicillium* and *Aspergillus* tested outstandingly more NaCl-resistant than any of the other organisms. The tolerance of certain sections of the penicillia, notably the Asymmetrica-velutina group (Table II, 2, 10), was exceptionally high while among the aspergilli, most members of the *A. flavipes, flavus, niger, ochraceous, terreus*, and *ustus* series could tolerate levels of 20% NaCl or more (Table II, 11, 19, 36, 40, 50, 51). Similar results were also obtained by Rai & Agarwar (31).

The environmental stresses faced by the microfungi in these ecosystems, periods of extreme drought, warm to hot temperatures, possibly high salt concentrations and alkaline conditions, ultra-violet irradiation, and/or low amounts of organic matter, produce a distinctive cluster of dominant soil fungi (Table II, 1, 2, 5, 6, 7, 8, 9, 10, 11, 16, 19) showing broad environmental tolerances and a widespread distribution in temperate and tropical areas (10). Although qualitatively the populations may resemble those isolated in more northernly climes, each ecosystem has a unique group of principal species selected by adaptation to a combination of environmental factors and a tolerance to each other. The remaining important species (Table II, 3, 4, 12, 13, 14, 17, 18) are plant or insect pathogens. These forms with the exception of *F. solani* rarely appear as principal species in lists of fungi recorded from soil. The high percentage of phytopathogens in the population, 17% of the total isolates (Table IV), is a typical feature of tropical soils (6).

The thermophilous population is qualitatively similar to those recorded from soil by other workers (3, 4, 5, 11, 44). Quantitatively, the number of propagules in the casuarina

forest is comparable to the 200 or less per gram found by Apinis (3, 4) and Waksman et al. (42) for mesic temperate soils. In the coconut grove the level is similar to that occurring in certain chalk soils (4) but in both ecosystems well below the 60,000 per gram reported for some cultivated grasslands in England (4).

Although the soil temperature in the forest is above the minimum required by most thermophiles (9) and all thermotolerant forms, it is apparently too low to allow these fungi to successfully compete with the mesophilous members of the population. The shift from the cooler forest soil to the highly insolated one in the coconut grove where temperatures often reach optimum levels results in a 30-fold increase in thermophilous fungi. This indicates that solar irradiation can produce sufficient heat for the development of these forms. However, other conditions also must be satisfactory if high propagule densities are to develop. Inadequate moisture and nutrient levels may account for the low ratio (1 : 10) of thermophiles to mesophiles and may also be the reason that true thermophiles form such an insignificant segment of a population characterized by thermotolerant aspergilli and chaetomia that typically inhabit hot dry soils.

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