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A PRELIMINARY SURVEY OF THE COPROPHILOUS FUNGI FROM A SEMI-ARID GRASSLAND IN COLORADO

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ABSTRACT

A survey was made of the kinds of coprophilous fungi which developed fructifications on different coprophilous substrates from a semiarid grassland in Colorado. A total of 53 species were found on approximately 650 g dry weight of feces. These included cattle feces (37 species/600 g), rabbit feces (27 species/30 g), pronghorn feces (17 species/20 g), and small mammal feces (12 species/1 g). Given the relatively small amount of substrate examined and the fact that collections came from adjacent pastures, the population of coprophilous fungi was remarkably diversified. Populations of coprophilous fungi on ruminant feces (cattle and pronghorn) were most similar in species composition, while those on pronghorn and small mammal feces showed the least similarity. Many of the species developed fruiting bodies on both freshly dried and partially decomposed cattle droppings during moist chamber incubation. Some of the problems associated with attempts at quantifying populations of coprophilous fungi are considered, and hypotheses explaining the apparently high diversity of species in this grassland are discussed.

INTRODUCTION

Coprophilous fungi are believed to play several important roles in the functioning of grassland ecosystems (Fig. 1). They assist in the decomposition and mineralization of herbivore feces (Angel and Wicklow, in press), serve as a nutritional base for coprophagous and mycophagous arthropods (Halffter and Matthews 1971; Malan and Gandini 1966), and may, be influencing microbial composition and activity in the rumen, affect the digestive efficiencies of sheep (Brewer and Taylor 1969; Brewer et al. 1972).

Coprophilous fungi are the most easily recognized component of the coprophilous microflora. They reproduce and spread mainly by spores which, after being eaten with grass, are stimulated to germinate during travel through the digestive tract (Webster 1970). Mycelium develops in the deposited feces, and following a period of incubation under suitable conditions, spore production and discharge occurs. Coprophilous fungi are particularly well adapted to grasslands. Their fructifications and/or spores are usually darkly pigmented, fruiting body development may be triggered by light, and spore discharge is directed phototropically. It is an essential feature of the life history of these fungi that discharged spores become attached to herbage selected by a warm-blooded herbivore

This investigation was conducted to compare the coprophilous fungal populations colonizing different types of herbivore feces from a shortgrass prairie. Shortgrass prairies seem ideally suited to comparative studies on coprophilous fungal populations since the vegetation, with its spore inoculum, is equally available to all herbivores. The Pawnee Site (Grassland Biome, U.S. International Biological Program), located in northeastern

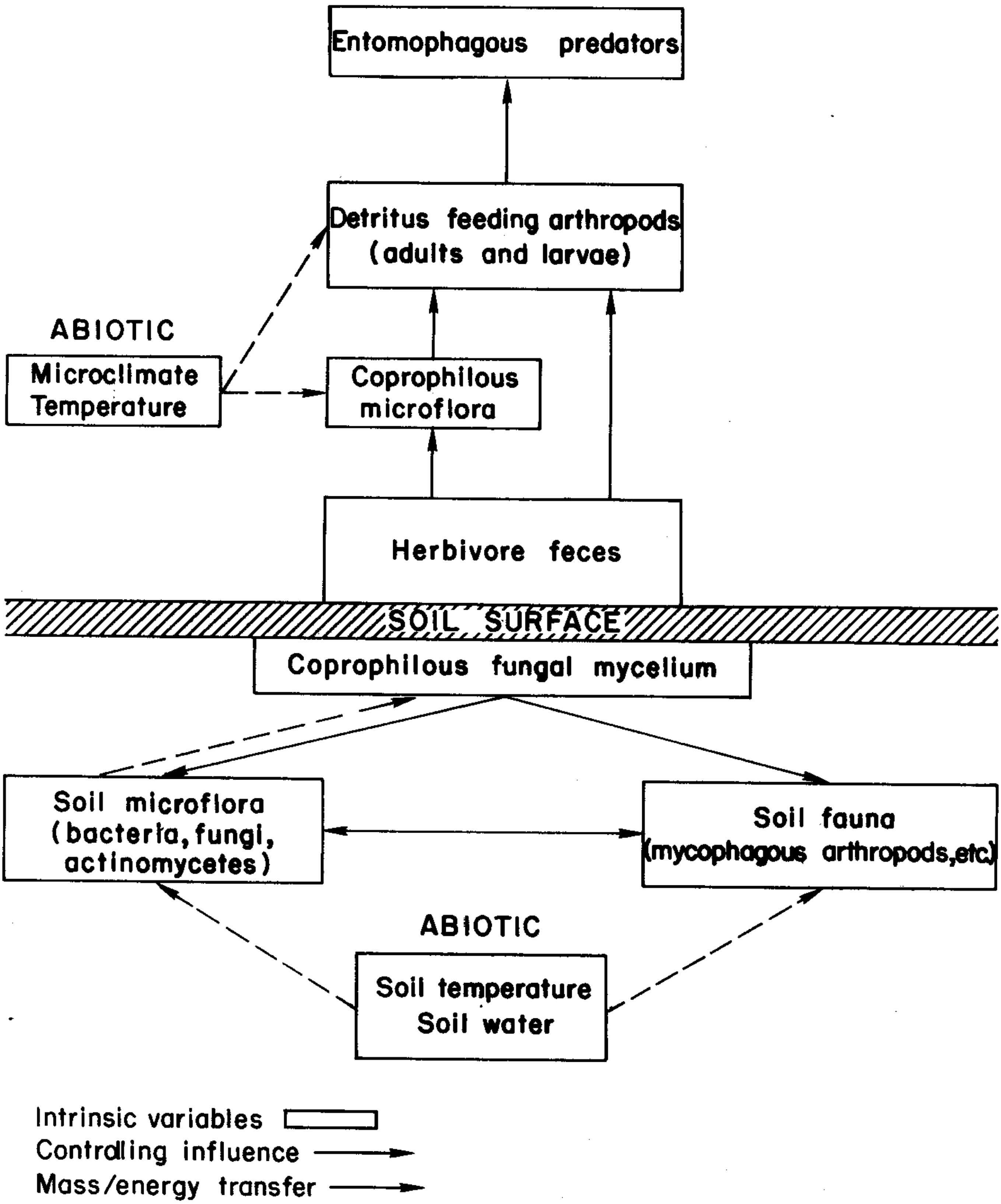

Fig. 1. Descriptive model of the relationships between coprophilous fungi and some prairie ecosystem compartments.

Colorado, is reputed to be the most intensively studied grassland ecosystem in the world, and so it seemed appropriate that someone make at least a cursory examination of the coprophilous mycoflora. Furthermore, since it has already been demonstrated that fungal colonization patterns differ on ostrich and goat feces collected from the same grassland (Mitchell 1970), it was of interest to compare populations of fungal colonists on feces of some of the large herbivores on the Pawnee Site.

MATERIALS AND METHODS

Feces were collected at the Pawnee Site on 27 October 1972 from pronghorn antelope, cattle, rabbits, and small mammals, all of which had been grazing within a short distance of one another. Some of the collections were recently voided feces which had dried thoroughly before any fungi could develop fructifications. Other collections were comprised of partially decomposed feces showing considerable weathering. Individual collections of freshly dried and partially decomposed cattle feces (280 to 320 g dry weight), rabbit feces of various ages (200 fecal pellets = 28 to 32 g dry weight), as well as freshly dried small mammal (20 fecal pellets = 0.5 to 1.0 g dry weight) and pronghorn feces (100 fecal pellets = 18 to 22 g dry weight), were divided into six subsamples of approximately equal size and placed on moist paper towels in individual Petri or specimen dishes. Samples were incubated for 60 days at 24°C and given daily exposures to artificial light. Substrate moisture was maintained at levels slightly below saturation by periodic additions of sterile distilled water. Feces were inspected for fungal fructifications at regular intervals during this incubation period, and semipermanent slide mounts were prepared for each species. Hyphomycetes were not included in the present survey.

An estimate of the similarity in the species composition among the sample populations was calculated using the Index of Similarity $S = \frac{2c}{a + b} \cdot 100$ described by Sorensen (1948). Whereas:

a = the number of species found on one type of feces,

b = the number of species found on a second type of feces, and

c = the number of species common to both types of feces.

RESULTS

Forty-five ascomycetes, 4 basidiomycetes, 3 myxomycetes, and 2 zygomycetes were recorded from the fecal samples (Table 1). The greatest number of different species was found on cattle feces (37), followed by rabbit feces (27 species), pronghorn feces (17 species), and small mammal feces (12 species). The distribution patterns exhibited by some of the predominant fungi are what might be expected based on a review solely of the literature. For example, *Ascobolus immersus, Iodophanus carneus, Sporormiella australis,* and *Tripterospora erostrata* developed fructifications on all four types of feces. Distribution records reveal that these and other fungi listed in Table 1 are widely distributed on different kinds of herbivore feces (Ahmed and Cain 1972; Van Brummelen 1967; Cain 1934; Cain 1956; Kimbrough 1966). In contrast species such as *Delitschia marchalii, Preussia isomera* and *Sporormiella affinis* ocurred only on rabbit feces. These species are cited as being especially common on this substrate (Ahmed and Cain 1972; Cain 1934; Cain 1961). Similarly, *Podospora pectinata* which fruited on cattle feces in the present study, was only recently described from this substrate by Lundqvist (1970). *Mycoarachis inversa* appeared on both cattle and pronghorn feces. Malloch and Cain (1970)

Table 1. Checklist of coprophilous fungi.[a/]

Taxa	Fecal Substrates			
	Rabbit	Pronghorn	Cow	Small Mammal
Mycomycetes				
Licea fimicola Dearn. & Bisby		+	+	
Licea tenera Jahn	+	+	+	
Didymium squamulosum (Alb. & Schw.) Fries	+		+	
Zygomycetes				
Pilobolus crystallinus (Wiggers) Tode			+	
Mucor sp.	+			+
Ascomycetes				
PYRENOMYCETES: NON-OSTIOLATE				
Kernia nitida (Saccardo) Neiuwland		+	+	
Mycoarachis inversa Malloch & Cain		+	+	
Preussia isomera Cain	+			
Tripterospora erostrata (Griff.) Cain	+	+	+	+
PYRENOMYCETES: OSTIOLATE				
Arnium sp. (Similar to *A. triepitheca*, but having only one appendage at each end)			+	+
Chaetomium cuniculorum Fuckel	+			
Chaetomium pulchellum Ames				+
Chaetomium subspirale Chivers	+	+		
Coniochaeta discospora (Auersw.) Cain	+		+	
Coniochaeta scatigena (Berkeley & Broome) Cain	+		+	
Delitschia marchalii Berl. & Vogl.	+			
Delitschia patagonica Speg.	+		+	+
Delitschia winteri Phill. & Plowr.	+		+	+

Table 1. Continued.

Taxa	Fecal Substrates			
	Rabbit	Pronghorn	Cow	Small Mammal
Hypocopra merdaria (Fries) Fries			+	
Phomatospora hyalina (Griff.) Cain	+	+	+	
Podosordaria sp.			+	
Podospora anserina (Ces. in Rabenh.) Niessl			+	
Podospora decipiens (Winter) Niessl			+	
Podospora hyalopilosa (Stratton) Cain	+			
Podospora pectinata Lunq.			+	
Podospora tetraspora (Winter) Cain	+			+
Podospora vesticola (Berk. & Broome) Mirza & Cain	+	+	+	
Sodaria fimicola (Rab.) Ces. et DeNot	+			
Sordaria macrospora Auerw.	+			
Sporormia fimataria DeNot			+	
Sporormiella affinis (Sacc. Bomm. & Rouss.) Ahmed & Cain	+			
Sporormiella australis (Sacc. Bomm. & Rouss.)	+	+	+	+
Sporormiella cymatomera Ahmed & Cain			+	
Sporormiella intermedia Auersw.	+	+	+	
Sporormiella lageniformis (Fuckel) Ahmed & Cain	+		+	
Sporormiella longisporopsis Ahmed & Cain	+			
Sporormiella minima (Auersw.) Ahmed & Cain		+	+	
Trichodelitschia bisporula (Crouan) Munk			+	
Zygopleurage zygospora (Speg.) Boedijn			+	
DISCOMYCETES				
Ascobolus immersus Pers. per Pers.	+	+	+	+

Table 1. Continued.

Taxa	Fecal Substrates			
	Rabbit	Pronghorn	Cow	Small Mammal
Coprotus disculus Kimbr., Luck-Allen & Cain			+	
Coprotus glaucellus (Rehm) Kimbrough			+	+
Coprotus sexdecimsporus (Cr. & Cr.) Kimbrough		+		
Coprotus winteri (Marchal) Kimbrough	+			
Iodophanus carneus (Pers.) Korf	+	+	+	+
Lasiobolus ciliatus (Schmidt ex Fries) Boud.		+	+	
Saccobolus globuliferellus Seaver				
Saccobolus truncatus Vel.		+	+	
Basidiomycetes				
Coprinus miser Karst			+	
Coprinus stercorarius (Scop. ex Fr.) Fr.	+	+	+	
Psilocybe coprophila (Bull. ex Fr.) Kumm.			+	
Sclerodermataceae (sterile)			+	

a/ Collected 27 October 1972: Incubated at room temperature (23° to 24°C) in artificial light, January to March 1973.

first described *M. inversa* from a specimen found on elephant feces collected at Queen Elizabeth National Park in Uganda, and it has also been reported on cattle feces from Cheyenne Co., Nebraska. *Coprotus winterii* was described from just one specimen which, interestingly enough, was found in 1910 on horse dung collected in Colorado (Kimbrough, Luck-Allen, and Cain 1972). We found *C. winterii* on rabbit feces. *Podospora tetraspora* originally described from a collection of mouse feces (Mirza and Cain 1969) was the only species of *Podospora* found on samples of small mammal feces and was the only ascomycete recorded from this substrate which was not found on either type of ruminant feces.

Similarity indices were calculated for populations of coprophilous fungi colonizing each type of feces (Table 2). The highest index of similarity among the fecal samples (S = 56) was associated with cattle and pronghorn feces. Fifteen of seventeen species found on pronghorn feces were also found on cattle feces. This might be explained by the fact that these animals are both ruminants, and a number of fungi appear to be associated with ruminant feces (Richardson 1972). However, with the exception of *Mycoarachis inversa*, species such as *Kernia nitida*, *Sporormiella minima*, and *Saccobolus truncatus*, which occurred only on ruminant feces in the present study, have been previously recorded from nonruminant feces. Populations of fungi on small mammal feces were most similar to those on rabbit feces (S = 41). Small mammal feces produced no myxomycetes or basidiomycetes and lacked genera such as *Coniochaeta* and *Saccobolus*. Furthermore, they showed few species of *Podospora* and *Sporormiella*, which were generally abundant on rabbit, cow, and pronghorn feces. Interestingly, *Coniochaeta* spp. and *Delitschia* spp. were found on lagomorph and cow feces, but not on

Table 2. Similarity indices among fungal populations colonizing four types of herbivore feces. Numbers of species found on both types of feces in parentheses.

Herbivore	Fungal Colonists	Pronghorn	Cattle	Rabbit	Small Mammal
Pronghorn	17 spp.	--	56 (15)	45(10)	28(4)
Cattle	37 spp.			47(15)	33(8)
Rabbit	27 spp.				41(8)
Small Mammal	12 spp.				--

pronghorn feces. Because of species associations such as these, the second highest similarity index (S = 47) was obtained for populations of cattle and rabbit feces.

A comparison of fungal populations colonizing freshly dried and partially decomposed cattle feces (Table 3) provides some information as to possible long-term fungal colonization patterns on these substrates. While *Didymium squamulosum*, *Licea fimicola* and *Phomatospora hyalina* appeared regularly on the freshly dried feces, none developed fructifications on the partially decomposed feces. In contrast, several species, including *Coniochaeta discospora, C. scatigena, Psilocybe coprophila*, and *Trichodelitschia bisporula*, appeared only on collections of decomposed feces. Even with these more obvious differences, populations on both types of cattle feces showed a high degree of similarity (S = 70).

DISCUSSION

There apparently have been only three previous attempts to quantify the relationships between individual species of coprophilous fungi and the feces of various herbivores. Mitchell (1970) recorded a predominance of discomycetes on South African ostrich feces and an abundance of pyrenomycetes on Angora goat feces collected from the same grassland enclosure. Lundqvist (1972) observed that most coprophilous ascomycetes from Sweden are specialized to one or a few categories of feces. Several of these species were found on feces from the Pawnee Site (Table 4). Richardson (1972) examined 137 collections of ruminant and lagomorph feces, primarily from England and Scotland. Certain fungi were associated with ruminant feces, others with lagomorph feces, and several were common to

Table 3. A comparison of species colonizing freshly dried and partially decomposed cattle feces.

Taxa	Freshly Dried Feces	Decomposed Feces
Licea fimicola	+	
Didymium squamulosum	+	
Phomatosproa hyalina	+	
Hypocopra merdaria	+	
Zygopleurage zygospora	+	
Podosordaria sp.	+	
Sclerodermataceae	+	
Licea tenera	+	+
Pilobolus crystallinus	+	+
Kernia nitida	+	+
Mycoarachis inversa	+	+
Tripterospora erostrata	+	+
Delitschia patagonica	+	+
Podospora pectinata	+	+
Podospora vesticola	+	+
Sporormiella australis	+	+
Sporormiella intermedia	+	+
Podospora decipiens	+	+
Sporormia fimataria	+	+
Ascobolus immersus	+	+
Coprotus glaucellus	+	+
Iodophanus carneus	+	+
Lasiobolus ciliatus	+	+
Saccobolus truncatus	+	+
Coprotus disculus	+	+

Table 3. Continued.

Taxa	Freshly Dried Feces	Decomposed Feces
Coprinus stercorarius	+	+
Coprinus miser	+	+
Arnium sp.		+
Coniochaeta discospora		+
Coniochaeta scatigena		+
Delitschia winterii		+
Podospora anserina		+
Sporormiella cymatomera		+
Sporormiella lageniformis		+
Sporormiella minima		+
Trichodelitschia bisporula		+
Psilocybe coprophila		+
Total number of species	27	30

Table 4. Species occurring on feces from the Pawnee Site which have a "host animal preference" in Sweden.[a,b]

Taxa	Host Animal Preference-Sweden	Substrate Occurrence-Pawnee Site
Coniochaeta discospora	Lagomorph	Bovine and Lagomorph
Coniochaeta scatigena	Equid	Bovine and Lagomorph
Delitchia winterii	Lagomorph	Bovine, Lagomorph, and Rodent
Podospora decipiens	Bovine	Bovine
Sordaria fimicola	Equid and Lagomorph	Lagomorph
Sporormiella lageniformis	Equid	Bovine and Lagomorph
Sporormiella minima	Bovine	Bovine and Antilocapridae
Zygopleurage zygospora	Rodent	Bovine

a/ See Lundqvist (1972).

b/ Lagomorph (i.e., hare, rabbit); Equid (i.e., horses, donkeys); Bovine (i.e., buffalos, cattle); Rodent (i.e., mice, rats, voles); Antilocapridae (i.e., pronghorn = *Antilocapra americana*).

both fecal types. Richardson's collections were presumably made from different habitats at different times of the year and included samples of horse, sheep, cow, roe deer, rabbit, and hare feces. It is clear that samples of ruminant feces outnumbered and presumably outweighed samples of lagomorph feces. We would suggest that some of the less prevalent species on lagomorph feces might have had higher frequencies if the weight of individual samples was equivalent to that of the ruminant feces. Wicklow and Moore (in press) have shown that the frequencies of different coprophilous fungi vary considerably among 3.0 to 3.8 g samples of rabbit feces. Since the chance that a particular fungal spore will be ingested and deposited with the feces is related, in part, to the quantity of forage going into those feces, it is important that detailed comparisons of fungal populations on different types of feces take into consideration the volume of feces comprising each sampling unit. This is one of the principal reasons that we find data obtained from such comparative studies so difficult to interpret. This statement can also be applied to portions of the data presented herein.

It is not known whether the passage of a similar population of fungal spores through the digestive tract of a lagomorph or ruminant has a selective effect on the population of fungi colonizing their feces. Nor is it known whether coprophilous fungi are able to grow during gut passage. The potential for such growth, however, would offer a distinct competitive advantage, since the fungus would be able to increase its propagule density inside the herbivore and distribute the inoculum in greater numbers of fecal droppings. Rates of mycelial spread of coprophilous fungi on feces or in culture differ considerably. We have noticed that while isolates of *Podospora* and *Sporormiella* grow more slowly in culture than those of *Ascobolus* or *Iodophanus*, they may initiate ascocarp production simultaneously on feces. It would appear that in order for these slower growing fungi to colonize the same fecal surface as the more rapid colonizers, spores of the former would have to be ingested in greater numbers or these fungi would have to be capable of multiplying during gut passage. Should a particular fungus be able to germinate and grow within the rumen, then the ingestion of a single spore could become inoculum for undetermined numbers of fecal droppings. Concentrations of ruminants in grasslands might contribute to a build-up of spore inoculum from these fungal types.

Fungal growth response may vary in feces of different nutrient composition, texture, or volume, thus affecting final densities of fruiting bodies on these fecal remains. For example, the coprophilous fungi on pronghorn antelope feces may be responding favorably to somewhat lower C/N ratios, since pronghorn have been found to have a dietary preference for herbage of relatively high nitrogen content (Hoover 1971).

Many of the coprophilous fungi identified from the Pawnee Site have also been reported from grasslands in other regions of North America and in other parts of the world. In fact, with the possible exception of a few species that we were unable to identify, none of the fungi from the Pawnee Site could be considered endemic to the region. This was entirely expected since coprophilous fungi have presumably adapted to microhabitats associated with fecal droppings. As yet no attempt has been made to experimentally demonstrate how coprophilous fungal populations respond to the different terrestrial habitats in which the feces they colonize have been deposited. Lundqvist (1972) noticed that several species were associated with the feces of forest animals in the taiga zone. Undoubtedly certain evolutionary strategies have developed around the warm-blooded herbivores, the coprophagous arthropods, and the abiotic conditions characteristic of shortgrass prairies.

The 53 species associated with the Pawnee collections (Table 1) represent a very diversified assemblage of coprophilous fungi, particularly when measured against the relatively small amount of fecal material examined. A species list provide by Larsen (1971) shows fewer kinds of fungi even though the amount of substrate examined was greater than in the present study. Similarly, our list of ascomycetes showed a greater amount of diversity than one compiled by Richardson (1972) for various dung types in Great Britain. There appears to have been only one collection which equals ours in diversity. R. F. Cain (personal communication) collected several dung types from a dry grassland near Greybull, Wyoming, on which developed a greater variety of coprophilous fungi (50 species) than any collection of feces he has had the opportunity to examine. This collection was one of a number he made while traveling through the western United States druing the summers of 1955, 1957, 1960, 1962, and 1964.

It is interesting to speculate why species diversity among coprophilous fungal populations on the Pawnee Site is so great in view of the observation by Coleman et al. (1973) that moisture variability in semiarid grasslands limits the numbers and kinds of consumers that can occupy such a system. Limited annual precipitation or extended periods of drought may contribute to reduced species diversity among some groups of consumers, but would not be expected to effect the species composition of coprophilous fungal populations. Reduced moisture levels could interrupt the growth and fruiting body development of these fungi, but would not eliminate them from the site. It also seems apparent to us that the longer feces survive fragmentation and eventual incorporation into the mineral soil, the greater chance they have of becoming colonized by additional species of coprophilous fungi. These may be present in the soil, arrive as airborne inoculum, or be transported by arthropod vectors.

A comparison of species lists obtained from examining collections of both freshly dried and partially decomposed cattle feces shows that the latter includes several species which were not found on the former. This observation would tend to support our contention that, given the length of time that feces persist in semiarid grasslands, there is a possibility that they will become inoculated with additional fungal colonists. One would expect that coprophagous arthropods could spread fungi from one fecal pile to another. Furthermore, soil probably serves as a reservoir for many of these fungi. Because these soils are dry during much of the year, the activities of potentially antagonistic soil microorganisms are limited. Under such circumstances the spores of many coprophilous fungi might be expected to survive in these soils for indefinite periods. When a self-heating pile of cattle feces is deposited over the soil in which these spores lie, this could serve as a stimulus to germination and eventual growth and fruiting body development on or within those feces.

Herbivore feces represent a significant portion of the aboveground detritus on the Pawnee Site, where limited annual precipitation (Rasmussen, Bertolin, and Almeyda 1971) and the absence of the earthworms retard their rate of disappearance. During the October site visit it was difficult to find a square meter of gound not showing any fecal remains. The time required for the disappearance of herbivore feces on the Pawnee Site is not known; however, it appears that some of the feces may have been there for several years. Under such circumstances, many coprophilous fungi are likely to be found in various stages of maturity with a capability for discharging spores whenever adequate moisture is available. In contrast, fecal droppings (rabbit, deer, and small mammal) which accumulate during the late fall and winter in a tallgrass prairie (Curtis Prairie, Madison, Wisconsin) completely disappear within a 3 to 4 week period in the spring that coincides with the emergence of new plant growth and abundant earthworm activity. Since earthworms seem to thrive in manure piles and are known to select from among the leaves in an oak forest (Edwards and Heath 1963), they might also be expected to selectively ingest herbivore feces. Any destruction of microhabitat resulting from the ingestion of feces by earthworms or any losses in spore inoculum through grassland fires could be considered catastrophic events in the life histories of many coprophilous fungi. These disturbances may contribute to dramatic changes in the species composition of coprophilous fungal populations, thereby reducing the diversity of species in a given collection of feces. On the Pawnee Site one would expect the coprophilous fungal population to be rather stable, since neither earthworms nor fires play a part in the ecology of this area.

In moist chambers the appearance of many of the same fungal fructifications on collections of both old and freshly dried cattle feces suggested that some coprophilous fungi may show recurrent growth and fruiting body development with successive moist periods on the Pawnee. Such a model suggests seasonal reductions in levels of microbial staling products or living microbial biomass before additional growth can take place. Preliminary results from some related experiments have shown that feces on which no new fungal fructifications appear after 40 days of an 80-day incubation period will, following freezing or air-drying, produce new fruiting bodies of many of the same species which appeared during the original incubation period. Hot summers and/or freezing winters probably contribute to conditions affecting a change in fecal composition. Resumption in microbial activity following adverse conditions of incubation has also been described for air-dried soils (Stevenson 1956; Griffiths and Birch 1961).

Future research should be directed at identifying the events controlling the fragmentation and rate of decomposition of feces in grasslands. The timing of events for both fungal and arthropod life histories may give some clues as to the interrelationships between these two groups of detritivores. It is important to note that no one has clearly shown that fungi are essential to the insects feeding on feces. Finally, we should determine whether coprophilous fungi have any effects on the microbial ecology of the rumen.

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