2001

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Mycologia, 93(3), 2001, pp. 432–439.

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Abstract: Biological soil crusts of arid and semiarid regions of the world are recognized as one of the least explored niches occupied by fungi. The principal species of fungi associated with biocrusts in desert grasslands and their associated soils in two geographically separated sites were identified and compared with species from a similar community in which the active crust had been destroyed by grazing. The results confirm the existence of a highly diverse and to some degree a host specific assemblage (mycosociety) of fungi. Comparison of the prevalent species by presence and commonness at the undisturbed and disturbed sites revealed both quantitative and qualitative changes. The forms absent or with a markedly reduced occurrence in the disturbed site were three dark-colored anamorphs of loculoascomycetes (*Bipolaris* sp., *Embellisia tellustris, Phoma anserina*) and two loculoascomycetes (*Graphyllium permundum, Pleospora richtophensis*). Fungi present at all sites included *Chrysosporium/Geomyces pannorum, Embellisia tellustris* and *Pseudozyma* sp. Crust associated fungi not previously reported from soil included a basidiomycete (*Cyphellostereum* sp.), five loculoascomycetes (*Kalmusia utahensis, Macroventuria wentii, Pleospora richtophensis, Phaeospora* sp., *Preussia* sp.) and three mitosporic species (*Heteroconium* sp., *Sclerococcum* sp., *Taeniolella* sp.). Overall, the commonly encountered crust-associated fungi were dark-colored mitosporic and sterile forms apparently adapted to desert environments.

Key Words: biocrusts, bryophilous fungi, *Embellisia,* graminicolous fungi, *Graphyllium, Kalmusia,* lichenicolous fungi, loculoascomycetes, *Macroventuria,* mycosociety, *Pleospora, Pseudozyma,* saprotroph, *Sclerococcum,* soil microfungi, *Taeniolella*

INTRODUCTION

Biological soil crusts, or biocrusts, are found worldwide in arid and semi-arid environments (West 1990, Eldridge and Greene 1994). Sometimes called cryptogamic or microphytic crusts because of the visual preponderance of cyanobacteria, algae, lichens and mosses, biologically active crusts stabilize and protect sparsely vegetated areas from the erosive forces of water and wind. In many cases they have been shown to promote the establishment of vascular plants through enhancement of nutrient flow and soil moisture conditions (West 1990, Belnap and Gardner 1993). In early biocrust studies free-living fungi were identified as conspicuous and important components of the crust structure (Fletcher and Martin 1948). Subsequent studies revealed extensive and persistent growths of hyphae that strongly influence the aggregation of soil particles and the crust-forming properties of soils collected from a wide range of arid and semi-arid environments (Bond and Harris 1964, Sutton and Sheppard 1976, Schulten 1985). Surprisingly, recent investigations of biocrusts rarely or only incidentally mention fungi and their possible relationships with other crust components. Furthermore there have been no studies that deal directly with the species composition of fungal communities associated with biocrusts and the soils beneath them.

Unique and biologically diverse fungal communities have been reported in arid-land soil surveys in the western US: Ranzoni (1968), the Sonoran desert; States (1978), cool deserts in Arizona and Utah; Christensen (unpubl), a sagebrush-grassland desert in south-central Wyoming. It is logical to surmise that the special environment inherent in biocrusts would support a novel fungal community as well. Nutrient, moisture and soil microstructural effects have been found to extend into the soil a full 10 cm beneath the biocrust (Belnap and Gardner 1993). The collective presence of cyanobacteria, algae, lichens and mosses adds a different and potentially new niche for fungal colonization. For example, lichen thalli have been found to support an unexpectedly rich community of mitosporic fungi (Petrini et al 1990, Girlanda et al 1997). Furthermore, grazing and trampling disturbance have been shown to have significant adverse effects on biocrust structure and function (Beymer and Klopatek 1992, Belnap et al 1994). Therefore, it was the purpose of this study to:(i) determine the principal species present in biocrusts of three arid sites in the western United States, (ii) as-

Accepted for publication November 28, 2000.
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sess the effect of recent disturbance and removal of an active biocrust on composition of the soil fungal community, and (iii) determine through comparison with other soil studies whether biocrusts support a diverse and unique fungal community.

MATERIALS AND METHODS

Site descriptions.—Three desert grassland communities were selected for study. Two of the sites, designated Stewart ranch near Dubois, Wyoming and Virginia Park in Canyonlands National Park, Utah, have well-developed biocrusts and relatively little grazing disturbance. The third area is a recently grazed allotment adjacent to the Wyoming Stewart site, known locally as the Rifle site. Apart from the marked reduction of crusts on the Rifle site, the sites are comparable in amount and composition of vegetative cover with *Stipa commata* Trin.&Ruper. and *Oryzopsis hymenoides* Michx. as the dominant perennial grasses, and *Artemisia tridentata* Nutt. and *Krascheninnikovia (Cerotoides) lanata* (Pursh) Meeuse&Smit as common shrubs (shrubs were not present in the immediate area where samples were collected). Soils at the Utah and Wyoming sites are uniformly sandy loams, high in calcium carbonates, pH 8.0–8.5, and they receive an average annual precipitation of 25 and 29 cm, respectively.

Biocrusts from the Utah and Wyoming sites are lichen dominated. Lichen thalli often are mixed with moss mats, mostly *Tortula ruralis* (Hedw.) Guertn., and clumps of free-living cyanobacteria including *Microcoleus vaginatus* (Vauch.) Gormont, *Nostoc muscorum* Agardh. and *Scytonema* spp. The continuity of the crusts is occasionally broken by the presence of perennial grasses and herbaceous annuals. *Collema tenax* (Schwartz) Ach.(a black gelatinous lichen), *Psora decipiens* (Hedwig) Holtman, *Catapyrenium (Placidium) squamulosum* (Ach.) Breuss, *Xanthoparmelia chlorochroa* (Tuck.) Hale, and *Fulgensia desertorum* (Tomini) Poelt are the most prevalent lichens of the Canyonlands site, while *Collema tenax, Psora decipiens, Caloplaca tominii* Savicz, *Xanthoparmelia wyomingica* (Gyelink) Hale, and *Endocarpon pusillium* Hedwig characterize the lichen community at the Stewart site.

Collection and examination of biocrusts.—Within the Canyonlands and Stewart sites (0.1 ha), three randomly selected collection points were positioned over well-developed biocrusts. The crusts were sampled in June at a time when the crusts were metabolically active. A metal soil container with a 10-cm-diam opening was placed over the crust and gently pushed downwards using a twisting action to separate the crust as an intact core inside the container. The container was then covered and the core sample was placed in cold storage at 7 C until examination in the laboratory 3 d later. Lichen thalli (at least one thallus per species in each core) were removed, rinsed thoroughly in tap water and subjected to 3 min soaking in 0.5% aqueous sodium hypochlorite. Tissues were cleared of sterilant using 10 serial washings in sterile distilled water with agitation. Intact thalli of each lichen species were incubated in sterile, humid chambers (glass petri dishes with filter paper continuously moistened with sterile water) illuminated with natural light for 3 wk at room temperature and examined weekly. Additional thalli of each species were cut into 5-mm-square segments and cultured on Malt extract agar according to the protocol of Petrini et al (1990). Three 5-mm segments of moss thalli and three 5-mm segments of incorporated grass litter taken from each biocrust sample were treated in a similar fashion. All material was examined over a 3 wk period for the presence of fungi which were then identified to genus when possible.

For the isolation of fungi by suspension plating, ten samples of crust plus soil (depth 0–5 mm; approximately 20–25 g per sample) were taken at regular intervals along a 100 ft transect at each site, placed in sterile plastic 6 oz bags, and stored at −7 C for 10 wk prior to processing. Soil suspension plating, described in detail elsewhere (Christensen 1969, Clarke and Christensen 1981), involved immediate mechanical homogenization of each sample in its collection bag, the removal of a 2.5 g subsample, and the addition of sterile distilled H_2O with mechanical agitation to yield 1:500–1:10 000 soil:water suspensions. One ml of each suspension was uniformly dispensed over the surface of an agar medium in a total of 150 petri plates (3 sites, 30 samples). The isolation medium was soil extract agar amended with streptomycin or streptomycin and rose bengal and incubation was at room temperature (Clarke and Christensen 1981). Following fungal isolation by both suspension plating and detritus particle plating using fresh soils, all cultures were compared, and the numbered and identified taxa were tabulated to show frequency (samples of occurrence as a percent of total samples examined) and relative density (isolates as a percent of total isolates) (Christensen 1969).

RESULTS

Biocrust fungi.—A community of fungi was found to colonize tissues of lichens, mosses, and associated grasses of biocrusts (TABLE I). As expected, several taxa appeared to be host specific. *Phaeospora, Taeniolella* and two entities provisionally assigned to the genera *Mycospherella* and *Sclerococcum* were found only on lichen thalli. All but *Mycospherella* have been reported on lichens by Hawksworth (1983). *Cyphellostereum* Reid cf. *laeve,* a rarely reported, stipitate, stereoid fungus on mosses and lichens, was the only basidiomycete recovered. The ascomycetes/loculoascomycetes isolated from grasses included *Leptosphaeria, Melanospora, Preussia, Chaetomium,* and *Graphyllium.* The latter two also were found in the suspension plating. Dark pigmented sterile colonies designated as *Mycelium sterile dematiaceum* (following the taxonomic solution of Girlanda et al 1997) were the most common cultural isolates from lichen and plant tissues (TABLE I). Similar results were obtained in the crust plus soil analysis.

TABLE I. Lichenicolous, bryophilous, and graminicolous fungi associated with biotic soil crusts of semidesert grasslands in Utah (U) and Wyoming (W). Notation (*) indicates occurrence also in crust associated soils (see TABLE III). Category headings and placement of species follow Barr (1987, 1990), Hawksworth et al (1995), and Cannon et al (1995)

Fungal categories	Lichenicolous/fungicolous fungi	Bryophilous/graminicolous fungi
Hymenoascomycetes		**Chaetominum* sp. U, W
Loculoascomycetes	*Mycosphaerella* sp. W	**Graphyllium* sp. U
	Phaeospora sp. W	*Leptosphaeria* sp. U, W
		Preussia sp. W
Lecanorales		*Poelcinula/Melanospora* sp. W
Basidiomycetes		*Cyphellostereum* sp. W
Anamorphic/mitosporic species	**Ascochyta* sp. U	*Acremonium* spp. U, W
	**Cladosporium* sp. U, W	**Alternaria* sp. U, W
	Heteroconium sp.? W	*Aureobasidium pullans* U, W
	**Monodictys* sp. U, W	**Bipolaris* spp. U, W
	**Myrothecium* sp. W	**Cladosporium* spp. U, W
	Sclerococcum sp. ? W	**Embellisia* spp. U, W
	**Stachybotrys* sp. W	**Epicoccum* sp. U, W
	Taeniolella sp. U, W	**Fusarium* spp. U, W
	Trichoderma sp. U, W	**Monodictys* sp. U, W
		Papulaspora sp. U, W
		**Phoma* spp. U, W
		**Stachybotrys* sp. W
		Trichoderma sp. W
		**Ulocladium* spp. U, W
Mycelia sterilia	*M. s. dematiaceum* spp. U, W	*M. s. dematiacium* spp. U, W

In analysis of crust and underlying soil by suspension plating, the average number of fungal units per gram of material was determined as 5800 and 11 350 at the biocrust sites, Stewart and Canyonlands respectively. They yielded fewer propagules than the soils at the Rifle site (28 800) which lacked a crust. Total isolates examined were 323 for the Stewart site (av 26.6 by suspension plating from each of the 10 samples plus 57 by particle plating), 306 for the Rifle site (av 27.4 per sample by suspension plating plus 32 by particle plating) and 314 for the Canyonlands site (av 25.9 per sample by suspension plating plus 55 by particle plating).

The principal species at each site are the quantitatively prevalent fungi isolated by suspension and particle plating. They are those taxa which occurred (i) at a frequency of 30% or more in suspension plating, (ii) at a frequency of less than 30% in suspension plating but with three or more total isolates, (iii) at a frequency of less than 30% in suspension plating but represented among isolates from particle plating, and (iv) absent in suspension plating but represented by at least two isolates in particle plating. The 26, 25 and 29 principal species at Stewart, Rifle and Canyonlands accounted for 76, 70 and 69% of total isolates, respectively.

TABLE II. Numbers of fungal taxa shared among sites[a]

Site	Stewart	Rifle	Canyonlands
Stewart	**89**	21	7
Rifle		**101**	5
Canyonlands			**108**

[a] Numbers in bold are total taxa isolated at the given site.

TABLE II is a tabulation of microfungal co-occurrences. The two species recorded at Stewart and Canyonlands but not at Rifle were minor: *Ulocladium* sp., St 34, and an unidentified form (St 96) had low frequencies and relative densities of only 1.9 and 0.4% among 943 isolates.

The 58 principal species isolated in this study are listed or accounted for in TABLE III. Collectively, they represent 72% of the 943 isolates. The taxa isolated as principal forms at all three sites were *Embellisia tellustris, Pseudozyma* sp. and the sterile form St-51 (slow-growing, black, chlamydosporic). Colonies of *Pseudozyma,* reportedly an anamorph in the Ustilaginales (Boekhout 1995), frequently were associated with blue-green algal filaments. *Trichoderma* and *Penicillium,* common in all except desert soils (Christensen 1981), were represented by 0 and 6 isolates, respectively, among the total of 943. Sterile dark forms, listed in TABLE III as *Mycelium sterile dematiaceum,* were abundant at all sites and collectively accounted for approximately 38% of all taxa and 20.5% of all isolates. Lyophilized preparations of the principal

TABLE III. Principal fungal species obtained by suspension plating and particle plating at three sites

			Sites[b]		
		Species[a]	Stewart	Rifle	Canyonlands
Hymenoascomycetes					
	R10[c]	*Chaetomium perlucidum*		**10** (3)	
Loculoascomycetes					
C[d]	St44	*Graphyllium permundum*	**30** (15)		
C	C94	*Kalmusia utahensis*			**50** (16)
C	C18	*Macroventuria wentii*			**30** (16)
	St20	*Pleospora richtophensis*	**10** (12)		
Anamorphic and mitosporic species					
C, L[d]	C16	*Alternaria tenuissima*			**30** (32)
L	R19	*Ascochyta/Phoma*		**10** (26)	
C	St11	*Aspergillus leporis*	**10** (15)	**40** (29)	
	C13	*Aspergillus ustus*			– (13)
C, L	St32	*Bipolaris* sp.	**50** (43)	**20** (31)	
C, L	St95	*Chrysosporium/Geomyces pannorus*	**10** (3)	**10** (3)	**10** (13)
L	St43	*Cladosporium herbarum*	**20** (12)		
L	C30	*Cladosporium macrocarpum*			**20** (25)
L	C12	*Embellisia chlamydospora*			**20** (41)
C, L	St27	*Embellisia tellustris*	**80** (99)	**70** (49)	**90** (83)
C	St6	*Epicoccum purpurascens*	**30** (31)		
	R3	*Fusarium equiseti*		– (13)	
C	St1	*Fusarium flocciferum*	**50** (53)	**70** (72)	
	St2	*Fusarium* sp.	**10** (50)		
C	R2	*Fusarium* sp.		**60** (26)	
	R4	*Fusarium* sp.		**10** (10)	
C	St45	*Monodictys putredinis*	**10** (3)	**50** (33)	
C	St63	*Mortierella alpina*	**20** (6)	**60** (36)	
	St94	*Mortierella* sp.	**20** (12)		
C, L	St68	*Phoma anserina*	**90** (62)	**40** (13)	
C, L	C23	*Phoma fimeti*			**50** (86)
L	C22	*Phoma leveillei*			**10** (6)
	C25	*Phoma nebulosa*			— (6)
C, L	St80	*Phoma* sp.	**70** (68)		
C	St74	*Pseudozyma* sp.	**40** (19)	**80** (131)	**70** (61)
	St90	*Stachybotrys cf cylindrospora*	**10** (3)	**20** (10)	
	C2	*Ulocladium chartarum*			— (16)
	St34	*Ulocladium cf. multiforme*	**10** (6)		**20** (12)
C	St12	Yeast	**10** (6)	**50** (16)	**40** (16)
	St14	Yeast	**20** (9)		
	C8	Yeast			**20** (16)
Mycelia sterilia[e]					
C	St47	*Mycelium sterile dematiaceum*	**70** (53)	**50** (26)	
C	St51	*Mycelium sterile dematiaceum*	**100** (93)	**40** (16)	**30** (25)
C	St78	*Mycelium sterile dematiaceum*	**50** (22)	**30** (10)	
C	R73	*Mycelium sterile dematiaceum*		**80** (59)	
C	C34	*Mycelium sterile dematiaceum*			**60** (35)
	Total taxa		89	101	108
	Total isolates		323	306	314
	Principal species: number and % of total isolates		26 (76%)	25 (70%)	29 (69%)

[a] Category headings and placement of species follow Barr (1987, 1990), Hawksworth et al. (1995), and Cannon et al (1985).

[b] Inserted figures indicate commonness: frequency % in bold face point and relative density × 10 in parentheses (see text).

[c] Rocky Mountain Fungi culture collection number, Botany Department, University of Wyoming, Laramie. Lyophilized preparations of the isolates are available upon request.

[d] C indicates species with one frequency of 30% or more. L indicates genera commonly considered to be anamorphic loculoascomycetes.

[e] Seventeen additional taxa identified as Mycelia sterilia met the criteria for principal species (see text), but had no site frequency above 40%.

species have been deposited in the Rocky Mountain Fungi (RMF) collection at the University of Wyoming and are available from the authors.

DISCUSSION

The most striking result of the biocrust examination was the discovery of a diverse assemblage of mitosporic species residing within lichen, moss, and vascular plant tissues. Many of these were also principal species in the suspension plating of crust plus underlying soil. Of the 20 genera isolated by suspension plating, 11 were represented in the tissues of treated and serially-washed biocrust components. In other studies, a large number of mitosporic fungi also were found to occur in both fruiticose lichens (Petrini et al 1990) and foliose lichens (Girlanda et al 1997). However, the majority of the taxa in those two studies were not found in our direct biocrust analysis; ca 25% were found in our suspension and particle plating. One leaf associated (foliicolous) taxon in the present study, *Heteroconium,* was found in the above studies, as were representatives of two common saprotrophic genera, *Cladosporium* and *Trichoderma* (interestingly, *Trichoderma* was not found in our soil survey). The remaining lichenicolous/fungicolous isolates were not recorded in the studies by Petrini et al (1990) and Girlanda et al (1997) (TABLE I). Four of these, *Ascocyhta, Monodictys, Sclerococcum* and *Taeniolella* are considered to be lichenicolous by Hawksworth (1983). In an effort to account for the large number of saprotrophic, mitosporic fungi in lichen thalli, Glenn et al (1997) suggested that terricolous lichens which lack defensive lichen products will be those most readily invaded. However Girlanda et al (1997) recorded a greater diversity of saprobes on foliose lichens that produce lichen products than on those that do not. They also suggested that the prevalence of saprobic fungi is promoted by prolonged hydration in a temperate environment. In contrast to Girlanda et al (1997), we obtained fewer total taxa (32 vs 117) and a lower presence of isolates per tissue segment (35% vs 70–90%).

A possible explanation for lower densities of fungal propagules at biocrust sites in comparison to densities at the non-crust site is existence of a relatively stable moisture regime fostered by the biocrust in contrast to a discontinuous organic substrate and fluctuating moisture in the non-crust surface soil (Fletcher and Martin 1948, Belnap and Gardner 1993). Propagule densities at the three sites are comparable to densities in other desert soils of the region (Ranzoni 1968, Christensen unpubl) and are lower than most densities reported for grassland and forest soils in the U.S. (Orpurt and Curtis 1957, Christensen 1969, Clarke and Christensen 1981). The relatively high number of taxa in relation to isolates indicates a low equitability among the prevalent species in each community (few species at high and intermediate levels of commonness), but cannot by itself be interpreted as indicative of high species richness (Christensen 1981, 1989).

The data in TABLE II, revealing that only 21 of 89 taxa from the Stewart site were present in the Rifle soils, is here interpreted as a disturbance effect. In the comparison of Stewart to Canyonlands, an effect apparently attributable to geographic separation precluded discovery of any taxa present in both biocrust soils but missing at the Rifle site.

Many of the identified species obtained by suspension and particle plating are not commonly encountered soil isolates. Thus, the Compendium of Soil Fungi (Domsch et al 1980), which treats 60 genera and 450 species of common soil fungi, contains descriptions of 14 of the 20 genera in TABLE III, but treats only 12 of the 27 identified principal species. All of the listed ascomycetes, along with *Embellisia, Monodictys* and about six species in *Aspergillus, Bipolaris, Phoma* and *Stachybotrys* apparently have only infrequently been reported from soil.

Black, chlamydosporic but otherwise sterile isolates, here accounting for high proportions of both taxa and isolates, reportedly are common in other desert soils (Gochenaur 1970, 1981, Ranzoni 1968, States 1978, Christensen 1981). Nicot (1960) has interpreted such forms as adapted to persistence in hot, dry soils. Recently Caldwell et al (2000) have shown that dark sterile endophytes from roots can degrade major detrital organic materials, either as biotrophs or saprotrophs. Girlanda et al (1997) isolated 9 distinct forms with dark sterile mycelia (11% of all taxa) from thoroughly washed fragments of foliose lichens from a *Larix-Picea* forest in northern Italy.

Of the genera common at these sites but apparently absent or rare in other soils (*Graphyllium* = *Comoclathris, Kalmusia, Macroventuria, Embellisia, Monodictys, Pseudozyma*), the first three are loculoascomycetes reported from plant materials (Farr et al 1989, Shoemaker and Babcock 1992, Barr pers comm). Six other genera in TABLE III (namely *Alternaria, Ascochyta, Bipolaris, Cladosporium, Embellisia* and *Phoma)* reportedly have loculoascomycetous teleomorphs (Hawksworth et al 1995).

Comparison of the prevalent species by presence and commonness at the undisturbed Stewart and disturbed Rifle sites supports the observations of others who have noted gradual or abrupt changes in soil mycofloras following disturbance (Gochenaur and Woodwell 1974, Stanton et al 1981, Zak 1992). At the

Rifle site, several species (*Aspergillus leporis,* Fusaria including *F. flocciferum, Mortierella alpina, Monodictys putredinis*) had markedly higher frequencies and densities than were recorded at the Stewart site, and all have been reported in other grassland and desert studies. The forms common to the biocrust of the Stewart site but significantly reduced in the disturbed site are two loculoascomycetes and three species in genera that have been identified as anamorphs of loculoascomycetes (*Bipolaris* sp., *Embellisia tellustris,* and *Phoma anserina).*

Several of the saprotrophic fungi isolated in this study from crusts and underlying soils have been reported from deserts or desert-like environments. Our unique finding was the relatively high proportions of taxa and isolates in Class Loculoascomycetes at the two biocrust sites. Thus, considering Christensen's (1981) analysis of 33 microfungal communities and her summary of species apparently characteristic in soils of five vegetation types, seven of the 27 identified principal taxa in the present study are in the list of desert-associated forms (*Alternaria, Chaetomium, Cladosporium, Stachybotrys, Aspergillus ustus, Fusarium* and *Ulocladium*), two taxa match grassland-associated fungi (*Fusarium* and *Mortierella alpina*), one may indicate a tundra-like environment (*Chrysosporium/Geomyces*), and no taxon is among the 31 forms listed as common in forest or heath soils. No loculoascomycetes were reported in the two soil studies wherein vegetative composition most closely resembles that in this study (Christensen unpubl, States 1978). Overall compositional similarities to those two studies, respectively, were 33% (12 taxa shared) and 13% (9 taxa shared).

Based on our observation that terrestrial lichens from a conifer forest in southern Germany (Petrini et al 1990) harbor within their thalli fungi characteristic of conifer forest soils (Christensen 1981), and that our desert biocrusts contain taxa characteristic of desert-grassland soils, we suggest that terrestrial lichens and biocrusts may support mycosocieties of fungi which can be categorized on the basis of unique physiological-ecological traits. Three such categories, proposed below as a slight modification of the groups of Hawksworth (1983) and Petrini et al (1990), are: (i) generalists, known to be biotrophic or early-succession colonizers of detritus world-wide; (ii) soil fungi characteristic of the site; and (iii) parasymbionts, species intimately associated with the biotic unit as a whole or an algal, lichen, or fungal member of the unit. We agree with Petrini et al (1990) that, irrespective of ecological group, it is likely that many of the regularly encountered fungi are intimately associated with a host.

The generalists of the first category, from this study and confirmed elsewhere (Frankland 1966, 1998, Visser and Parkinson 1975, Hudson 1986), include: many of the saprotrophic species in *Alternaria, Aureobasidium, Bipolaris, Cladosporium, Epicoccum, Fusarium, Mycosphaerella, Myrothecium, Phoma* and *Trichoderma.* Several species in three of the above genera (*Alternaria, Cladosporium, Fusarium*) also are common in desert grassland soil, apparently as early colonizers of grass roots and litter.

The separation of soil fungi, the second category, from generalists was clearer in the forest study (Petrini et al 1990) than in our desert grasslands study. Thus, the fungi from the carefully washed thalli in the former study that also are characteristic in forest soils are: *Mortierella vinacea* and species in *Oidiodendron, Paecilomyces, Penicillium, Thysanophora,* and *Trichoderma* (Christensen 1981). Taxa in the present study and characteristic of desert grassland soils (Ranzoni 1968, States 1978, Christensen 1981, Abdullah et al 1986) but rarely or not listed as primary colonizers include: *Aspergillus leporis, A. ustus, Chaetomium* spp., *Embellisia* spp., *Monodictys putredinus, Mortierella alpina,* and certain species in *Leptosphaeria, Melanopsora* and *Ulocladium.*

The environments and lichen genera examined in the studies of Petrini et al (1990) and Girlanda et al (1997) were very different from those of this study. The only apparently parasymbiotic genus in common is *Heteroconium.* Other fungi from this study that may be parasymbionts in the soil biocrust include: *Cyphellostereum* sp., *Graphyllium/Comoclathris* spp., *Kalmusia utahensis, Macroventuria wentii, Phaeospora* sp., *Pleospora richtophensis, Preussia* sp., *Sclerococcum* sp. and *Taeniolella* sp.

The commonly encountered taxonomic groups in and associated with our biocrusts were dark-colored mitosporic species (both hyphomycetous and coleomycetous) and dark sterile forms, along with eight genera of loculoascomycetes, *Pseudozyma* sp., and species in *Fusarium* and *Aspergillus.* We found them to be difficult to isolate as well as to identify. It is possible that many of the forms, especially the dark sterile forms, are representatives of host specific lichenicolous, fungicolous, bryophilous or graminicolous fungi, or as generalists or site specialists, they may be more general cozy niche inhabitants (Richardson 1999). Additional ecological studies are needed to further characterize fungal communities associated with biological crusts.

ACKNOWLEDGMENTS

The authors gratefully acknowledge Drs. Thomas H. Nash III and Roger Rosentreter for assistance in lichen identification, and the following people for assistance in fungal

identifications: Drs. Margaret Barr Bigelow, Teun Boekhout, Walter Gams, R.A. Samson, R.A. Shoemaker, and Emory Simmons. Our capable assistants were Diantha States, C. Lynn Kinter and Dan Fitzgerald. The study was supported in part by NSF Grant DEB-9632880.

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