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# Soil fungi of virgin and restored tallgrass prairies in central Iowa

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# Soil fungi of virgin and restored tallgrass prairies in central Iowa

by

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# INTRODUCTION

The soil is an extremely complex heterogeneous assemblage of organic and inorganic components. Whereas the abiotic component of soils has been extensively examined and characterized, the biotic component has remained poorly known.

Fungi are only one group of the wide array of soil inhabitants. Decomposer fungi form the largest population of the total microorganisms in the soil (Paul et al., 1979). The substrates available to these organisms include above ground litter, organic residues in the soil, living and dead roots and their exudates, and living and dead microorganisms. These substrates can be thought of as microsites for a succession of microorganisms in the decomposition process. The succession of organisms gradually reduces the capacity of the habitat to support life and the end result is not a climax association, but zero living units (Garrett, 1955). The activities of microorganisms are essential to soil building processes, nutrient cycling, and the total energy dynamics of the soil ecosystem.

Most fungal soil studies characterize the soil mycoflora as being almost exclusively Hyphomycete genera. That Hyphomycetes are important soil organisms is well-established, but other fungal species may be equally important in the decomposition process and their presence in the soil ecosystem is poorly documented. Ascomycetes and Basidiomycetes, good decomposers of cellulosic substrates, are generally absent from soil lists except as infrequent forms.

A detailed picture of the fungal community in prairie soils was the focus of the present study. Laboratory plating of preburn and numerous postburn soil samples collected during the growing season provided documentation on the effects of spring burning as well as the response to seasonal changes by the fungal community. Prairie vascular plant flora changes constantly throughout a growing season but it is unknown if the fungal community exhibits similar seasonal fluctuations and diversity differences over the same time period. To date, few seasonal trends have been observed in fungal populations (Widden, 1981).

Extended incubation periods of soil plates allowed a wide range of rarely reported and unusual soil fungi to develop and sporulate. Periodic observations of culture plates throughout the incubation period gave a detailed picture of the succession of fungal organisms which colonize and break down organic residues in the soil.

Re-established prairie rarely has the diversity of native vascular plant flora that is found on virgin prairie. It is unknown if the soil mycoflora reflects a similar corresponding change in species diversity. Gochenaur (1981) reviewed the effects of various disturbance factors on the fungal community and concluded that cultivation increases the productivity of opportunistic decomposers but has variable effects on species diversity. Sampling of virgin and restored prairie sites should add valuable insight into the effect of cultivation on soil mycoflora of the prairie ecosystem.

# LITERATURE REVIEW

Since Müller in 1883 first noted the presence of fungal hyphae in soil (Waksman, 1916), many workers have attempted to qualitatively and quantitatively assess the fungal community in soils of all types, locations, and vegetation histories. The potential numbers of fungal species and fungal community composition and structure remain poorly defined for most soils.

Griffin (1972) published a collection of lectures as one of the first treatises devoted exclusively to aspects of soil fungal ecology. Additional historical developments in soil microbial ecology have been reviewed recently in books by W. B. Cooke (1979) and R. C. Cooke and Rayner (1984). Wicklow and Carroll (1981) served as editors for the most up-to-date treatment of fungi in the framework of contemporary ecological thought. The series of contributed papers by leading mycologists and ecologists addressed such topics as fungal populations and communities, competition and species interactions, productivity, nutrient cycling, and community development. It has brought into focus the role and importance of fungi in ecosystems but it has also emphasized that much work remains.

Tremendous impetus was given to studies of grassland soil fungal ecology by the implementation of the International Biological Program in the 1960s. Stemming from participation in the Grassland Biome segment of the program, Clark and Paul (1970) summarized accumulated information on the range of soil microflora, including fungi, of grassland. On an

international scale, Kjoller and Struwe (1982) compiled and published data derived primarily from worldwide IBP fungal studies of grassland, desert, woodland, and tundra soils. Comparisons of biomass, productivity, and occurrence of fungi in different ecosystems worldwide provide a valuable contribution to soil fungal ecology.

After years of fungal ecological research, Griffin (1972) defined the two major difficulties facing fungal ecologists as: (1) the complex physical and chemical environment of the soil, and (2) the microscopic nature of the soil organisms. Furthermore, accurate descriptions of fungal communities are complicated, according to States (1981), by environmental factors which favor some prolific species, and by difficulties in separating the soil inhabitants from those species occupying plant debris as it is incorporated into the soil. Two significant trends appear consistent in all fungal communities examined critically since 1950 (Christensen, 1981): (1) microfungal species diversity appears to be correlated with vascular plant diversity, and (2) species composition seems clearly correlated with the vegetation cover of the community.

When soil microbial studies first began during the early years of the 20th century, grassland soils were largely ignored. Most published accounts of that era (Waksman, 1916; Werkenthin, 1916; Brown, 1917; Brierley, 1923) dealt with agricultural or forest soils. It was not until Paine (1927) undertook a study of forest and pasture soils in Iowa that information about fungi in grasslands began to accumulate. Temperate grasslands once covered vast expanses of North and South

America, Asia, Africa, and Australia (Raven et al., 1981). All are characterized by climates that support a vegetation cover dominated by grasses, but include a wide array of herbaceous plants and an almost lack of woody vegetation.

Since 1927, grassland soil studies have been reported from Africa (Eicker, 1970; 1974; Papendorf, 1976), New Zealand and Australia (Thornton, 1958; 1960; 1965; Jackson, 1965; Ruscoe, 1973), South America (Gochenaur, 1970; Goos, 1960; 1963), Asia (Mukerji, 1966; Dwivedi, 1966; Chu and Stephen, 1968; Mishra, 1965; 1966; Mishra and Kanaujia, 1973), Europe (Brown, 1958; Warcup, 1951; 1957; Apinis, 1958; 1963; 1964a,b; 1972; Ciborska and Zadura, 1974; Park, 1963), and North America (Bisby et al., 1933; 1935; McElroy et al., 1952; England and Rice, 1957; Orpurt and Curtis, 1957; Gordon, 1954; 1956; Swift, 1929; Wicklow, 1973; 1975; Wicklow and Hirschfield, 1979; Herman and Kucera, 1979; Clarke and Christensen, 1981; Pamperin, 1981).

Almost all of the published reports are derived from soil studies of planted pastures or grasslands that have been heavily grazed or mowed. Few have dealt with natural grassland communities.

In North America prior to settlement, grasslands extended from the Rocky Mountains eastward to Indiana. Although the eastern United States was dominated by hardwood forests, prairie did occur in scattered pockets from Ohio east to Long Island, New York. The tallgrass prairie or true prairie encompassed an area roughly 574,000 $km^2$ (Risser et al., 1981). Within the grassland formation of North America, the tallgrass prairie receives the most rainfall, has the greatest north-south diversity, and

the greatest number of major dominant species of any association (Risser et al., 1981).

Following the last major glaciation of North America, tallgrass prairie became the dominant vegetation in Texas about 12,000 years ago and the grassland range extended northward and eastward reaching maximum extension about 2000 years ago (Delcourt and Delcourt, 1987). Prairie has been slowly receding since that time.

The extensive root systems of the prairie grasses and forbs modified and broken down by the decomposition processes of soil microorganisms gave rise to the richest agricultural land in the world. Yet little is known about the fungal community which contributed to the development of the soils of the tallgrass or true prairie ecosystem.

Studies of soil fungi have of necessity been studies based on a variety of laboratory isolation procedures developed over the last 100 years. The most widely used techniques are described by Johnson and Curl (1972), Warcup (1960), and Montegut (1960). These procedures, by their selective nature, often yield an inaccurate assessment of the relative importance of certain groups of fungal species and a lack of appreciation for the role others may play in the soil ecosystem. Because fungi vary considerably in their nutritional, physiological, and environmental needs and tolerances, no one isolation procedure results in a complete picture of the soil microflora. Only a combination of procedures can depict the full range of fungal species which occur in different soils.

The earliest recorded study of fungi from tallgrass prairie soil was by Paine (1927) when he sampled a grazed but untilled pasture in Iowa.

In the past sixty years, few reports have come from these soils or from grassland soils in contiguous areas.

Researchers have adopted different sampling techniques for studying prairie soil fungi. Frequency of sampling has varied from only once (Paine, 1927; Swift, 1929; Gordon, 1956; Orpurt and Curtis, 1957; Wicklow, 1973; Huang and Schmitt, 1975; Wicklow and Hirschfield, 1979) to two or more times per site (England and Rice, 1957; Herman and Kucera, 1979; Clarke and Christensen, 1981; McMullen and Stack, 1983; Wicklow, 1975).

Single sample collections were made during various months of the growing season, April to November, but absent during the winter months, December through March. When sampling a site more than once, sampling criteria were based on seasonality (Clarke and Christensen, 1981; McMullen and Stack, 1983), a monthly schedule (England and Rice, 1957), or relation to a particular management practice such as burning or mowing (Wicklow, 1973; Herman and Kucera, 1979).

Vertical soil sampling has varied from surface sampling (Wicklow, 1973) to coring to a depth of 120 cm for one sample (Swift, 1929). Most soils have been sampled within the top 10 cm. Warcup (1951) determined from grassland soil studies that species numbers and species diversity decreased with increasing sampling depth.

Isolation techniques have varied greatly among studies of prairie soils. Dilution plating alone was used by Paine (1927), Clarke and Christensen (1981), Wicklow (1973), Herman and Kucera (1979), Gordon (1954, 1956), and Orpurt and Curtis (1957). Soil plating was the

technique of choice for Swift (1929) and England and Rice (1957). McMullen and Stack (1983) used a combination of plating techniques in their Fusarium studies, but abandoned dilution plating in favor of soil plating, citing ease of use and greater diversity of species recovered. Huang and Schmitt (1975) used dilution plating, alcohol treatment, heat incubation, and hair-baiting. Wicklow (1975) directly baited soil samples with pieces of oat straw and filter paper to stimulate ascomycete development in his studies of prairie soils in Wisconsin.

Culture incubation time varied among workers from as few as three days (Paine, 1927) to a maximum of 50 days (Wicklow, 1975) before counting, identifying or subculturing colonies from isolation plates. Most investigations used about seven days.

Early studies of tallgrass prairie soils resulted in reports of few fungal species, 19 by Paine (1927) and 39 by Swift (1929). Both investigators isolated a prevalence of species in the Hyphomycetes, particularly Aspergillus fumigatus and a lack of Zygomycetes, particularly Mucor, from untilled soils. Subsequent studies revealed a regularity of occurrence of Zygomycetes, including Mucor, from virgin soils (Orpurt and Curtis, 1957; England and Rice, 1957; Huang and Schmitt, 1975).

The most commonly isolated fungi from prairie soils were species of Fusarium, Penicillium, Trichoderma, Alternaria, Paecilomyces, Chrysosporium, Aspergillus, Mortierella, and Mucor. Fusarium spp. have been universally equated with grassland soils. They accounted for 16 percent of all isolates in a soil study of cereal plots in Canada

(Gordon, 1954). Subsequently, Gordon (1956) reported that Fusarium oxysporum was the most prevalent species in grassland soils, followed by Fusarium equiseti and F. solani.

Soil studies of North Dakota grasslands (McMullen and Stack, 1983) gave further support to Gordon's findings; F. oxysporum and F. equiseti had frequencies of 100 percent within each of six study sites. The proportions varied from site to site, leading the authors to hypothesize that F. oxysporum thrives in undisturbed grasslands whereas F. equiseti is most favored by continued disturbance.

A seasonal preference was postulated for Fusarium species (McMullen and Stack, 1983) related to nutrient levels in early season from seedling exudates and in late season by root decomposition. Clarke and Christensen (1981) also reported that slight seasonal trends existed in soil fungi from a short-grass prairie in South Dakota.

Orpurt and Curtis (1957) investigated soil fungi relative to higher plant associations in 65 Wisconsin prairies. Some species, such as Fusarium solani, were equally common in all prairie types whereas others showed site preferences along a moisture gradient. Numbers of species were greatest in the mesic prairie with fewer numbers in both wet and dry sites. One of the major contributions of the study was the idea that microfungal communities reflect definite relationships to the higher plant communities.

Garrett (1950; 1954; 1955) developed a successional hypothesis of fungal substrate utilization, later coined the "nutritional hypothesis" by Webster (1970). The idea that sugar fungi are primary colonizers

followed by cellulose and lignin decomposers was seriously questioned by Frankland (1966) after a detailed, 5-year study of decomposition of bracken petioles. Initial colonizers were cellulose and lignin decomposers, followed by Hyphomycetes, and lastly sugar fungi which existed on the by-products of cellulose decomposition.

A tallgrass prairie soil study by Herman and Kucera (1979) indicated a sequential appearance of Zygomycetes (sugar fungi), followed by Ascomycetes and their imperfect stages and finally Basidiomycetes and their imperfect stages (cellulose and lignin decomposers). The two studies, although apparently contradictory, analyzed different phases in the decomposition process: the former litter decomposition, the latter organic residues.

Ascomycetes, although reported infrequently, are probably common regular inhabitants of grassland soils. Wicklow (1973) found that two species of the pyrenomycete genus Coniochaeta were common isolates from burned prairie soil, leading him to postulate that a "fungal bloom" resulted from heat activation of the spores. By utilizing heat stimulation methods, Huang and Schmitt (1975) selectively isolated 36 Ascomycetes from grassland soil in Ohio.

Slow growing ascomycetes are most likely overlooked or selected against when isolations are discontinued after a seven-day incubation of soil plates. Wicklow (1975) found no ascomycetes on baited prairie soil plates after 7 days incubation time, but by day 14, five species had matured and by day 50, three additional species developed.

Studies of basidiomycetes as soil fungi are rare. That

basidiomycetes are present in grassland communities was documented by Shantz and Piemeisel (1917) and Bayliss Elliot (1926) in fairy ring studies of Calvatia gigantea and Marasmius oreades in short grass prairies. Techniques for isolation of basidiomycetes from soils are tedious and fungal identification remains difficult because most of them do not readily sporulate in culture.

Prior to 1982, tallgrass prairie communities had not been surveyed for vescicular arbuscular mycorrhizal (VAM) fungi. Hetrick and Bloom (1983) identified 20 VAM species from six collection sites on the Konza Prairie in Kansas. Species of Glomus and Gigaspora occurred with the greatest frequency. Maximum numbers of spores were retrieved from spring rather than fall collections, a contradiction of previous reports from other soils. Prairie soils also yielded a greater diversity of fungal species than did soils of nearby winter wheat fields.

Abiotic factors may influence the fungal component of soils. Not only do the physical, chemical, and mechanical properties of soil play a role in the distribution and composition of the fungal community (Park, 1968), but environmental conditions may cause fluctuations in fungal populations. Optimum conditions of moisture availability, favorable temperatures, and sufficient organic substrates lead to maximum fungal diversity in spring, followed by a decline under hotter and drier conditions during summer (Ulehlova, 1979). Numbers often increase in fall as moisture and temperature conditions once again approach optimum levels.

Management practices such as burning, mowing, and grazing are

reported to alter the fungal community. Burning in particular is a common management practice on almost all tallgrass prairies. Both Wicklow (1973) and Herman and Kucera (1979) found changes in species composition and diversity by burn manipulation of prairie stands in Wisconsin and Missouri, respectively.

# MATERIALS AND METHODS

## The Study Sites

Four tallgrass prairies in Story County, Iowa, were selected as study sites (Fig. 1). Three of the prairies sampled, Ames High Prairie, Doolittle Prairie, and Doolittle Prairie Plover Tract, have never been plowed and are considered virgin prairie. All three have a past history of disturbance by mowing and/or grazing. The fourth site, Norton Prairie, is a planted prairie on land that was previously cropped. It was replanted to prairie grasses 6 years prior to the study.

Story County lies in the Clarion-Nicollet-Webster soil association. The soils are derived from parent material of glacial origin, primarily glacial till. The area was covered by continental ice at least twice (Soil Survey of Story County, Iowa, 1984). The latest ice sheet, the Des Moines Lobe of the Wisconsin glacier, receded from central Iowa approximately 14,000 years ago.

The topography of the region is level to gently rolling. Small depressions or prairie potholes were abundant in low-lying areas throughout most of central and north-central Iowa at presettlement. Draining and tiling activities have almost eliminated these poorly drained areas from most of the region, but they remain common on Doolittle Prairie and Plover Tract.

The mid-continental climate of central Iowa is characterized by (1) seasonal fluctuations in temperature (winter and summer means are -6 C and 21 C, respectively), (2) an annual precipitation near 96 cm, 75% of

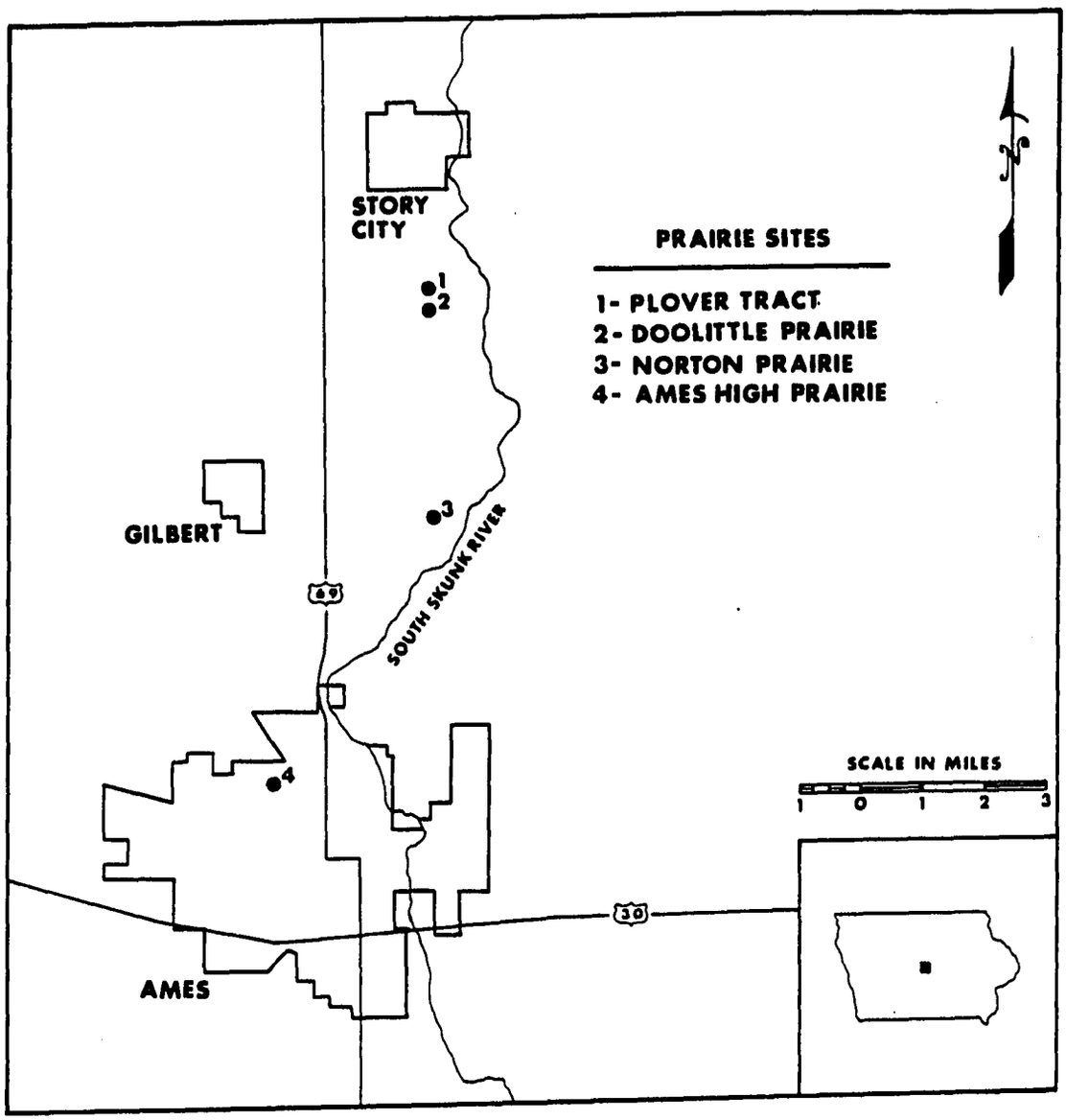


Figure 1. Map of prairie sites, Story County, Iowa

which occurs April-September as a result of thunderstorms, and (3) a frost-free period of about 151 days (Soil Survey of Story County, Iowa, 1984).

Past vegetational history in Story County following glacial retreat was boreal forest, replaced by deciduous forest over a 6,000 year span, and finally grassland communities which developed between 8,000 and 3,000 years ago. At presettlement, the entire county was tallgrass prairie dissected by deciduous forest along the waterways.

The collection sites are all classified as tallgrass prairie communities. The dominant grasses on the virgin prairie sites are Andropogon gerardii Vitman and Sorghastrum nutans (L.) Nash. The drier slopes at Ames High Prairie support stands of Andropogon scoparius Michx., Sporobolis heterolepis Gray and Bouteloua curtipendula (Michx.) Torr. In moister areas of Doolittle Prairie and Plover Tract, Panicum virgatum L., Spartina pectinata Link and Calamagrostis canadensis (Michx.) Beauv. are the more common associates of the dominant species. The re-established Norton Prairie is dominated by planted stands of Andropogon gerardii Vitman, Sorgastrum nutans (L.) Nash, Andropogon scoparius Michx. and Agropyron smithii Rhyb. Some of the more common prairie plant species which occur on the study sites are listed in Appendix A.

The study sites have a history of periodic spring burning as a management practice. All were partially burned in the spring of the year in which they were sampled.

## Collection and Isolation Procedure

Plots within the sampling sites were selected from burned and unburned treatments. On each study site, preburn soil samples and 2 da, 14 da, 30 da, 60 da, and 180 da postburn soil samples were collected. Six plots were sampled at the Norton site and eight plots were sampled at each of the virgin prairie sites at each collecting period. The virgin prairie sites were sampled over one growing season, the Norton prairie was sampled during two consecutive growing seasons.

Within each plot, at sampling time, a small area was cleared of standing vegetation and surface litter. Soil samples were collected from the surface to a depth of 4 cm with a trowel. Approximately 1 liter of soil from each plot was placed in a sterile plastic bag, and transported to the laboratory in an ice-cooled chest. All samples were frozen immediately and kept at -5 C until processed. The trowel was sterilized with 95% ethyl alcohol prior to use on each plot.

Soil samples from the study sites were analyzed by the ISU Soil Testing Laboratory. Data on pH, % organic matter, phosphorus and potassium from spring and fall collections for burned and unburned areas are presented in Table 1.

A modified soil plate method was used for soil fungal isolations. Two types of agar media, corn meal agar and non-carbon agar, were used for soil plate preparation. Twenty-five ml aliquots of non-carbon agar were added to glass petri plates containing either 1-g samples of sterilized grass culm pieces of Andropogon gerardii or 1 g of sterilized sawdust pieces. Twenty-five ml aliquots of corn meal agar were added to

Table 1. Spring and fall measurements of percent organic matter, pH, phosphorous and potassium from burned and unburned prairie plots, Story County, Iowa[a]

| | Spring | | | | Fall | | | |
|---|---|---|---|---|---|---|---|---|
| | % Org. matter | pH | P kg/ha | K kg/ha | % Org. matter | ph | P kg/ha | K kg/ha |
| | | | | Burned | | | | |
| Plover | 5.30 | 7.27 | 33.00 | 405 | 4.00 | 7.79 | 20.22 | 523 |
| Doolittle | 10.10 | 6.79 | 38.47 | 569 | 9.50 | 7.15 | 61.36 | 490 |
| Ames | 7.10 | 8.03 | 45.47 | 663 | 4.10 | 7.69 | 29.20 | 395 |
| Norton 1 | 5.10 | 7.01 | 25.16 | 902 | 4.00 | 7.08 | 15.69 | 715 |
| Norton 2 | 4.00 | 7.28 | 56.16 | 692 | 4.20 | 7.00 | 61.55 | 563 |
| | | | | Unburned | | | | |
| Plover | 11.70 | 7.79 | 95.75 | 1045 | 5.50 | 7.38 | 16.99 | 308 |
| Doolittle | 14.50 | 6.93 | 35.94 | 617 | 13.40 | 7.51 | 29.07 | 489 |
| Ames | 6.00 | 7.83 | 12.36 | 500 | 4.20 | 6.86 | 14.19 | 440 |
| Norton 1 | 4.00 | 7.04 | 21.79 | 1085 | 3.70 | 7.35 | 64.35 | 553 |
| Norton 2 | 5.30 | 6.96 | 23.47 | 906 | 14.80 | 7.04 | 22.58 | 658 |

[a]Soil samples were analyzed by the Soil Testing Laboratory, Iowa State University.

sterile glass plates. Streptomycin sulfate was added to all media prior to pouring to inhibit bacterial growth. The plates were held for a minimum of 3 days prior to inoculation. Contaminated plates were discarded.

Each soil sample was thawed and thoroughly mixed. Approximately 1 g of soil was placed on the agar surface at one side of the petri plate. Five replicate plates (15 per sample) were inoculated for each of the three media used. One control plate for each medium type was held throughout the observation period. The remaining soil was reserved for VAM examination.

The soil plates were incubated at room temperature and were examined at approximate intervals of 7, 30, 60, and 90 da. Fungi which appeared on the plates were recorded, identified when possible, and/or transferred to low sugar potato dextrose (PDA) agar plates or tubes for later identification.

Most isolates were identified from subcultures made on low sugar PDA plates. Penicillium and Aspergillus isolates were plated on Czapek's agar and malt extract agar for identification. Cylindrocarpon and Fusarium species were cultured on low sugar PDA and 2% water agar. References used for fungal species identification are listed in Appendix B.

### Vesicular Arbuscular Mycorrhizal Isolation Procedure

Soil samples were processed for VAM fungi by using the centrifugation gradient procedures of Walker et al. (1982). Material collected on the final sieving was washed into vials with a 5% formaldehyde solution

and stored at room temperature until examined.

Vial contents were washed into a 5-cm watch glass for observation. Relative spore counts were made by using a dissecting microscope set at 30x. Individual spores were transferred to glass slides with a micropipette for microscopic examination and identification.

## Data Analyses

Frequency data for the fungal species were based on presence/absence tabulations from the inoculation plates for each soil sample. A density rating for each species was determined by the formula D = P/N where P = the number of incubation plates in which the species occurred and N = the total number of incubation plates per soil sample. Composite density data from all collections were used to determine the most common 100 fungal species. The densities of these top 100 species for each plot sampled were used as input for the ordination program. The results were ordinated by detrended correspondence analysis (Hill, 1979).

# RESULTS AND DISCUSSION

## Fungi of Central Iowa Tallgrass Prairie Soils

Four hundred eighty-three species of soil-inhabiting fungi have been identified from tallgrass prairie sites in central Iowa (Appendix C). Included are 7 Myxomycetes, 6 Basidiomycetes, 62 Zygomycetes, 112 Ascomycetes, 35 Coelomycetes and 261 Hyphomycetes.

Myxomycetes and Basidiomycetes are infrequently recorded on soil fungal species lists. Myxomycetes, common on decomposing organic matter, are not represented on soil lists because traditional isolation techniques do not allow their development on culture plates. Use of a mass soil sample rather than a dilution series allowed colony development not only from spores and hyphal fragments, but from larger survival propagules such as sclerotia. Retention of plates for 3 months provided ample time for development of Myxomycete plasmodia and sporangia in culture.

Throughout a growing season, grassland communities accumulate ample organic substrates to support Myxomycete fungi through litter decomposition and buildup of microorganism populations. The mobility of a plasmodium enables continuous invasive capabilities into new soil microsites.

Many Myxomycetes can produce enzymes, sterols, and antibiotics (Martin and Alexopoulos, 1969), thereby enhancing their competitive potential in the soil ecosystem. Both sexual reproduction and sclerotial formation assure survival during unfavorable environmental

conditions.

A complete assessment of the presence and frequency of occurrence of Basidiomycetes was not attempted during the study. Commonly used soil fungal isolation techniques rarely result in Basidiomycete colonies. Field observations of basidiocarps of Agaricus, Leucoagaricus, Coprinus, Lycoperdon, and Calvatia reinforce the hypothesis that a large and diverse population of this group inhabits prairie soils.

Basidiomycetes with cellulose and lignin degrading capabilities would potentially find suitable substrates among the litter and organic residues from prairie plant decomposition.

Most of the fungal species isolated from soil come from four major groups of fungi: Zygomycetes, Ascomycetes, Coelomycetes, and Hyphomycetes. A ranking of the thirty principal species by relative densities on the study sites (Table 2) shows that these groups are represented by 8, 3, 1 and 18 species, respectively. The thirty principal species differ somewhat if plot frequency, rather than densities of the fungi, is used (Table 3). The numbers of taxa in the major groups then total 5, 3, 2, and 20 species, respectively. Acremonium sp., Sphaerodes retispora, Chrysosporium sp., and Pyrenochaeta sp. replace Zygorhynchus moelleri, Coemansia pectinata, Absidia glauca, and Chaetomium seminudum with higher frequencies (68.5, 56.0, 56.5, 55 vs. 41.5, 38.5, 50.5, 36.0) but lower densities on the sites (20.84, 18.11, 15.68, 16.48 vs. 37.17, 22.13, 35.81, 25.74).

Zygomycetes are common inhabitants in soils worldwide. Most are saprobes, deriving their nutrition from simple carbohydrates (Griffin,

Table 2. Density rankings of principal species of fungi isolated from tallgrass prairie soils, Story County, Iowa

| Species | Plover | | Ames | | Doolittle | | Norton 1 | | Norton 2 | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | U | B | U | B | U | B | U | B | U | |
| Trichoderma hamatum | 11.86 | 9.99 | 17.40 | 18.20 | 15.92 | 15.72 | 14.07 | 15.24 | 13.67 | 11.14 | 143.21 |
| Gliocladium roseum | 13.88 | 15.74 | 12.00 | 12.65 | 10.88 | 9.14 | 12.39 | 11.82 | 12.66 | 11.80 | 122.96 |
| Staphlotrichum coccosporum | 15.93 | 17.00 | 12.19 | 9.43 | 12.11 | 10.32 | 10.32 | 8.27 | 12.74 | 11.19 | 119.50 |
| Gliocladium viride | 5.75 | 4.52 | 8.94 | 9.99 | 6.53 | 2.27 | 12.73 | 13.66 | 13.00 | 13.31 | 90.60 |
| Mucor hiemalis | 11.19 | 12.67 | 8.03 | 9.46 | 5.15 | 10.54 | 6.26 | 5.74 | 9.25 | 7.54 | 85.83 |
| Ramichloridium schulzeri | 12.16 | 12.12 | 8.66 | 7.45 | 5.73 | 4.74 | 6.81 | 6.07 | 9.05 | 9.26 | 82.04 |
| Alternaria alternata | 3.54 | 8.00 | 12.92 | 10.59 | 10.34 | 9.89 | 6.40 | 5.93 | 3.28 | 5.06 | 75.95 |
| Mariannaea elegans | 1.94 | 1.67 | 4.88 | 8.07 | 6.66 | 2.81 | 8.73 | 7.35 | 8.38 | 8.47 | 58.96 |
| Paecilomyces marquandii | 11.27 | 10.02 | 9.80 | 6.99 | 6.41 | 9.79 | 0.86 | 1.60 | | | 57.83 |
| Cunninghamella elegans | 6.48 | 3.19 | 11.79 | 11.86 | | | 1.08 | 3.14 | 4.72 | 6.39 | 49.79 |
| Penicillium janthinellum | | 2.47 | 8.68 | 7.66 | 3.81 | 7.14 | 3.95 | 3.65 | 3.92 | 4.34 | 46.94 |
| Cladosporium cladosporoides | 2.15 | 5.26 | 6.59 | 3.60 | 5.06 | 5.69 | 4.94 | 5.87 | 2.33 | 4.87 | 46.36 |
| Chaetomium globosum | 3.73 | 3.39 | 4.39 | 4.33 | 5.75 | 5.27 | 3.15 | 4.20 | 5.28 | 4.27 | 43.76 |
| Fusarium oxysporum | 4.07 | 5.47 | 4.79 | 4.55 | 5.76 | 5.49 | 4.19 | 3.08 | 1.81 | 1.81 | 41.02 |
| Myrothecium verrucaria | 1.62 | 4.00 | 6.27 | 2.15 | 2.46 | 1.54 | 4.15 | 3.33 | 6.61 | 7.82 | 39.95 |
| Phoma sp. | | 2.86 | | 2.06 | 1.54 | 2.09 | 7.93 | 6.47 | 6.80 | 5.94 | 37.72 |
| Zygorhynchus moelleri | 9.52 | 4.54 | 5.54 | 13.07 | 3.01 | 0.87 | | | 0.21 | 0.62 | 37.17 |
| Mortierella sp. | 7.12 | 5.28 | 3.20 | 2.99 | 2.53 | 4.07 | 2.81 | 1.47 | 4.01 | 3.13 | 36.61 |

Table 2. (Continued)

| Species | Plover | | Ames | | Doolittle | | Norton 1 | | Norton 2 | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | U | B | U | B | U | B | U | B | U | |
| Absidia glauca | 8.74 | 11.06 | 2.14 | 2.40 | 4.26 | 6.73 | | | | | 35.81 |
| Penicillium simplicissium | 5.66 | 6.39 | 5.15 | 2.80 | 2.48 | 4.07 | 1.81 | 2.06 | 2.13 | 2.14 | 34.69 |
| Arthrobotrys oligospora | 2.02 | 3.04 | 3.13 | 3.33 | 4.27 | 3.60 | 3.65 | 3.80 | 4.13 | 4.68 | 33.59 |
| Syncephalis furcata | 9.20 | 8.36 | 3.40 | 5.66 | 2.73 | 3.20 | | | | | 33.23 |
| Aspergillus flavipes | 6.67 | 3.91 | 3.08 | 2.00 | 1.54 | 2.28 | 3.86 | 1.68 | 1.87 | 1.56 | 31.68 |
| Papulaspora immersa | 2.35 | 3.46 | | | 4.06 | 2.14 | 3.81 | 3.54 | 3.20 | 3.94 | 28.46 |
| Epicoccum purpurascens | | 3.27 | 5.20 | 4.55 | 4.08 | 4.15 | 2.01 | 2.22 | | | 27.82 |
| Sordaria fimicola | 1.81 | | 7.94 | 4.68 | 1.08 | 1.23 | 2.00 | 0.87 | 2.27 | 2.66 | 25.95 |
| Chaetomium seminudum | 7.16 | 5.47 | 3.45 | 4.79 | 4.60 | | | | | | 25.74 |
| Fusarium solani | 4.27 | 3.08 | 1.88 | | 1.41 | 1.81 | | 2.14 | 4.21 | 2.27 | 22.82 |
| Coemansia pectinata | 2.53 | 2.14 | 7.53 | 4.60 | 2.35 | | | | 1.82 | | 22.13 |
| Rhizopus stolonifer | 2.14 | | 1.54 | 2.13 | 2.14 | 3.35 | 2.00 | 3.79 | 1.74 | 1.41 | 21.66 |
| Acremonium sp. | 2.74 | 11.06 | 1.55 | 2.42 | 2.94 | 2.20 | 1.46 | 0.68 | 1.14 | 1.80 | 20.84 |
| Curvularia inaequalis | 5.46 | 5.93 | 2.20 | | 1.94 | 1.94 | | | | | 20.04 |
| Spinalia tenuis | | 2.65 | | 1.61 | 3.49 | 5.72 | 1.67 | | | 2.40 | 18.96 |
| Scopinella sp. | 5.35 | | | | | | 3.35 | 1.93 | 3.32 | 2.74 | 18.77 |
| Sphaerodes retispora | | | 2.48 | 1.87 | | | 1.53 | 2.93 | 4.07 | 2.80 | 18.11 |
| Gliomastix murorum | 3.07 | 3.53 | 3.74 | 2.48 | 2.14 | 2.35 | | | | | 17.78 |
| Pyrenochaeta sp. | 2.02 | 3.81 | 1.08 | | | 2.08 | | 1.15 | 2.14 | 2.42 | 16.48 |
| Pithomyces chartarum | | 1.60 | 1.88 | 4.06 | 2.27 | 2.16 | | 2.13 | | | 15.99 |
| Chrysosporium sp. | | | 1.68 | 1.41 | 1.81 | | 2.02 | 0.94 | 2.73 | 2.67 | 15.68 |
| Melanospora zamiae | 4.34 | 3.06 | 2.20 | 3.47 | 1.02 | | | | | | 14.98 |

Table 3. Percent frequency rankings of the principal fungal species from tallgrass prairie soils, Story County, Iowa

| Species | Plover | | Doolittle | | Ames | | Norton 1 | | Norton 2 | | Average | | Average |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | U | B | U | B | U | B | U | B | U | B | U | |
| Trichoderma hamatum | 95 | 100 | 100 | 100 | 95 | 100 | 100 | 100 | 100 | 100 | 98 | 100 | 99.0 |
| Gliocladium roseum | 100 | 100 | 95 | 90 | 100 | 100 | 100 | 100 | 100 | 100 | 99 | 98 | 98.5 |
| Mucor hiemalis | 95 | 95 | 85 | 100 | 100 | 100 | 100 | 93 | 100 | 100 | 96 | 98 | 97.0 |
| Ramichloridium schulzeri | 100 | 100 | 85 | 75 | 100 | 100 | 100 | 93 | 100 | 100 | 97 | 94 | 95.5 |
| Alternaria alternata | 80 | 95 | 95 | 95 | 100 | 100 | 100 | 100 | 87 | 100 | 92 | 98 | 95.0 |
| Staphlotrichum coccosporum | 100 | 100 | 85 | 70 | 100 | 95 | 100 | 100 | 100 | 100 | 97 | 93 | 95.0 |
| Chaetomium globosum | 95 | 95 | 85 | 85 | 85 | 95 | 100 | 100 | 99 | 87 | 93 | 92 | 92.5 |
| Gliocladium viride | 75 | 70 | 95 | 65 | 75 | 90 | 100 | 100 | 100 | 100 | 89 | 85 | 87.0 |
| Cladosporium cladosporoides | 70 | 90 | 85 | 85 | 100 | 80 | 93 | 93 | 67 | 87 | 83 | 87 | 85.0 |
| Marinnaea elegans | 65 | 35 | 90 | 60 | 70 | 95 | 100 | 93 | 100 | 100 | 85 | 77 | 82.0 |
| Fusarium oxysporum | 90 | 95 | 95 | 95 | 95 | 70 | 93 | 80 | 53 | 53 | 85 | 78 | 81.5 |
| Phoma sp. | 40 | 75 | 55 | 95 | 55 | 95 | 100 | 100 | 100 | 100 | 70 | 93 | 81.5 |
| Mortierella sp. | 100 | 100 | 45 | 65 | 70 | 75 | 60 | 40 | 100 | 93 | 75 | 75 | 75.0 |
| Penicillium janthinellum | 35 | 45 | 80 | 95 | 90 | 85 | 80 | 67 | 87 | 87 | 74 | 76 | 75.0 |
| Arthrobotrys oligospora | 65 | 55 | 85 | 65 | 30 | 75 | 93 | 87 | 93 | 100 | 73 | 76 | 74.5 |
| Papulaspora immersa | 70 | 75 | 70 | 70 | 40 | 60 | 73 | 80 | 87 | 100 | 68 | 77 | 72.5 |
| Paecilomyces marquandii | 95 | 100 | 70 | 75 | 100 | 100 | 47 | 40 | 33 | 47 | 69 | 72 | 70.5 |
| Rhizopus stolonifer | 60 | 70 | 65 | 70 | 55 | 85 | 80 | 80 | 73 | 67 | 67 | 74 | 70.5 |
| Myrothecium verrucaria | 40 | 80 | 65 | 45 | 85 | 55 | 73 | 80 | 87 | 93 | 70 | 71 | 70.5 |
| Acremonium sp. | 70 | 100 | 70 | 65 | 60 | 80 | 60 | 47 | 60 | 73 | 64 | 73 | 68.5 |
| Sordaria fimicola | 70 | 55 | 40 | 65 | 100 | 95 | 67 | 40 | 87 | 60 | 73 | 63 | 68.0 |
| Aspergillus flavipes | 95 | 95 | 45 | 45 | 65 | 55 | 73 | 67 | 47 | 80 | 65 | 68 | 66.5 |
| Epiccoccum purpurascens | 35 | 80 | 75 | 80 | 85 | 95 | 73 | 73 | 27 | 33 | 59 | 72 | 65,5 |
| Cunninghamella elegans | 100 | 40 | 30 | 20 | 90 | 100 | 47 | 53 | 73 | 93 | 68 | 61 | 64.5 |
| Penicillium simplicissimum | 75 | 90 | 50 | 60 | 80 | 45 | 47 | 47 | 63 | 63 | 63 | 61 | 62.0 |
| Chrysporium sp. | 40 | 35 | 50 | 25 | 60 | 55 | 80 | 47 | 80 | 93 | 62 | 51 | 56.5 |

Table 3. (Continued)

| Species | Plover | | Doolittle | | Ames | | Norton 1 | | Norton 2 | | Average | | Average |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | U | B | U | B | U | B | U | B | U | B | U | |
| Sphaerodes retispora | 30 | 25 | 35 | 20 | 55 | 55 | 80 | 87 | 100 | 73 | 60 | 52 | 56.0 |
| Fusarium solani | 85 | 75 | 40 | 35 | 45 | 30 | 27 | 60 | 100 | 67 | 59 | 53 | 56.0 |
| Pyrenochaeta sp. | 60 | 65 | 40 | 50 | 50 | 25 | 53 | 60 | 73 | 87 | 55 | 57 | 56.0 |
| Syncephalis furcata | 95 | 100 | 60 | 50 | 75 | 100 | 13 | 7 | 27 | 7 | 54 | 53 | 53.5 |
| Absidia glauca | 90 | 100 | 70 | 80 | 65 | 55 | 0 | 14 | 7 | 27 | 46 | 55 | 50.5 |
| Gliomastix murorum | 85 | 85 | 70 | 70 | 95 | 70 | 0 | 0 | 27 | 7 | 55 | 46 | 50.5 |
| Gonytrichum macrocladium | 55 | 25 | 60 | 20 | 20 | 65 | 60 | 53 | 87 | 53 | 56 | 43 | 49.5 |
| Spadicoides obovata | 60 | 45 | 30 | 30 | 70 | 50 | 60 | 20 | 67 | 60 | 57 | 41 | 49.0 |
| Nigrospora sphaerica | 45 | 45 | 5 | 20 | 75 | 90 | 47 | 47 | 60 | 60 | 46 | 52 | 49.0 |
| Spinalia tenuis | 30 | 50 | 75 | 75 | 15 | 40 | 80 | 7 | 27 | 60 | 45 | 45 | 45.5 |
| Pithomyces chartarum | 25 | 35 | 35 | 65 | 35 | 100 | 20 | 60 | 20 | 27 | 27 | 57 | 42.0 |
| Zygorhynchus moelleri | 100 | 45 | 35 | 10 | 70 | 90 | 0 | 13 | 47 | 7 | 50 | 33 | 41.5 |
| Coemansia pectinata | 45 | 35 | 35 | 20 | 85 | 80 | 13 | 27 | 47 | 0 | 45 | 32 | 38.5 |
| Scopinella sp. | 55 | 45 | 5 | 5 | 10 | 0 | 60 | 27 | 87 | 87 | 43 | 33 | 38.0 |

1972), but a few are parasites of plants, animals, or other fungi. They are generally characterized by rapid growth and high spore producing capacity, making them effective in quickly invading and colonizing new substrates.

Six of the eight principal Zygomycetes, Mucor hiemalis, Absidia glauca, Zygorhynchus moelleri, Mortierella sp., Rhizopus stolonifer, and Cunninghamella elegans, have been reported from grasslands worldwide. Species of Syncephalis, parasitic on other Mucorales, and of Coemansia appear commonly in soil cultures (Benjamin, 1959), but they have never been reported as principal forms in soil studies.

Syncephalis furcata and other species of Syncephalis isolated from prairie soil may be much more common than heretofore recognized. Isolation techniques which allow parasite and host to develop together potentially portray a more realistic picture of interactions in the soil ecosystem.

Although the Coelomycetes are a main component of the parasitic fungal flora on prairie plants, they are poorly represented in prairie soils. Phoma and Pyrenochaeta were the only genera consistently observed on soil plates.

The Ascomycetes, accounting for nearly one quarter of the total species, are represented in the 30 principal forms by Chaetomium globosum, C. seminudum, and Sordaria fimicola. Chaetomium globosum is one of the most common and cosmopolitan of all Ascomycete soil species (Domsch et al., 1980). C. seminudum and Sordaria fimicola have been infrequently reported from soil although both develop rapidly and

sporulate readily on soil plates. All are reported to be excellent cellulose decomposers.

Studies of soil fungi in various parts of the world have established that the Hyphomycetes are the most common components of the soil mycoflora. Dematiaceous and moniliaceous species were almost equally represented among the principal forms in prairie soils. All of the species are treated in depth by Domsch et al. (1980), but a few deserve special comment.

The Trichoderma complex of species has long been recognized as a main component of the soil mycoflora (Rifai, 1969). Trichoderma hamatum had the highest composite frequency and relative density from all prairie sites. Good degradative properties, wide-ranging mycostatic, antifungal, and parasitic activity (Domsch et al., 1980) and very rapid colony development, within three to seven days, make Trichoderma species very successful soil organisms.

Gliocladium roseum, with similar physiological characteristics to T. hamatum, developed at a much slower rate. While abundant on plates after 3-4 weeks, it was rarely evident at seven days. Slow growth rate probably accounts for the absence of G. roseum from most grassland lists. It was one of the most abundant species in all prairie sites in central Iowa.

Previously unreported as principal forms from soil studies, Staphlotrichum coccosporum and Ramichloridium schulzeri were two of the most frequently isolated fungi from all sites and plots at every collection period. Both are reported capable of cellulolytic activity

(Domsch et al., 1980) and would potentially be good decomposer organisms of prairie plant parts. These two taxa may be more common in tallgrass prairie soil in central Iowa than in other parts of the tallgrass prairie range, but isolation techniques probably account for their absence from other soil reports.

Arthrobotrys oligospora, an adhesive net-forming, nematophagous fungus, was included among the principal taxa. Species of Arthrobotrys are rarely reported as dominant fungi in soils although these net-formers are highly competitive in the soil ecosystem. They possess high saprophytic abilities in the early stages of decomposition plus a nematode-trapping ability which allows them an additional source of energy unavailable to other soil fungi (Cooke, 1962).

The remaining 13 Hyphomycetes which are dominant taxa in Iowa tallgrass prairie soils are known to occur in other prairie soils, but only species in the genera Fusarium, Penicillium, Cladosporium, and Alternaria have been recognized as principal forms.

## Ordination Results

One hundred fungal species ranked by composite density data from all plots, burned and unburned, and all sampling periods provided the detrended correspondence analysis (DECORANA) input. The first and second axis ordination scatter diagram of Iowa tallgrass prairie plots is shown in Figure 2. The plots separate into two distinct groups. One group includes the two prairie potholes from Doolittle Prairie and the twelve plots from the restored Norton prairie. The six remaining Doolittle

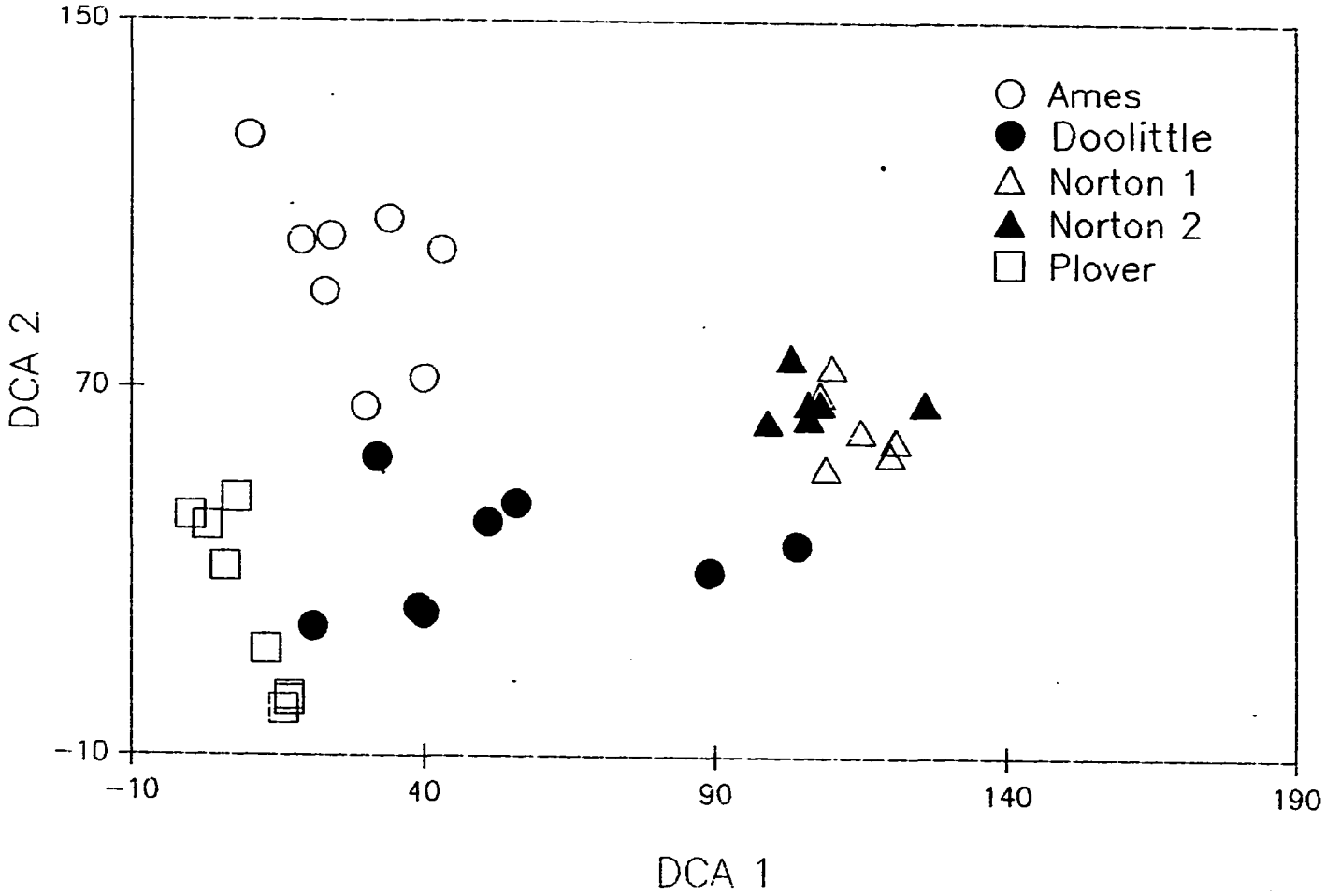


**Figure 2.** Detrended correspondence analysis ordination of tallgrass prairie plots based on the density of the 100 most frequent fungal species, axis 1 v. axis 2

plots cluster with the plots from Ames High Prairie and Plover Tract. Soil factor data, including pH, percent organic matter, phosphorous and potassium levels (Table 1), do not account for the separation of the plots into the two distinct groups. Disturbance seems to be the major factor giving rise to the patterns evident in the scatter diagram.

The complex structure of the total prairie community developed over thousands of years was destroyed by the original breaking of the prairie sod on the Norton site. Subsequent years of tilling and agricultural cropping changed the soil environment and consequently the community of organisms which exist in the soil.

The pothole plots have never been plowed, but these glacial depressions have been subjected to continuing disturbance by fluctuating water levels since glacial retreat. In years of average rainfall, the potholes have ephemeral high water levels followed by a summer drydown period. During years of high rainfall, the depressions retain standing water throughout the growing season, whereas during drought periods, the soils remain dry.

The cluster of prairie plots from Ames, Doolittle, and Plover, although disrupted by grazing and/or mowing, have never been disturbed by plowing. A gradient among these plots is evident along DCA axis 2. Topography and its corresponding effect on soil moisture is the major factor which gives rise to the gradient. Ames High Prairie, situated on a glacial ridge, has moderately sloping topographical features. Mesic to mesic-dry prairie plant species dominate the well-drained slopes. Doolittle and Plover Prairies, located on flattened glacial terrain, are

poorly drained and support mesic to mesic-wet prairie plant species. Soil moisture conditions affect the fungal community, both directly and indirectly. Moisture directly affects germination and growth of individual fungal species. Moisture plays a large part in the development of the vascular plant community and thus indirectly the composition of the fungal community.

The first and third axis ordination separates the Doolittle prairie potholes from the Norton plots (Figure 3). These glacial depressions are distinctly different from all other plots in the scatter diagram both in soil type and in vascular plant cover. The pothole vegetation is dominated by sedges, whereas the remaining virgin and restored pots are dominated by various grass species.

Soil type is the other major factor which separates the plots. The prairie pothole depressions sampled on Doolittle Prairie are distinctly different from all other plots. The Okoboji soils of these plots are very poorly drained and subject to pooling. Kossuth silty clay loams which are poorly drained and found on level terrain characterize the remaining plots on Doolittle and those of the Plover Prairie. The Norton restored site has Lester soils which are well-drained with gently to moderately sloping topography. Ames High Prairie is primarily Storden loam characterized by moderately steep well-drained slopes which have rapid surface runoff.

From the 100 total species used in the ordination, forty of the most common fungal taxa from all sites (Table 4) were selected for the species scatter diagrams. The first and second axis ordination based on density

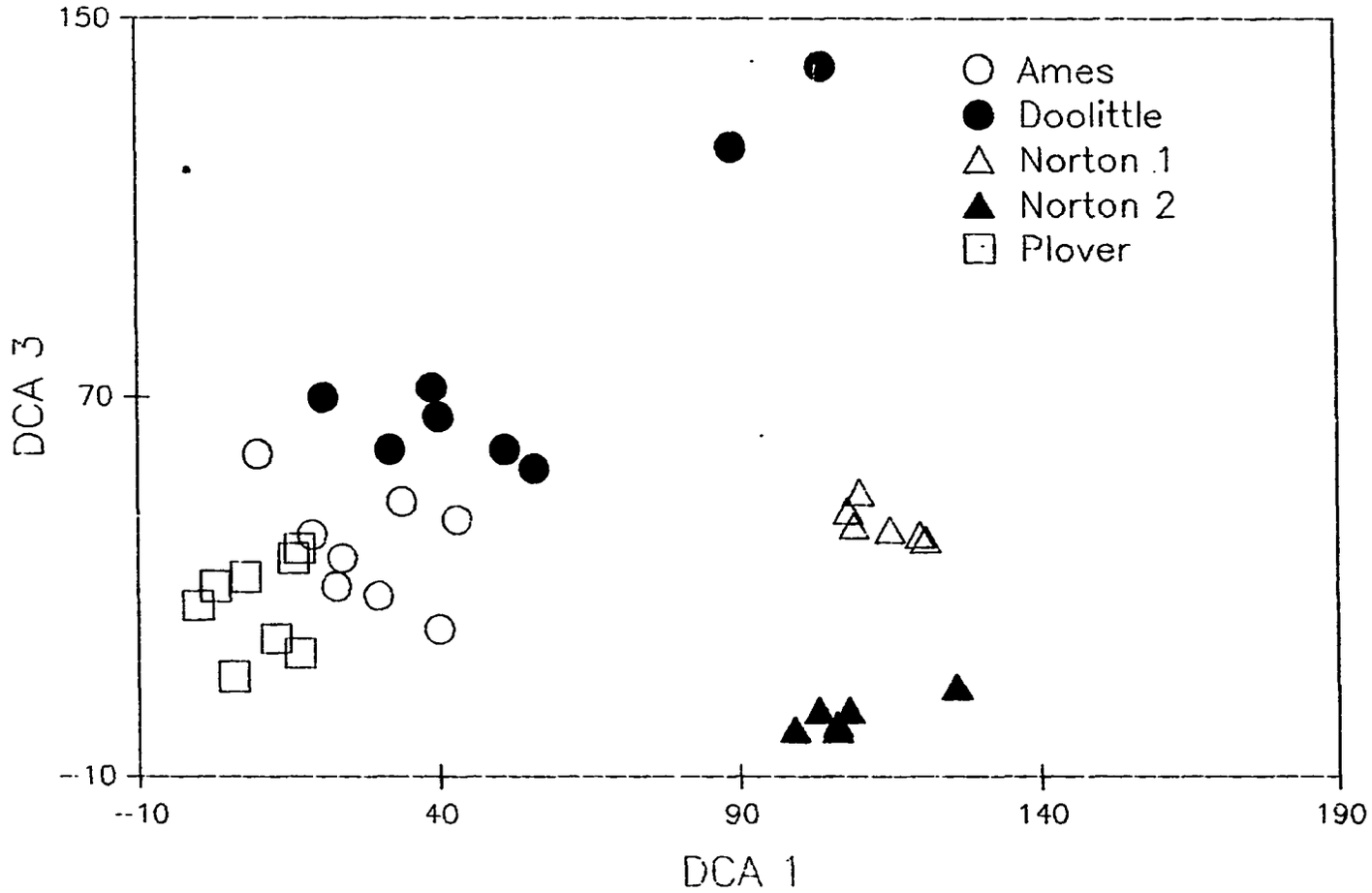


**Figure 3. Detrended correspondence analysis ordination of tallgrass prairie plots based on the density of the 100 most frequent fungal species, axis 1 vs. axis 3**

Table 4. Abbreviations used for fungal species in the DECORANA scatter diagrams presented in Figures 4 and 5

| | |
|---|---|
| Abgl | *Absidia glauca* |
| Alal | *Alternaria alternata* |
| Arol | *Arthrobotrys oligospora* |
| Asfl | *Aspergillus flavipes* |
| Chgl | *Chaetomium globosum* |
| Chse | *Chaetomium seminudum* |
| Clcl | *Cladosporium cladosporoides* |
| Cope | *Coemansia pectinata* |
| Crsp | *Chrysosporium* sp. |
| Cuel | *Cunninghamella elegans* |
| Eppu | *Epiccoccum purpurascens* |
| Fuox | *Fusarium oxysporum* |
| Fuso | *Fusarium solani* |
| Glro | *Gliocladium roseum* |
| Glvi | *Gliocladium viride* |
| Glmu | *Gliomastix murorum* var. *felina* |
| Mael | *Mariannaea elegans* |
| Meza | *Melanospora zamiae* |
| Muhi | *Mucor hiemalis* |
| Myve | *Myrothecium verrucaria* |
| Pama | *Paecilomyces marquandii* |
| Paim | *Papulaspora immersa* |
| Peja | *Penicillium janthinellum* |
| Pesi | *Penicillium simplicissimum* |
| Phsp | *Phoma* sp. |
| Pich | *Pithomyces chartarum* |
| Ppcr | *Piptocephalis cruciata* |
| Pysp | *Pyrenochaeta* sp. |
| Rasc | *Ramichloridium schulzeri* |
| Rhst | *Rhizopus stolonifer* |
| Scsp | *Scopinella* sp. |
| Sofi | *Sordaria fimicola* |
| Spob | *Spadocoides obovata* |
| Spre | *Sphaerodes retispora* |
| Spte | *Spinalia tenuis* |
| Stco | *Staphlotrichum coccosporum* |
| Syfu | *Syncephalis furcata* |
| Thte | *Thielavia terricola* |
| Trha | *Trichoderma hamatum* |
| Zygo | *Zygorhynchus moelleri* |

patterns of fungal species in tallgrass prairie plots is presented in Figure 4. From left to right along DCA axis 1, the fungi may be increasingly tolerant to disturbance. The fungal species on the right side of the scatter diagram are either residual species that were able to survive changes in the soil environment due to disturbance or they were introduced through agricultural practices.

Scant ecological information is available for each of the individual fungal species. Some general characteristics of taxa most frequently isolated from soil are reviewed by Domsch et al. (1980) and Christensen (1981). Of fourteen taxa described as broad amplitude grassland fungi by Christensen (1981), Fusarium oxysporum, F. solani, Gliomastix, Papulaspora, Pyrenochaeta, and Zygorhynchus moelleri are illustrated in the scatter diagrams. Zygorhynchus moelleri and Gliomastix murorum are more common on virgin prairie sites, Pyrenochaeta sp., Fusarium oxysporum, and F. solani are equally common on virgin and restored sites, and Papulaspora immersa is more common on the restored plots.

The first and third axis ordination of fungal species (Figure 5) has a very similar scatter pattern to that of the first and second axis ordination (Figure 4). Well-defined clusters of species are not apparent from the ordination. Superimposing site preference for each individual species shows a trend toward site specificity for a few fungi. Broad amplitude species found on both virgin and disturbed sites are generally unpatterned ecologically. In a review of soil fungi, they have been consistently recorded in 4 or more distinct community types (Christensen, 1981). Scattered among them are species which are known primarily from

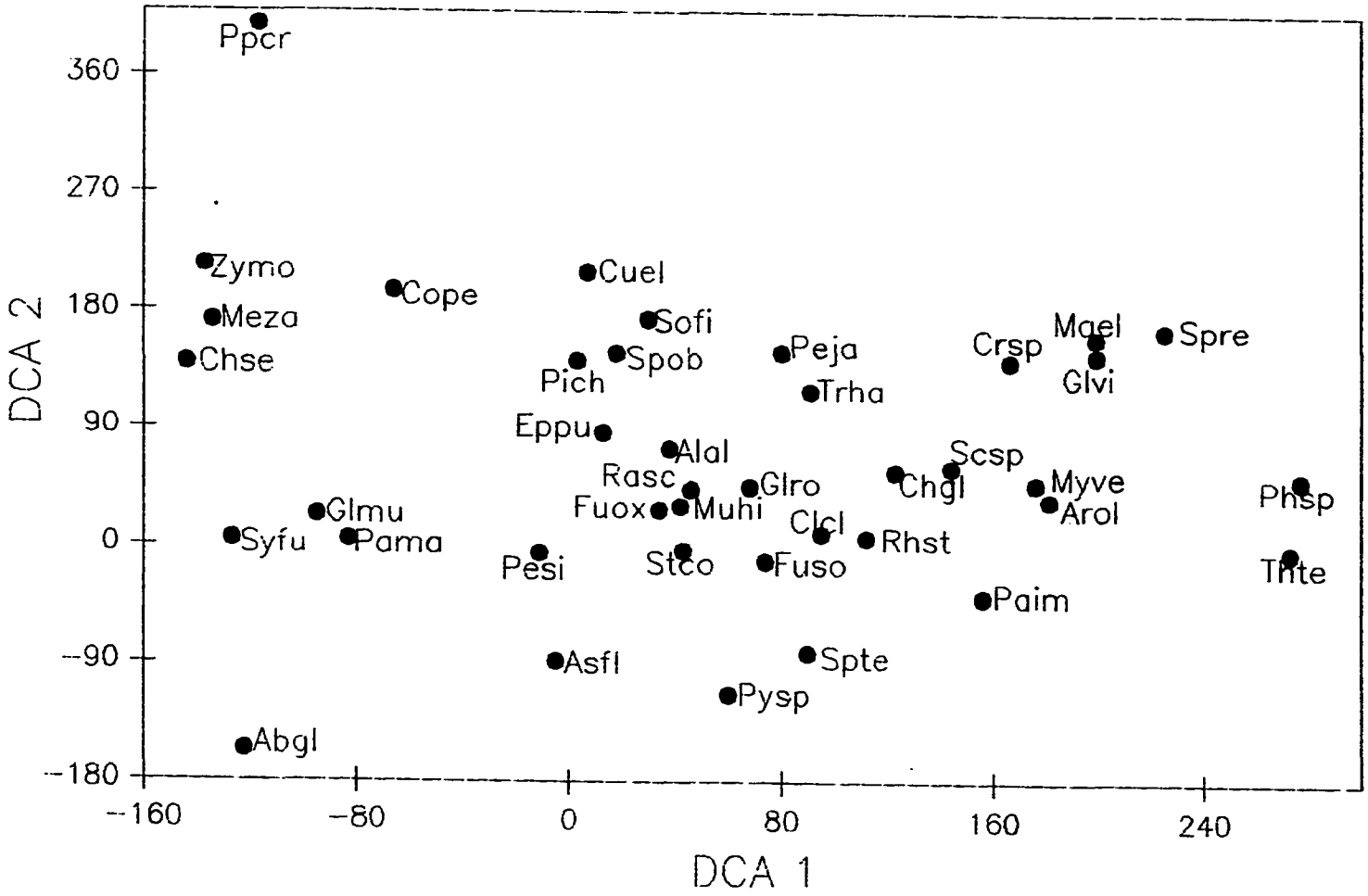


**Figure 4.** Detrended correspondence analysis ordination of thirty-nine principal species from tallgrass prairie sites based on density of the 100 most frequent fungal species, axis 1 v. axis 2

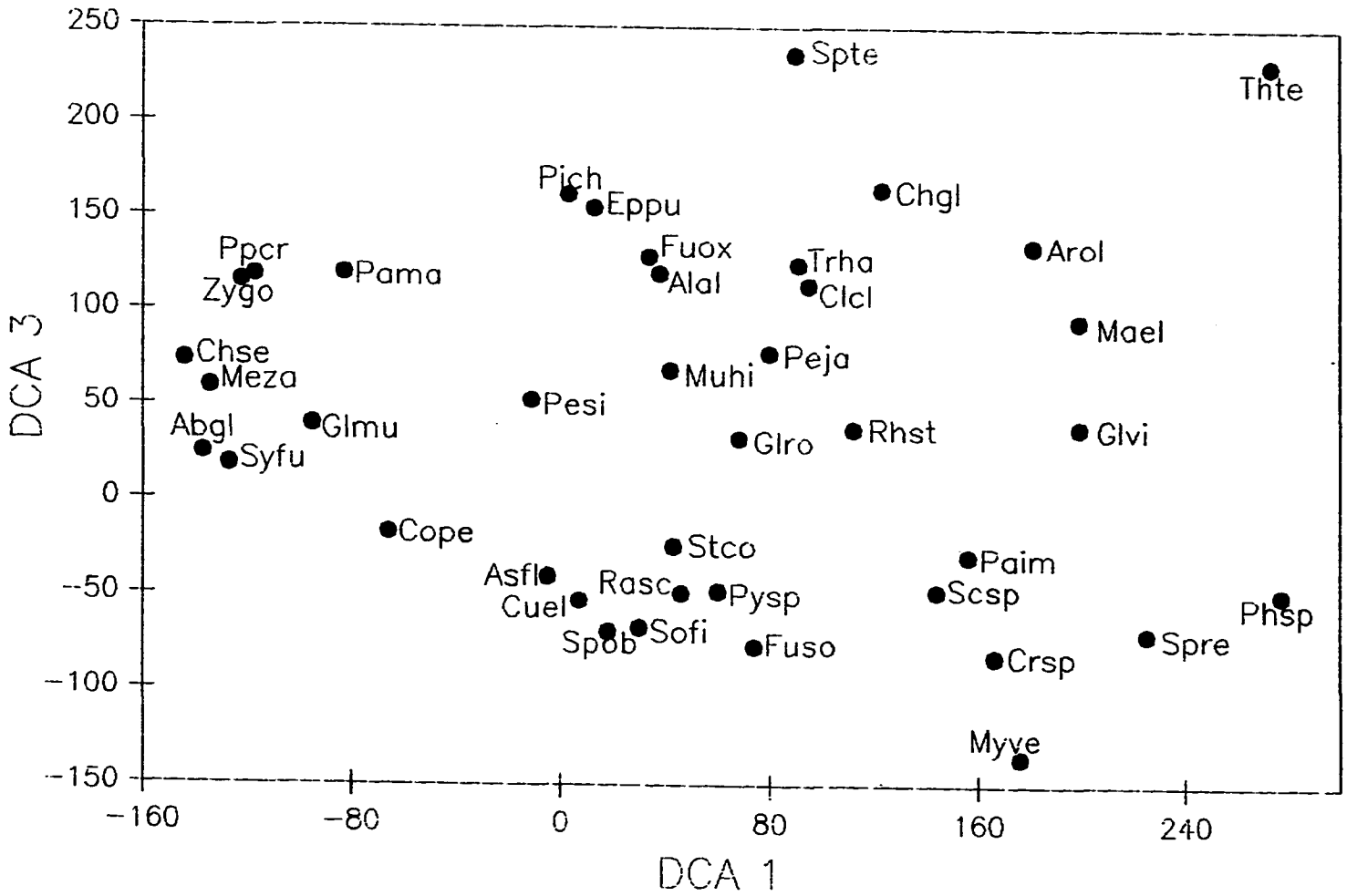


**Figure 5.** Detrended correspondence analysis ordination of thirty-nine principal species from tallgrass prairie sites based on density of the 100 most frequent fungal species, axis 1 v. axis 3

agricultural situations.

Species which seem specific for virgin prairie sites have a known restricted distribution for grassland and/or forest sites (Domsch et al., 1980; Christensen, 1981) or they are mycoparasites for which site preference information is not available.

When a prairie community is physically and biologically altered by agricultural disturbance, the diversity of microsites available for fungal decomposer organisms is reduced. Competition for the available organic substrates is increased. The success of a fungus to colonize and hold onto these substrates then depends on its competitive saprophytic ability and its inoculum potential (Frankland, 1981). To be successful in colonization of organic substrates according to Frankland, a fungus requires high growth rates, rapid germination, and the production of specific enzymes and antibiotics.

Species on the first and third axis ordination diagram (Figure 5) which produce toxins are indicated by a "T" in Figure 7. The toxin producers are found in both virgin and disturbed sites and tend to cluster together. Most of these toxin-producing fungi are also unpatterned in their habitat preference (Figure 6). Toxin producers may well have an advantage over non-toxin producers in competing for microsites in new environments. This may be particularly important in occupying disturbed sites where the heterogeneity of microsites is significantly reduced and the soil environment is more homogeneous.

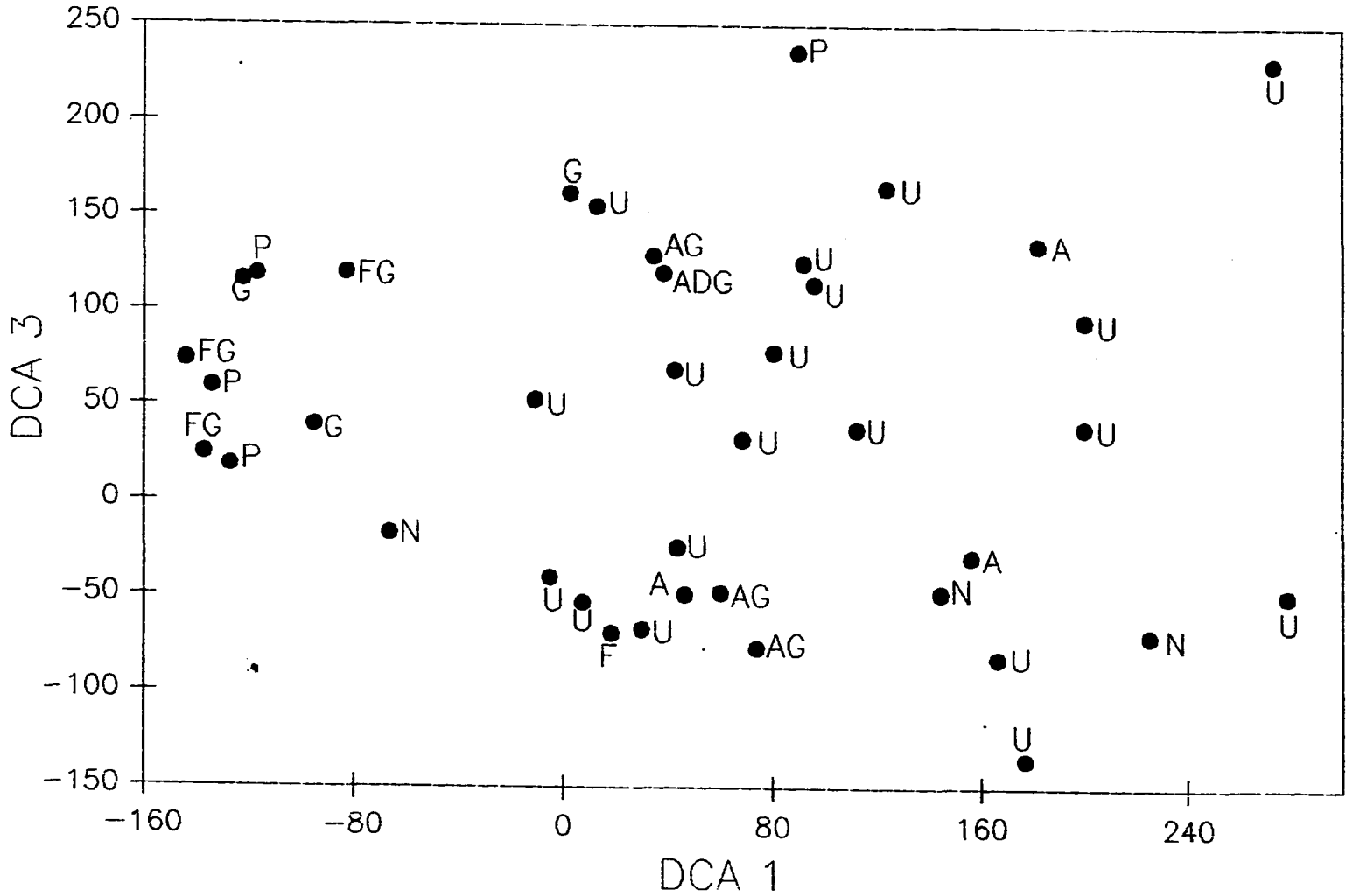


Figure 6. Detrended correspondence analysis of thirty-nine principal species from tallgrass prairie sites (Figure 5) with habitat preference superimposed on species name, axis 1 v. axis 3. A - Cultivated fields; D - Desert; F - Forest; G - Grassland; P - Parasite (habitat depends on host); U - Unpatterned; N - Undetermined

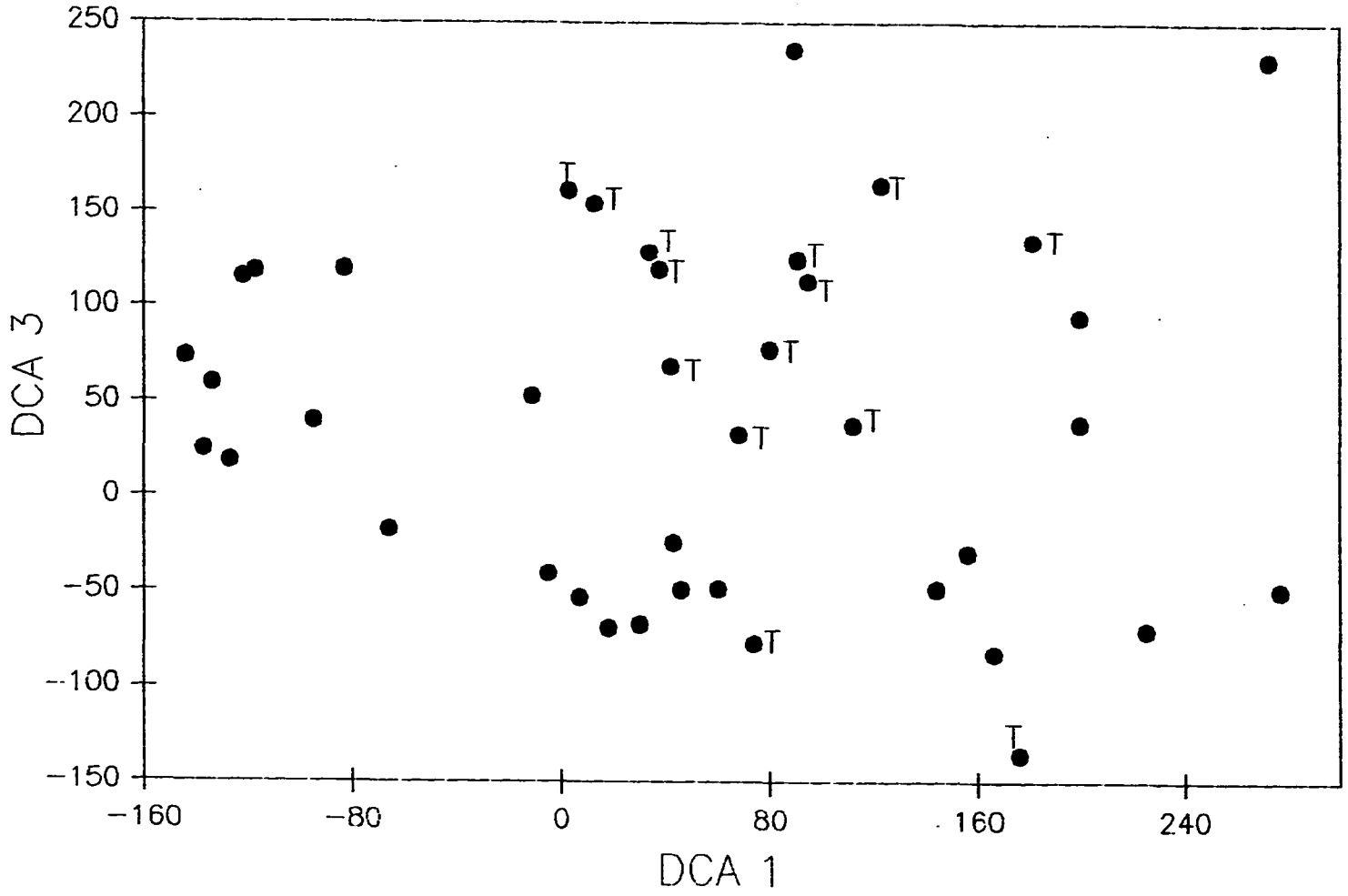


**Figure 7.** Detrended correspondence analysis ordination of thirty-nine principal species from tallgrass prairie sites (Figure 5) with a "T" superimposed on toxin-producing fungal species

## Comparisons of Fungal Populations from Soil Studies within the Tallgrass Prairie Ecosystem

Comparisons between Iowa tallgrass prairie and grassland soil mycofloras of other regions in the world were made by using a simple coefficient of similarity index (Table 5). A composite list of the thirty principal fungal species of Iowa prairie soil was compared with the principal species in other habitats and areas.

Table 5. Comparison of grassland soil microfungi from Iowa, Africa, New Zealand, and Britain using the C = 2w/(a + b) coefficient of similarity

| | Iowa | Africa | New Zealand | | Britain |
|---|---|---|---|---|---|
| | | | 1958 | 1973 | |
| Iowa | — | 20.7 | 33.3 | 25.4 | 21.0 |
| Africa[a] | | — | 17.4 | 15.0 | 18.1 |
| New Zealand | | | | | |
| 1958[b] | | | — | 32.7 | 27.6 |
| 1973[c] | | | | — | 36.4 |
| Britain[d] | | | | | — |

[a]Arid savanna in Africa (Papendorf, 1976).
[b]Tussock grassland (Thornton, 1958).
[c]Irrigated pasture (Ruscoe, 1973) in New Zealand.
[d]Coastal dunes in England (Brown, 1958).

The mycoflora of tallgrass prairie soils are unlike those from grassland soils from other continents (C < 35). Fungi from Iowa prairie soils are more similar to tussock grassland (C = 33.3) than coastal dunes, savanna, or irrigated pasture (C = 20.7-25.4). Tussock grassland has a large proportion of root biomass and the main organic matter

addition comes from root origin (Thornton, 1958), suggesting that soil development is similar to that of prairie ecosystems. Latitude, geologic history, and vascular plant cover all influence development of the mycofloral communities of these two soils and presumably account in large part for their differences.

In an attempt to discover if tallgrass prairie soils have a characteristic mycoflora, the principal species from the combined study sites in Iowa were compared with the principal species from a restored prairie (Wicklow, 1973) and a series of mesic tallgrass prairies (Orpurt and Curtis, 1957) in Wisconsin, grasslands in Ohio (Huang and Schmitt, 1975), a virgin prairie in Missouri (Herman and Kucera, 1979) and a tallgrass prairie (Pamperin, 1981), a cropfield (Pamperin, 1981), and an agricultural field (Wacha and Tiffany, 1979) in Iowa.

Presence/absence information of the principal fungal species from each of the studies was used as input for DECORANA ordination. Specific patterns between study areas are not apparent from the first and second axis scatter diagram (Figure 8). When isolation technique used in the soil fungal analysis is superimposed on the ordination diagram, a relationship becomes more apparent (Figure 9). Fungi from studies 2, 3, 4, 5, and 8 were isolated by dilution plating. The soil isolation techniques used in studies 1, 6 and 7 varied from each other and from dilution plating. Modified plating and extended incubation was used for study 1, soil plating alone was used for study 7, and a series of techniques including dilution plating, hair baiting, heat and alcohol treatment were used for study 6.

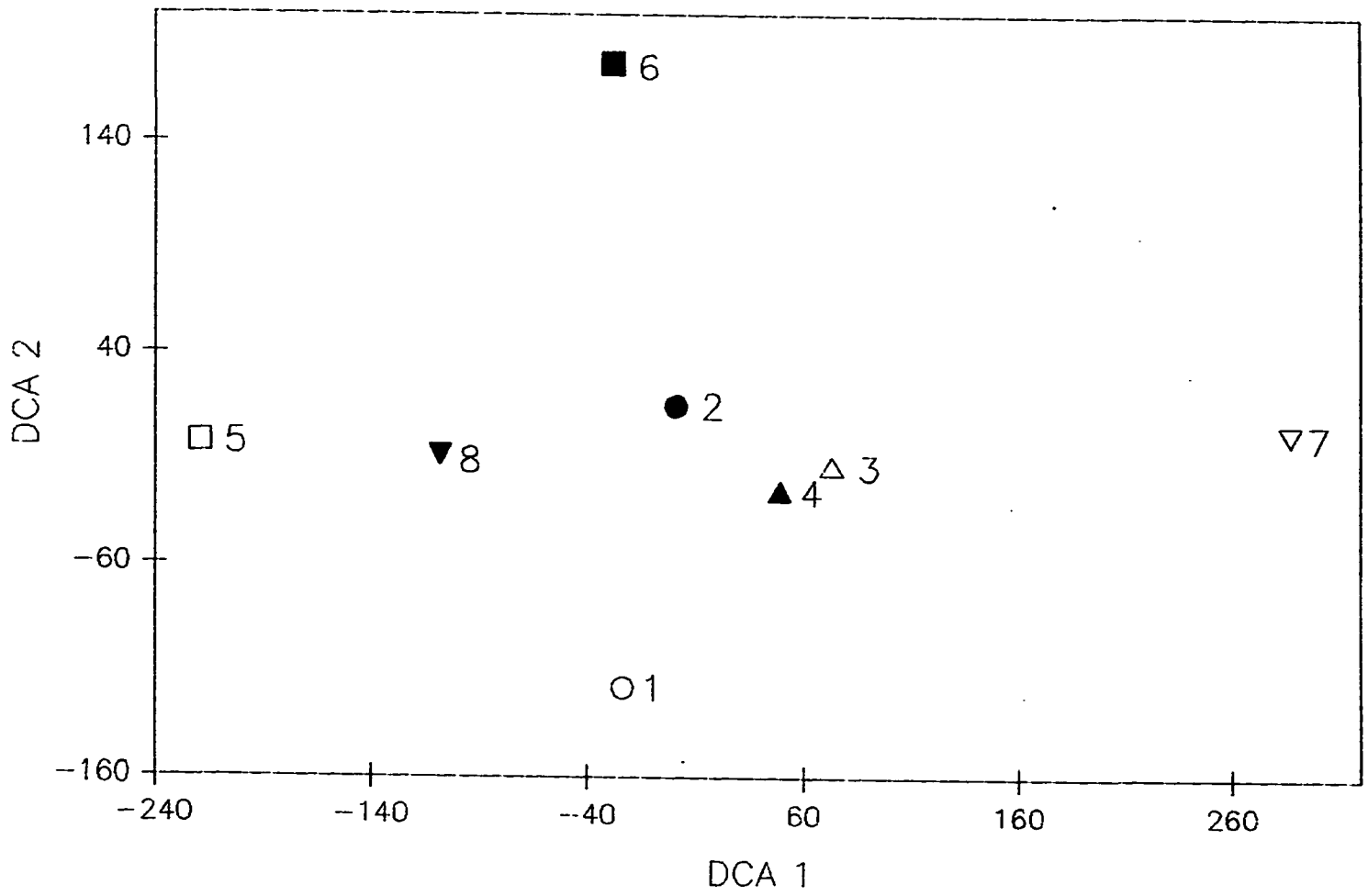


**Figure 8.** Detrended correspondence analysis ordination of sites utilized for fungal soil survey studies in central United States based on presence/absence data of the principal fungal species, axis 1 v. axis 2

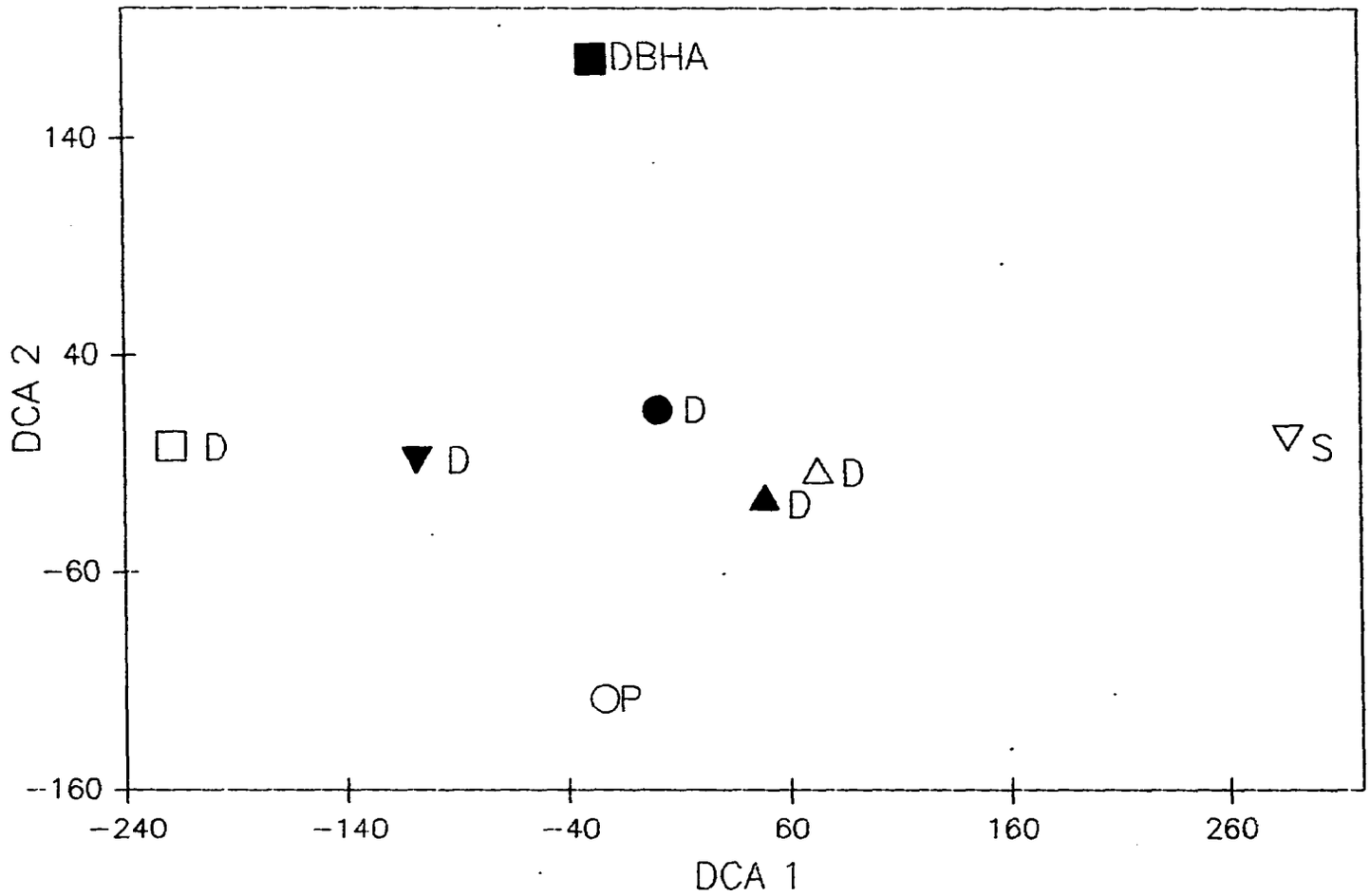


Figure 9. Detrended correspondence analysis ordination of sites utilized for fungal soil survey studies (Figure 8) with isolation technique(s) superimposed on study site number. A - Alcohol treatment; B - Hair baiting; D - Dilution plating; H - Heat treatment; P - Modified soil plate; S - Soil plating

The first and third axis ordination (Figure 10) shows some separation of the fungal communities into two groups based on historical and/or current land use. The study sites in the lower right corner area all have a history of soil disruption by plowing. The fungal species complexes from studies 3 and 7 were isolated from soils which were cropped at the time of the study. Site 2 study area was a restored prairie which had previously been cropped.

The study sites in the upper left corner of Figure 10 were virgin prairie or grassland complexes which included virgin prairies. Most closely related to the principal fungi of the Iowa tallgrass study (1) are the fungal communities of grasslands in Ohio (6) and mesic prairies of Wisconsin (8). The fungi of study 4 isolated from Doolittle Prairie, a site included in study 1, does not closely pattern with fungal populations from studies 1, 6 and 8. Doolittle Prairie is a wet-mesic prairie and the fungi from that one site would be expected to be different from the principal species derived from soils of a series of grassland sites as in studies 1, 6, and 8.

Study site 5 was a virgin prairie site in central Missouri. Herman and Kucera (1979) reported major differences between the principal fungal species of Missouri prairie and those of the wet-mesic Wisconsin prairies (Orpurt and Curtis, 1957). They reported these dissimilarities were more a factor of using Curtis's higher plant indicator series criteria for classifying Tucker Prairie in Missouri as a wet-mesic prairie. If the fungi from the total prairie continuum of Wisconsin were used for analysis, the two studies had many more species in common.

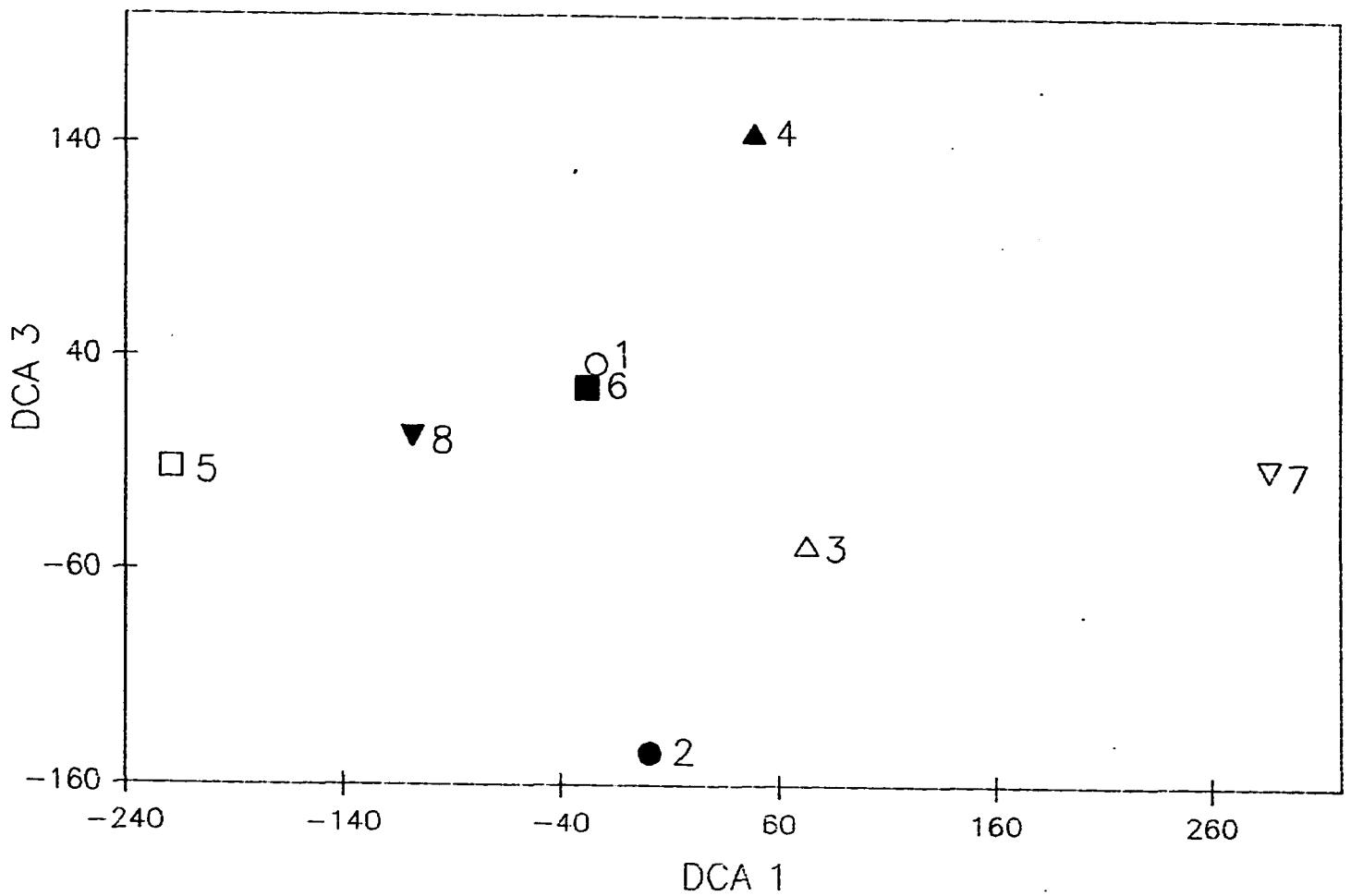


Figure 10. Detrended correspondence analysis ordination of sites utilized for fungal soil survey studies in central United States based on presence/absence data of the principal fungal species, axis 1 v. axis 3

A gradient between the virgin grassland sites is evident. The dominant grass species on Tucker Prairie in Missouri (Herman and Kucera, 1979) suggest a mesic to mesic-dry prairie site (5). The prairie sites from Wisconsin (8) were classified as mesic prairies. The grasslands of Ohio, although not characterized by Huang and Schmitt (1975), are assumed to be mesic because of the high rainfall patterns in the eastern United States. The complex of grasslands from central Iowa (1) ranged from mesic-dry to mesic-wet and Doolittle Prairie (4) is a wet-mesic prairie site.

## Comparisons of Fungus Populations of Agriculturally Modified Soils with Fungal Populations of Virgin Prairie Soils in Central Iowa

Relative density data were tabulated for each fungal species isolated from soil on each of the prairie sites in central Iowa. Fungal species were subdivided into four groups based on the abundance values. Ubiquitous species occur on all prairie types in high densities. Species classified as common occur on all prairie sites but in lower numbers. Other species are either site specific or occur preferentially in virgin rather than agriculturally disturbed soil.

Eight species were ubiquitous with relative densities greater than 20.0 on all sites (Table 6). Staphlotrichum coccosporum and Ramichloridium schulzeri were included by Domsch et al. (1980) in the Compendium of Soil Fungi, but they have not previously been reported as principal forms from grassland soils. Species of Mucor, Alternaria,

Table 6. Fungal species with relative density greater than 20.0 from tallgrass prairie sites, Story County, Iowa

| | Plover | Doolittle | Ames | Norton |
|---|---|---|---|---|
| Staphlotrichum coccosporum | 81.9 | 55.6 | 54.3 | 70.0 |
| Trichoderma hamatum | 54.5 | 79.5 | 88.9 | 89.6 |
| Mucor hiemalis | 59.8 | 38.2 | 44.6 | 49.4 |
| Alternaria alternata | 29.5 | 51.1 | 58.9 | 34.2 |
| Gliocladium roseum | 73.1 | 50.5 | 60.0 | 80.5 |
| Gliocladium viride | 24.5 | 20.5 | 46.7 | 87.8 |
| Ramichloridium schulzeri | 59.4 | 27.5 | 41.0 | 52.1 |
| Fusarium oxysporum | 23.4 | 29.5 | 24.6 | 23.9 |
| Cladosporium cladosporoides | 21.1 | 25.9 | 25.6 | 31.0 |

Gliocladium, Trichoderma, and Cladosporium have long been recognized as grassland fungi (Clark and Paul, 1970). Alternaria and Cladosporium are often present as primary invaders on senescing plant parts even before they become part of the litter layer (Webster, 1956; 1957). Below-ground litter invaders of root surfaces are Trichoderma, Gliocladium and Cladosporium (Waid, 1957). All of the ubiquitous species except Staphlotrichum coccosporum survive continued disturbance and are frequently recovered from agricultural soils (Domsch et al., 1980).

Sixteen species are common soil inhabitants on two or more of the prairie sites (Table 7). Only Sphaerodes retispora and Arthrobotrys oligospora have not been included in previously published studies of tallgrass prairie soil fungi. Penicillium simplicissimum and Penicillium janthinellum are members of a series of penicillia which occur abundantly in soil and on vegetation in the later stages of decay (Raper et al., 1949). Through analysis of the numbers and distributions of the

Table 7. Fungal species which commonly occur on 2 or more tallgrass prairie sites with relative density less than 20.0 on one or more of the sites

| | Plover | Doolittle | Ames | Norton |
|---|---|---|---|---|
| Penicillium simplicissimum | 32.4 | 15.0 | 18.1 | 14.0 |
| Mortierella sp. | 31.8 | 16.7 | 15.7 | 21.0 |
| Fusarium solani | 17.9 | 7.6 | 6.4 | 15.6 |
| Acremonium sp. | 16.6 | 12.9 | 10.4 | 7.8 |
| Pyrenochaeta sp. | 15.8 | 7.2 | 3.9 | 10.6 |
| Fusarium equiseti | 9.4 | 2.3 | 3.8 | 4.8 |
| Chaetomium globosum | 17.6 | 28.7 | 22.1 | 28.4 |
| Rhizopus stolonifer | 8.5 | 15.4 | 9.7 | 13.3 |
| Penicillium janthinellum | 10.6 | 29.6 | 41.2 | 25.9 |
| Epicoccum purpurascens | 11.3 | 21.6 | 24.7 | 9.5 |
| Myrothecium verrucaria | 13.5 | 9.7 | 23.0 | 37.3 |
| Arthrobotrys oligospora | 13.8 | 20.1 | 11.2 | 27.2 |
| Papulaspora immersa | 14.1 | 16.3 | 6.8 | 25.4 |
| Sphaerodes retispora | 2.0 | 3.5 | 10.3 | 19.5 |
| Chrysosporium sp. | 4.7 | 5.2 | 8.2 | 14.0 |
| Gonytrichum macrocladium | 5.5 | 6.0 | 7.5 | 8.2 |

janthinellum series, Raper et al. (1949) suggested that they must play an active role in decomposition.

Although F. equiseti and F. solani as well as F. oxysporum have been reported as plant pathogens, they are good cellulolytic decomposers and their role in grasslands is primarily as saprophytes (Gordon, 1956; Burgess, 1981). Highest densities for Fusarium solani and Fusarium equiseti were from undisturbed Plover Prairie soils and replanted Norton prairie soil.

Recovery rates of F. solani and F. equiseti were higher in the undisturbed tallgrass soils in Iowa than those in North Dakota (McMullen and Stack, 1983). F. equiseti was recovered at very high levels from

cultivated fields in North Dakota, leading McMullen and Stack (1983) to suggest that disturbance and monoculture favored its development. The relative density of F. equiseti on the disturbed Norton site was relatively low. Reestablishment of this site to prairie grasses may have offset the effect of cultivation and resulted in a decrease in the numbers of this particular species. There is evidence, however, that the distribution of F. equiseti in Iowa soils may differ from North Dakota because Wacha and Tiffany (1979) found more isolates of F. equiseti in no-tillage soils than plowed soils in Iowa.

Six of the species with common occurrence had their highest density on the restored Norton site. The history of cultivation on the site may have favored some fungal species. Gochenaur (1981) reported that opportunistic decomposers show increased productivity with cultivation and monocropping. Six additional species on the Norton plots ranked second in density values. Secondary succession on the Norton site has produced changes in the soil from root biomass accumulation and decomposition and in the terrestrial environment from the vascular plant community development. The residual effects of cultivation combined with the reestablishment of grassland may result temporarily in increased numbers of fungal species on the site. Over time, changes in the vascular plant community will regulate the decomposer community (Frankland, 1981).

The principal fungi and their relative densities will be expected to change with time. The Norton site may never develop a fungal community structure closely resembling that of predisturbance because the vascular

plant community may never develop the species richness or diversity of presettlement tallgrass prairie.

Nine species with high composite densities are found consistently in higher numbers on the virgin prairie sites than on restored prairie (Table 8). Paecilomyces marquandii and Absidia glauca have been reported with equal frequencies from grassland and forest ecosystems. Zygorhynchus moelleri and species of Gliomastix and Humicola are considered grassland specific species by Christensen (1981).

Table 8. Relative densities of fungal species frequent on virgin prairie but uncommon or absent on restored prairie, Story County, Iowa

| | Plover | Doolittle | Ames | Norton |
|---|---|---|---|---|
| Paecilomyces marquandii | 54.3 | 41.8 | 41.5 | 6.1 |
| Absidia glauca | 49.8 | 31.0 | 12.4 | 1.2 |
| Syncephalis furcata | 44.2 | 14.8 | 22.5 | 1.2 |
| Melanospora zamiae | 19.1 | 3.8 | 14.5 | 1.0 |
| Gliomastix murorum | 16.0 | 10.4 | 14.9 | 1.0 |
| Humicola grisea | 12.6 | 2.5 | 6.5 | 0.5 |
| Penicillium raistrickii | 10.8 | 6.1 | 4.0 | 0.0 |
| Zygorhynchus moelleri | 35.9 | 10.2 | 45.5 | 1.6 |
| Gongronella butleri | 9.3 | 4.8 | 10.8 | 2.3 |

Syncephalis furcata is a parasite on species of Mucor and Mortierella. Few reports have addressed the role of mycoparasites in natural systems. Richardson and Leadbeater (1972) suggested that habitat had a greater influence than the current presence of the host on the parasites. Their research showed that species of Syncephalis and Piptocephalis were most closely associated with closed grasslands even

though host species Mucor and Mortierella were present throughout the entire study area. The incidence of mycoparasites preferentially on virgin sites in Iowa support site selectivity as one factor. Mycoparasites would be expected to have a lower tolerance than nonspecialized saprophytic fungi to disturbance. Eradication or reduction of host numbers by disturbance would eliminate or reduce survival changes of a mycoparasite. Microbe-microbe interactions may occur in later successional stages as has been suggested for plant-animal, plant-plant, and plant-microbe interactions (Barbour et al., 1980).

Several species among the frequently isolated taxa are site specific (Table 9). One of the determining factors for this distribution

Table 9. Relative densities of fungal species which are specific to a particular prairie site, Story County, Iowa

| | Plover | Doolittle | Ames | Norton |
|---|---|---|---|---|
| Aspergillus flavipes | 35.5 | 10.3 | 13.7 | 15.5 |
| Arthrinium phaeosporum | 16.1 | 1.5 | 1.1 | 1.3 |
| Fusarium poae | 13.8 | 6.2 | 1.3 | 2.1 |
| Penicillium herquei | 10.5 | 0 | 0 | 0 |
| Spinalia tenuis | 8.6 | 22.0 | 4.6 | 7.5 |
| Emericellopsis mirabilis | 0 | 3.8 | 0 | 0 |
| Cunninghamella elegans | 22.7 | 2.7 | 56.3 | 25.1 |
| Sordaria fimicola | 7.8 | 6.3 | 31.9 | 12.2 |
| Coemansia pectinata | 12.7 | 6.9 | 27.9 | 4.0 |
| Piptocephalis cruciata | 1.0 | 1.0 | 25.0 | 0 |
| Spadicoides obovata | 6.6 | 3.5 | 16.3 | 6.8 |
| Gelasinospora calospora | 1.0 | 1.0 | 9.6 | 2.0 |
| Verticimonosporium diffusum | 0 | 0 | 9.3 | 0 |
| Phoma sp. | 8.8 | 10.2 | 8.1 | 45.7 |
| Aspergillus fumigatus | 1.0 | 1.0 | 4.1 | 9.4 |
| Camposporium pellucidum | 1.0 | 0 | 0 | 8.0 |
| Drechslera sativus | 1.5 | 1.4 | 1.0 | 7.9 |
| Chaetomium succineum | 0 | 1.0 | 0 | 4.3 |

may be moisture. Orpurt and Curtis (1957) reported that certain fungal species were more prevalent on particular sites depending on a moisture gradient. Plover and Doolittle Prairies are wet-mesic sites, Ames High is a dry prairie, and Norton prairie is a mesic reconstituted site.

Whereas species compositions between restored and virgin prairies differ, total numbers of species isolated were nearly equal on all sites (Figure 11). The native soil mycofloral species sensitive to soil disturbance were eliminated and replaced by agriculturally adapted species in the restored prairie soil. All sites showed a slight decline in species numbers at the first 2 da postburn collection. Species numbers fluctuated following the burn but equaled preburn collection by fall, 6 months after the spring burn.

## Effect of Fire on Fungus Populations of Tallgrass Prairie Sites in Central Iowa

Fire was a major evolutionary force in the development of grassland communities (Komarek, 1964). Whether from natural causes or human intervention, fire was historically a common phenomenon on tallgrass prairie. Most naturally occurring fires resulted from lightning strikes during summer drought periods.

Today most prairie remnants are managed in part by prescribed burning. In Iowa, burns are usually scheduled in early spring prior to new plant growth. Spring burning was carried out on selected sections of each of the study sites. These controlled, fast-burning surface fires remove the litter layer but cause little heating of the organic layer at

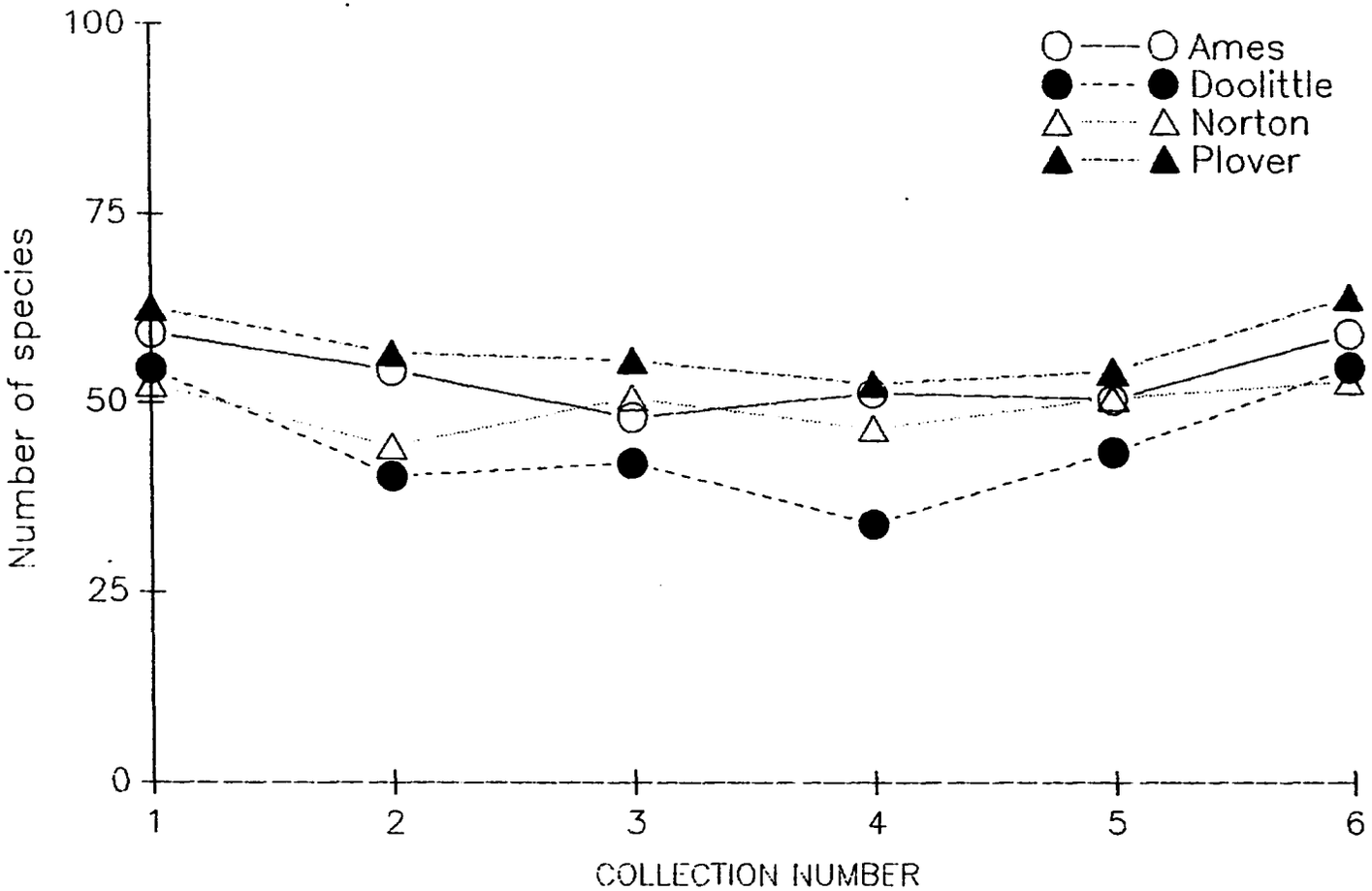


**Figure 11.** Average number of fungal species isolated from prairie sites, Story County, Iowa, at specific sampling times: 1) preburn, 2) 2 da, 3) 14 da, 4) 30 da, 5) 60 da, 6) 180 da

the soil surface. In the weeks following the burn, increased evaporation rates combined with higher temperatures on the burned sites affect species of fungi at or near the soil surface. Temporary changes in nutrient levels as a direct result of burning could cause fluctuations in the fungal population.

Fire is reported to reduce fungi, not only due to the heat of the fire but to changes in the postburn environment (Barbour et al., 1980). Most accounts refer to decreases in the number of fungal propagules following fire (Meiklejohn, 1955; Wright and Bollen, 1961; Ahlgren and Ahlgren, 1965; Jalaluddin, 1969), rather than to qualitative changes in the mycoflora.

To assess burning effects on the principal taxa of the fungal community, relative densities of species from preburn and postburn 2 da and 14 da samples were compiled (Table 10). Two criteria were used to assess a potential species response to burning: (1) a change from the preburn density of at least 10 units in the burned plots while deviating less than 2 units in the unburned plots, and (2) a sustained response between 2 da and 14 da postburn collections.

Only seven of the forty most commonly isolated taxa showed a response to burning. Four dematiaceous Hyphomycete species, Cladosporium cladosporoides, Papulaspora immersa, Epicoccum purpurascens, and Pithomyces chartarum, declined in colony numbers following burning. These cellulolytic decomposers, often early secondary invaders on all sorts of plants (Ellis, 1971), show response to the immediate effect of burning and litter removal at the soil surface by destruction or

Table 10. Relative densities for forty principal fungi from preburn and 2 da and 14 da soil samples from tallgrass prairie sites, Story County, Iowa

| | Preburn | Burn plots 2 da | Burn plots 14 da | Unburn plots 2 da | Unburn plots 14 da |
|---|---|---|---|---|---|
| Trichoderma hamatum | 78 | 89 | 74 | 80 | 66 |
| Gliocladium roseum | 61 | 76 | 74 | 57 | 71 |
| Mucor hiemalis | 54 | 42 | 39 | 49 | 39 |
| Ramichloridium schulzeri | 48 | 50 | 42 | 45 | 49 |
| Alternaria alternata | 44 | 30 | 35 | 48 | 42 |
| Staphylotrichum coccosporum[a] | 62 | 72 | 73 | 60 | 60 |
| Chaetomium globosum | 28 | 22 | 26 | 27 | 20 |
| Gliocladium viride | 43 | 56 | 43 | 54 | 42 |
| Cladosporium cladosporoides[b] | 33 | 20 | 17 | 32 | 32 |
| Marinnaea elegans | 36 | 46 | 31 | 39 | 22 |
| Fusarium oxysporum | 26 | 24 | 22 | 26 | 26 |
| Phoma sp. | 24 | 21 | 18 | 28 | 22 |
| Mortierella sp. | 31 | 14 | 15 | 26 | 13 |
| Penicillium janthinellum | 33 | 34 | 25 | 31 | 33 |
| Arthrobotrys oligospora | 24 | 18 | 11 | 26 | 22 |
| Papulaspora immersa[b] | 21 | 11 | 12 | 21 | 20 |
| Paecilomyces marquandii | 38 | 27 | 32 | 34 | 29 |
| Rhizopus stolonifer | 2 | 10 | 13 | 9 | 13 |
| Myrothecium verrucaria | 26 | 20 | 19 | 19 | 21 |
| Acremonium sp. | 10 | 8 | 9 | 11 | 8 |
| Sordaria fimicola | 13 | 20 | 17 | 11 | 19 |
| Aspergillus flavipes | 26 | 35 | 18 | 21 | 13 |
| Epicoccum purpurascens[b] | 21 | 4 | 10 | 20 | 14 |
| Cunninghamella elegans | 16 | 27 | 22 | 25 | 20 |
| Penicillium simplicissimum | 19 | 19 | 20 | 24 | 7 |
| Chrysosporium sp. | 9 | 7 | 10 | 6 | 8 |
| Sphaerodes retispora | 10 | 15 | 9 | 11 | 11 |
| Fusarium solani | 9 | 15 | 11 | 11 | 12 |
| Pyrenochaeta sp. | 13 | 7 | 6 | 8 | 11 |
| Syncephalis furcata | 19 | 25 | 18 | 26 | 13 |
| Absidia glauca | 33 | 21 | 15 | 21 | 19 |
| Gliomastix murorum | 6 | 11 | 8 | 6 | 9 |
| Gonytrichum macrocladium | 5 | 9 | 5 | 4 | 5. |
| Spadicoides obovata | 7 | 12 | 12 | 8 | 3 |
| Nigrospora sphaerica | 18 | 8 | 5 | 13 | 7 |

[a]Increases.
[b]Decreases.

Table 10. (Continued)

| | Preburn | Burn plots 2 da | Burn plots 14 da | Unburn plots 2 da | Unburn plots 14 da |
|---|---|---|---|---|---|
| *Spinalia tenuis* | 7 | 3 | 5 | 14 | 12 |
| *Pithomyces chartarum*[b] | 15 | 2 | 1 | 13 | 12 |
| *Zygorrhynchus moelleri* | 23 | 16 | 31 | 25 | 15 |
| *Coemansia pectinata*[a] | 8 | 22 | 7 | 8 | 5 |
| *Scopinella* sp.[a] | 2 | 14 | 11 | 4 | 5 |

reduction of viable propagative units.

Populations of Epicoccum, Papulaspora, and Pithomyces reduced by the spring burn exceeded preburn levels by the fall. The flush of litter accumulation in late fall could lead to coincident increases in these fungi at the last collection period.

Density increases were recorded for Staphylotrichum coccosporum and Scopinella sp. following the burn. Coemansia pectinata exhibited a high increase in the 2 da postburn plots, but dropped to preburn levels by the 14 da collection. Burning may have induced a spore germination response previously unreported for this species. All three species are relatively slow growing and may be given an advantage by reduction in density of more competitive soil species.

Numbers of isolated species of four large groups of fungi (Moniliaceous Hyphomycetes, Dematiaceous Hyphomycetes, Ascomycetes, and Zygomycetes) at each collection period at each site are presented in Figures 12-16. Moniliaceous fungal species decreased in numbers of 2 da postburned plots of Doolittle and Plover and increased slightly on Ames and Norton prairies. At the same collection period, the dematiaceous species numbers decreased on all sites except Norton 1. Fungal species numbers in these two groups declined in subsequent postburn collections but reached preburn levels by 6 months after the prairie burn. Species of Ascomycetes and Zygomycetes showed very little variation in species numbers between collection periods. Zygomycetes, pioneer fungal species capable of utilizing simple carbohydrates, are early invaders on new microsites. These microsites accumulate at a fairly constant rate in

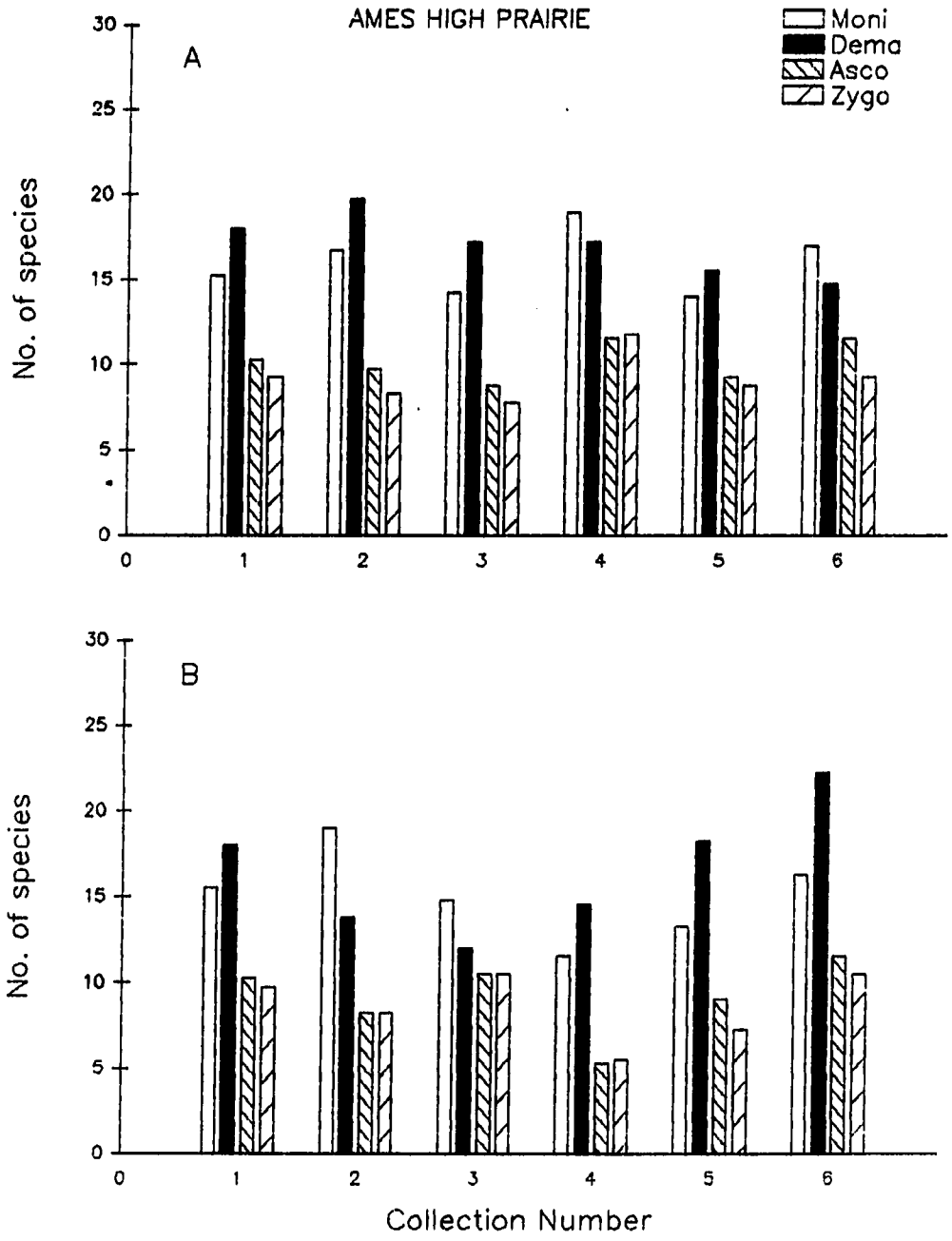


Figure 12. Numbers of fungal species grouped by major taxonomic categories isolated from soil samples, Ames High Prairie, Story County, Iowa, preburn (1) and at postburn 2 da (2), 14 da (3), 30 da (4), 60 da (5), and 180 da (6) intervals from unburned (A) and burned (B) plots

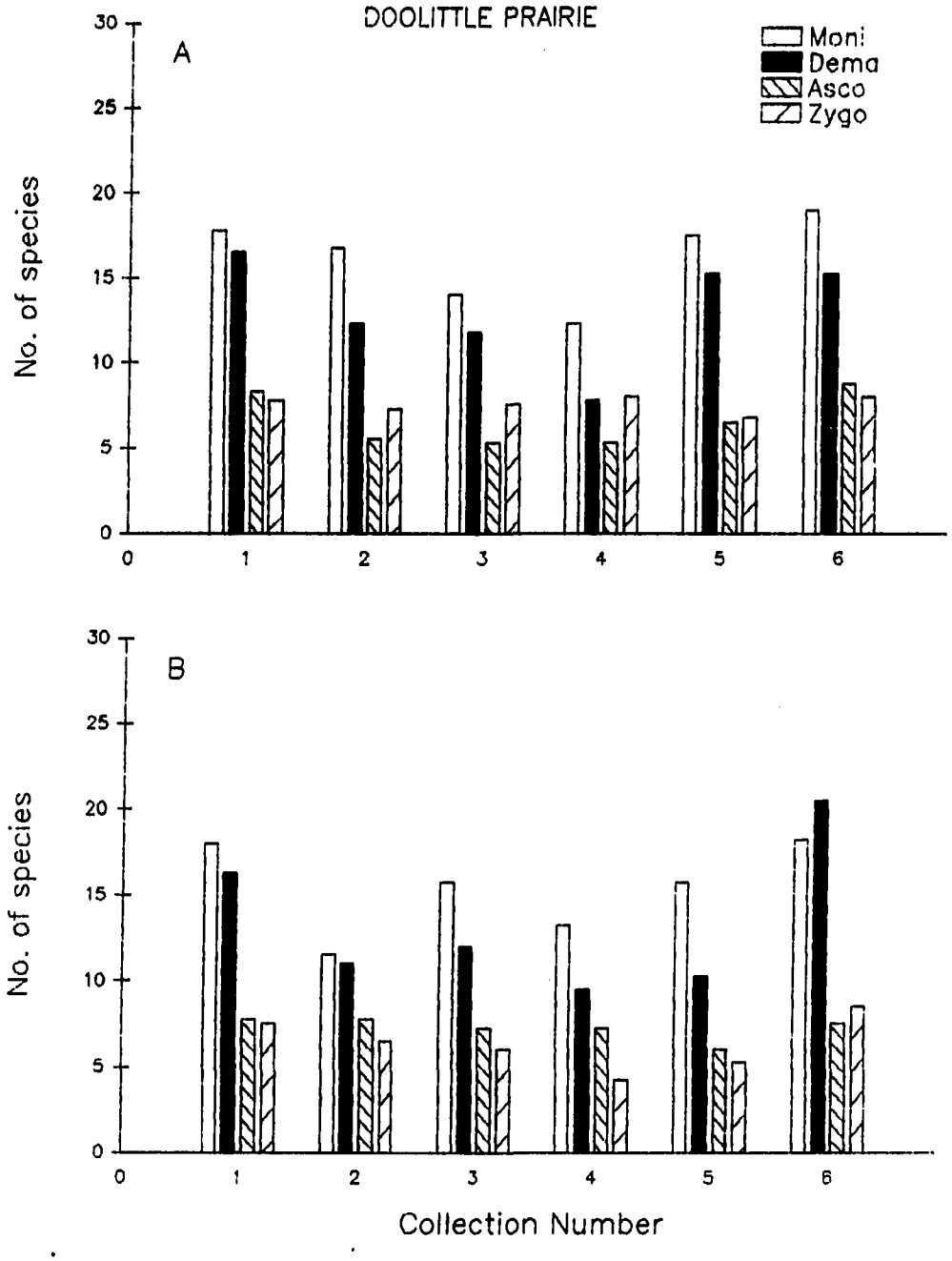


Figure 13. Numbers of fungal species grouped by major taxonomic categories isolated from soil samples, Doolittle Prairie, Story County, Iowa, preburn (1) and at postburn 2 da (2), 14 da (3), 30 da (4), 60 da (5), and 180 da (6) intervals from unburned (A) and burned (B) plots

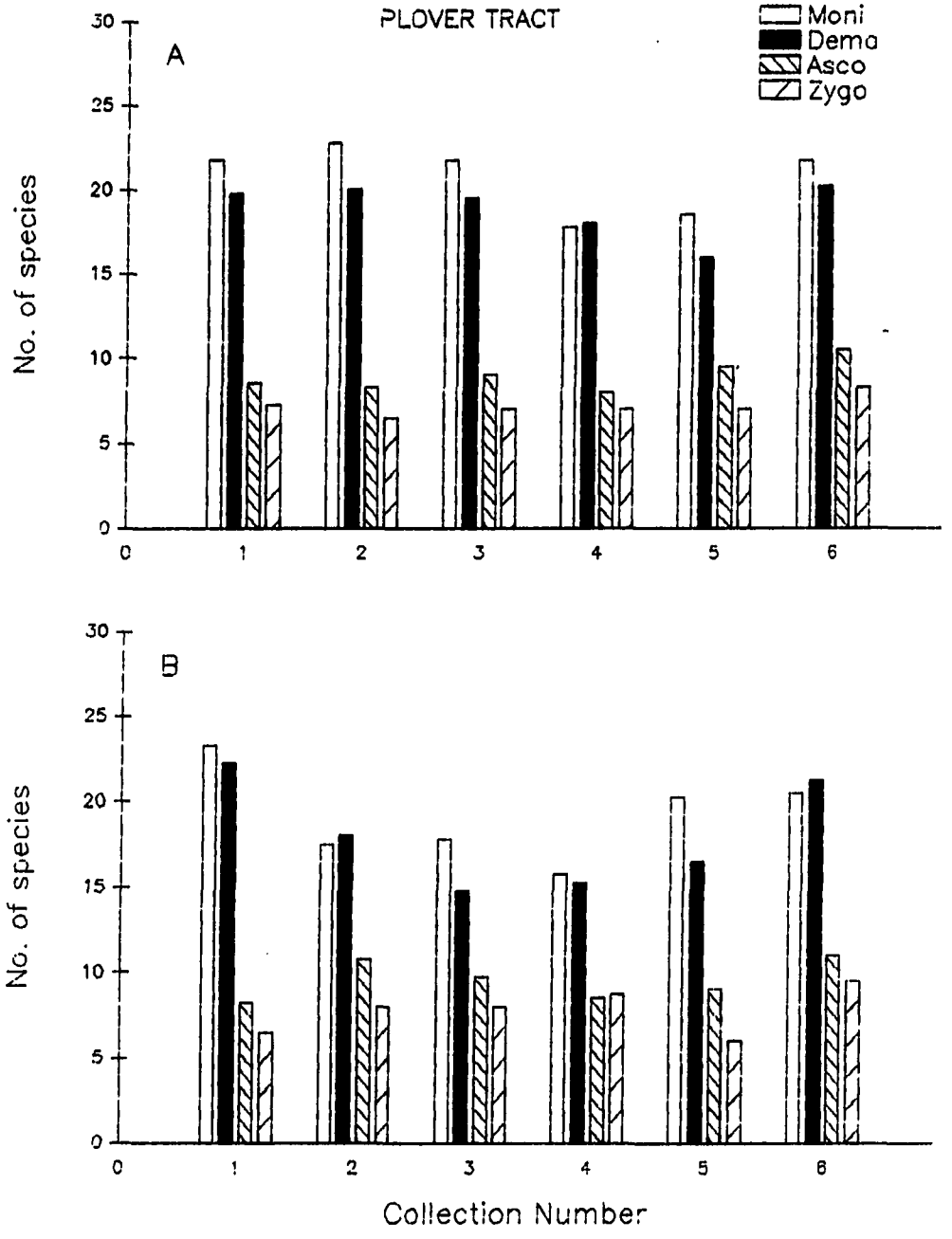


Figure 14. Numbers of fungal species grouped by major taxonomic categories isolated from soil samples, Plover Prairie Tract, Story County, Iowa, preburn (1) and at postburn 2 da (2), 14 da (3), 30 da (4), 60 da (5), and 180 da (6) intervals from unburned (A) and burned (B) plots

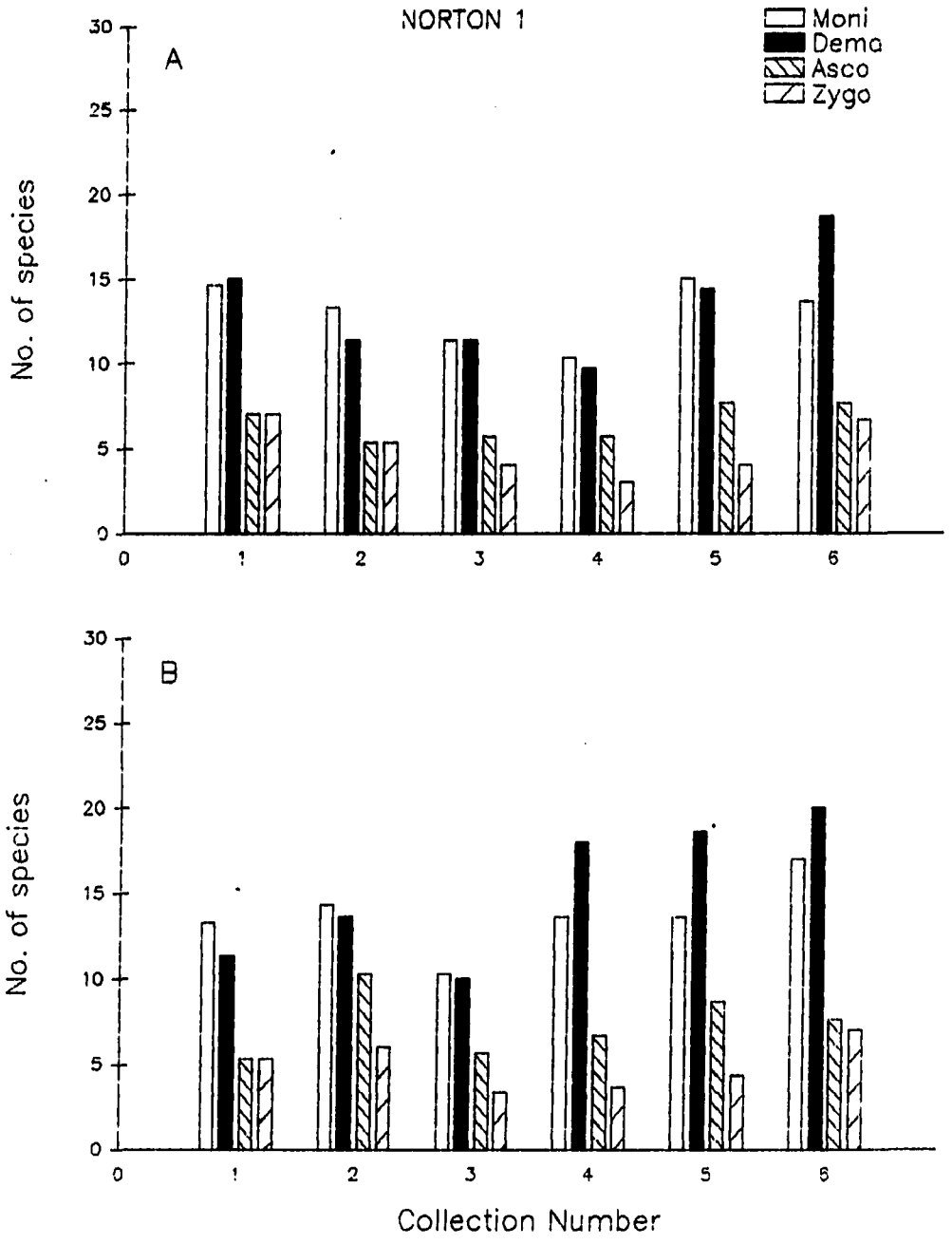


Figure 15. Numbers of fungal species grouped by major taxonomic categories isolated from 1st year soil samples, Norton Prairie, Story County, Iowa, preburn (1) and at postburn 2 da (2), 14 da (3), 30 da (4), 60 da (5), and 180 da (6) intervals from unburned (A) and burned (B) plots

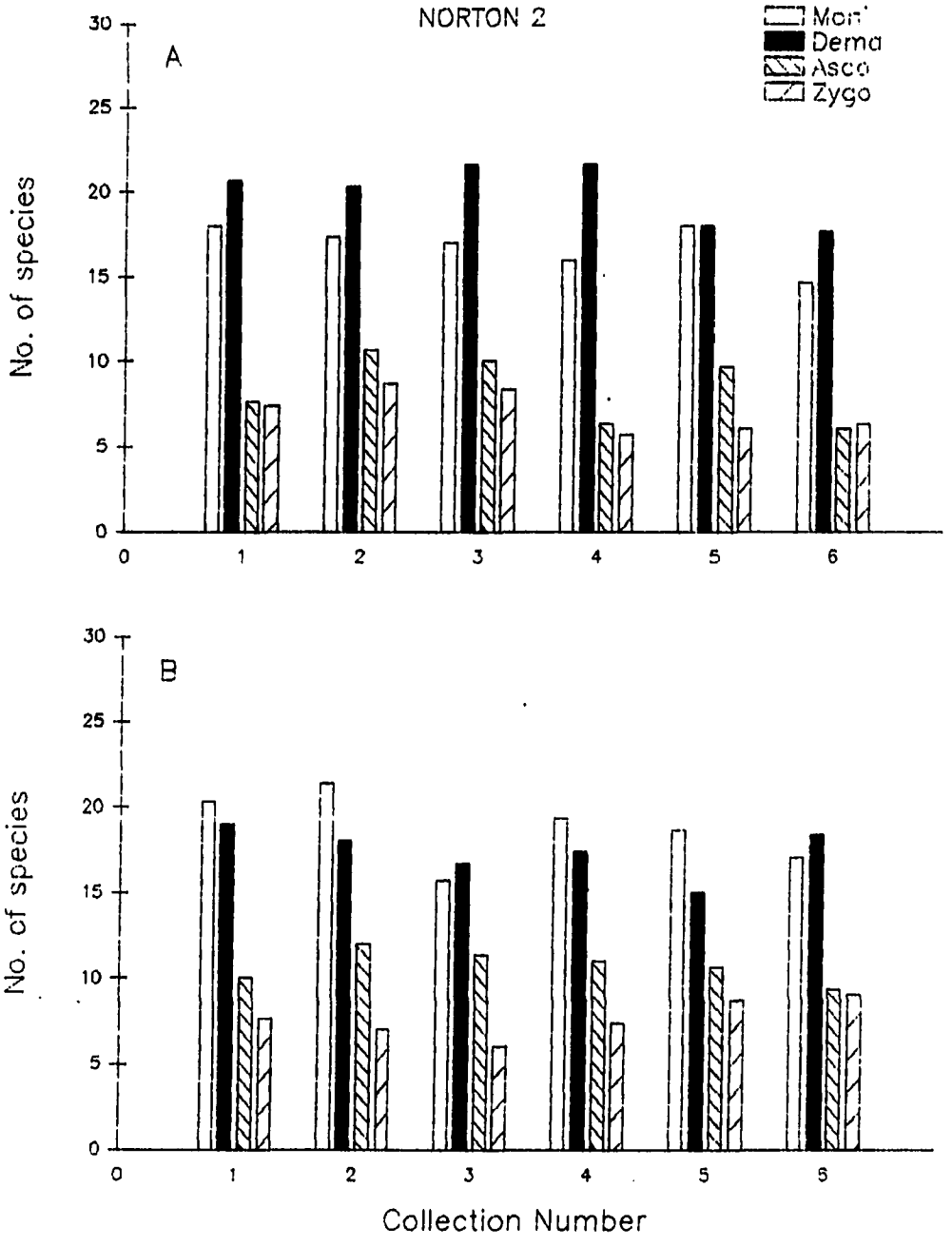


Figure 16. Numbers of fungal species grouped by major taxonomic categories isolated from 2nd year soil samples, Norton Prairie, Story County, Iowa, preburn (1) and at postburn 2 da (2), 14 da (3), 30 da (4), 60 da (5), and 180 da (6) intervals from unburned (A) and burned (B) plots

grassland communities during a growing season. Ascomycetes, by utilizing the more recalcitrant components of the microsites, are probably a constant though slow growing component of the soil flora.

The results of several studies were summarized by Gochenaur (1981); they revealed a great reduction in species diversity, particularly in the top layers of soil following a burn. The results of a study of slash burning on soil microorganisms (Deka and Mishra, 1983) revealed that numbers of fungi were reduced at the soil surface by burning, but below a depth of 2 cm no changes in fungal numbers could be detected. Fungal populations subsequently increased and reached a peak within a month after the fire.

Other investigators (Ahlgren and Ahlgren, 1965; Wicklow, 1973; Ahlgren, 1974) report substantial increases in fungal numbers later in the season following a burn, particularly after the first rain.

Although a dramatic decline in species numbers was not found in tallgrass prairie soils, Hyphomycete numbers were generally lower following the burn but reached preburn levels by six months after the burn.

Widden and Parkinson (1975) observed changes in the mycofloral component following fire in a forest community. Species of Trichoderma and Penicillium were killed by the heat of the fire, while Cylindrocarpon destructans and Gelasinospora sp. were stimulated to germinate and grow. None of the principal species in the present study were completely killed by the heat of the burn. Trichoderma increased while the Penicillium species remained unchanged immediately following the burn. Deka and

Mishra (1983) reported that Trichoderma, Penicillium, Aspergillus, Cladosporium, and Cephalosporium were early colonizers and became the dominant fungi in the burnt soils of forested areas of India. These particular species were a constant component of prairie soils at all collection times although fluctuations in densities did occur.

Wicklow (1975) suggested that a "fungal bloom" of Ascomycetes developed following fire on a midwestern prairie. The most common Ascomycetes and their percent densities from the combined plot data for burned and unburned treatments are shown for each of the collection periods in Table 11. A "fungal bloom" of Ascomycetes following fire did not occur on the Iowa study sites. Colony numbers of Chaetomium seminudum and Scopinella sp. increased substantially following the spring burn and densities for these two species remained consistently higher in the burned plots throughout the growing season. Most Ascomycetes were recorded in such low numbers that variation in plot densities was not a reliable indication of burning response.

Germination of some ascospores is reported to be stimulated by burning or heating. Such a response was not detected during the present study. Quick controlled burns may not reach temperatures which would have stimulated germination of fire-sensitive Ascomycetous fungal species. Furthermore, soil temperatures associated with early spring burns may not be high enough to support good fungal growth following a burn. Late spring and summer prairie burns may have a greater effect on fire-related species.

Table 11. Preburn and postburn relative density of common Ascomycetes on burned and unburned tallgrass prairie plots, Story County, Iowa

| | Pre-burn | 2 da | | 14 da | | 30 da | | 60 da | | 180 da | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | B | U | B | U | B | U | B | U | B | U |
| Chaetomium globosum | 28 | 22 | 27 | 26 | 20 | 22 | 25 | 25 | 27 | 30 | 20 |
| Sordaria fimicola | 15 | 20 | 11 | 17 | 19 | 12 | 13 | 22 | 11 | 13 | 7 |
| Chaetomium seminudum | 13 | 20 | 11 | 23 | 13 | 10 | 10 | 17 | 14 | 15 | 10 |
| Melanospora zamiae | 11 | 7 | 8 | 15 | 6 | 8 | 4 | 10 | 14 | 4 | 6 |
| Sphaerodes retispora | 10 | 15 | 11 | 9 | 11 | 11 | 10 | 9 | 8 | 9 | 7 |
| Syspatospora parasitica | 9 | 3 | 7 | 3 | 4 | 2 | 6 | 4 | 6 | 6 | 5 |
| Podospora curvicolla | 8 | 2 | 2 | 3 | 2 | 0 | 7 | 4 | 6 | 3 | 7 |
| Thielavia terricola | 6 | 7 | 8 | 8 | 6 | 10 | 9 | 14 | 8 | 10 | 4 |
| Gelasinspora calospora | 5 | 2 | 2 | 10 | 5 | 2 | 0 | 2 | 1 | 3 | 3 |
| Scopinella sp. | 2 | 14 | 4 | 11 | 3 | 13 | 7 | 18 | 8 | 14 | 10 |
| Talaromyces flavus | 3 | 9 | 5 | 6 | 2 | 4 | 6 | 3 | 5 | 3 | 3 |
| Chaetomium crispatum | 3 | 3 | 1 | 1 | 0 | 2 | 3 | 3 | 2 | 3 | 2 |
| Coniochaeta leucoplaca | 2 | 3 | 0 | 5 | 0 | 3 | 2 | 5 | 0 | 3 | 2 |
| Ascobolus furfuraceous | 3 | 2 | 3 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 |
| Hypocrea gelatinosa | 0 | 2 | 3 | 1 | 2 | 0 | 0 | 2 | 0 | 2 | 0 |

## Seasonality and Fungus Populations in Tallgrass Prairie Sites in Central Iowa

Conflicting reports exist about the seasonality of fungal species in all soil types and localities. England and Rice (1957) reported that most fungal species in tallgrass prairie soil in Oklahoma were seasonal or sporadic in occurrence. Spring and fall peaks in fungal numbers were reported by Brierley (1923) and Badurowa and Badura (1967). Highest species numbers were reported in fall collections in India (Rama Rao, 1966; Joshi, 1983) where numbers of isolates were correlated with dry and rainy season variations. Thornton (1965) reported that mycelium reached maximum levels in soil during summer. Sewell (1959) and Williams and

Parkinson (1970) observed that no significant changes occurred in the fungal community with seasonal changes.

Seasonal trends were not observed in the majority (62.5%) of commonly isolated fungi of tallgrass prairie soils in Iowa (Table 12). Species that increased in densities from spring to autumn were Hyphomycetes, Alternaria alternata and Fusarium solani and one Zygomycete, Cunninghamella elegans. A forest soil study in Poland (Badurowa and Badura, 1967) showed that in autumn the highest numbers of isolates came from these two groups of fungi.

Five species, Fusarium oxysporum, Penicillium janthinellum, Myrothecium verrucaria, Aspergillus flavipes, and Nigrospora sphaerica decreased by an average of 12 units between spring preburn and autumn collections. According to the data obtained by Clarke and Christensen (1981), seasonal spring peaks were recorded for Paecilomyces marquandii, Fusarium solani, Aspergillus niveus, and Aspergillus fumigatus and a fall peak for Penicillium janthinellum in short grass prairie soils. These species which are a common component of grassland soils may respond more to local environmental conditions of moisture and temperature than seasonal factors.

Seven species, Marrinnaea elegans, Arthrobotrys oligospora, Epicoccum purpurascens, Absidia glauca, Mortierella sp., Pithomyces chartarum, and Zygorhynchus moelleri, had density peaks in spring and fall. Reports from studies of forest soil fungi and aquatic microfungi show that these trends are common in other communities (Widden, 1981). Summer declines in species numbers were attributed to nutrient levels

Table 12. Relative densities of forty principal fungal species from unburned prairie plots, Story County, Iowa, at preburn and several postburn samplings

| | Preburn | Spring | Summer | Fall |
|---|---|---|---|---|
| Trichoderma hamatum | 78 | 80 | 85 | 81 |
| Gliocladium roseum | 61 | 57 | 71 | 63 |
| Mucor hiemalis | 54 | 49 | 68 | 58 |
| Ramichloridium schulzeri | 48 | 45 | 39 | 48 |
| Alternaria alternata[a] | 44 | 48 | 43 | 87 |
| Staphylotrichum coccosporum | 62 | 60 | 67 | 63 |
| Chaetomium globosum | 28 | 27 | 27 | 20 |
| Gliocladium viride | 43 | 54 | 49 | 53 |
| Cladosporium cladosporoides | 33 | 32 | 23 | 27 |
| Marrinnaea elegans[b] | 36 | 39 | 25 | 39 |
| Fusarium oxysporum[c] | 26 | 26 | 25 | 14 |
| Phoma sp. | 24 | 28 | 18 | 23 |
| Mortierella sp.[b] | 31 | 26 | 17 | 26 |
| Penicillium janthinellum[c] | 33 | 31 | 30 | 21 |
| Arthrobotrys oligospora[b] | 24 | 26 | 11 | 27 |
| Papulaspora immersa | 21 | 21 | 16 | 15 |
| Paecilomyces marquandii | 38 | 34 | 32 | 41 |
| Rhizopus stolonifer | 2 | 9 | 14 | 10 |
| Myrothecium verrucaria[c] | 26 | 19 | 24 | 14 |
| Acremonium sp. | 10 | 11 | 14 | 18 |
| Sordaria fimicola | 15 | 11 | 11 | 7 |
| Aspergillus flavipes[c] | 26 | 21 | 19 | 11 |
| Epicoccum purpurascens[b] | 21 | 20 | 13 | 23 |
| Cunninghamella elegans[a] | 16 | 25 | 26 | 36 |
| Penicillium simplicissimum | 19 | 24 | 18 | 29 |
| Chrysosporium sp. | 9 | 6 | 10 | 9 |
| Sphaerodes retispora | 10 | 11 | 8 | 7 |
| Fusarium solani[a] | 9 | 11 | 16 | 22 |
| Pyrenochaeta sp. | 13 | 8 | 10 | 14 |
| Syncephalis furcata | 19 | 26 | 15 | 24 |
| Absidia glauca[b] | 33 | 21 | 17 | 37 |
| Gliomastix murorum | 6 | 6 | 14 | 11 |
| Gonytrichum macrocladium | 5 | 4 | 10 | 9 |
| Spadicoides obovata | 7 | 8 | 7 | 12 |
| Nigrospora sphaerica[c] | 18 | 13 | 8 | .8 |
| Spinalia tenuis | 7 | 14 | 12 | 18 |

[a]Fall relative density peak.
[b]Preburn/spring and fall relative density peaks.
[c]Preburn relative density peak.

Table 12. (Continued)

| | Preburn | Spring | Summer | Fall |
|---|---|---|---|---|
| *Pithomyces chartarum*[b] | 15 | 13 | 8 | 20 |
| *Zygorhynchus moelleri*[b] | 23 | 25 | 17 | 27 |
| *Coemansia pectinata* | 8 | 8 | 5 | 13 |
| *Scopinella* sp. | 2 | 4 | 8 | 10 |

rather than climatic factors. This may not be the case in prairie systems where organic material is constantly accumulating. Summer in prairie ecosystems is the time when moisture is the most limiting factor to fungi near the soil surface.

Numbers of species in unburned prairie plots (Figures 12-16) remained relatively constant throughout the growing season on most sites. Doolittle Prairie (Figure 13) and Norton 1 (Figure 15) had decreasing numbers of Hyphomycetes in unburned treatments in the first three post-burn collections. The decline in species numbers can be attributed to moisture stress on the sites. Doolittle, a wet-mesic prairie, and Norton, a mesic prairie, had very low moisture levels during the first 2 months of the sampling period. The potholes on Doolittle Prairie were completely dry by collection 3. The unusual environmental conditions on these sites decreased decomposition rates and fungal populations during those periods.

Season is not a major factor affecting total soil fungal species numbers. In seasons with normal moisture levels, a mat of litter at the soil surface combined with the shading effects of the standing vegetation provides an environmentally insulated habitat for the soil fungi.

## Vesicular Arbuscular Fungi in Tallgrass Prairie Soils in Central Iowa

Sixteen species of vesicular arbuscular mycorrhizal (VAM) fungi were found in tallgrass prairie soils of central Iowa (Table 13). Fifteen of these species were from virgin prairie soils of Plover,

Table 13. Occurrence of vesicular arbuscular mycorrhizal fungi in tallgrass prairie sites, Story County, Iowa

| | Plover | Doolittle | Ames | Norton |
|---|---|---|---|---|
| Acaulospora scrobiculata | x | | | |
| Gigaspora calospora | x | x | x | x |
| Gigaspora gigantea | | | | x |
| Gigaspora sp. | x | | | |
| Glomus caledonicum | | | x | |
| Glomus etunicatum | x | x | x | x |
| Glomus fasciculatum | x | x | x | x |
| Glomus geosporum | x | x | x | x |
| Glomus intraradices | | x | | |
| Glomus macrocarpum | x | x | x | |
| Glomus microcarpum | x | | | |
| Glomus monosporum | x | x | x | x |
| Glomus mosseae | x | x | x | x |
| Glomus pallidum | | | x | |
| Glomus sp. | x | x | x | x |
| Sclerocystis rubiformis | x | | | x |

Doolittle and Ames prairie sites. Only nine species, or 56% of the total number of VAM fungi, were isolated from restored prairie soil at the Norton Prairie. Hetrick and Bloom (1983) also found a wider diversity of VAM fungal species in virgin prairie than in planted winter wheat field soil in Kansas.

The Norton soils contained half the number of Glomus species found in virgin prairie soils. Similar results were found by Hetrick and Bloom (1983) where winter wheat fields had less than half the Glomus species of virgin tallgrass prairie soils.

VAM fungi are cosmopolitan inhabitants of the roots of a wide variety of host plants (Hetrick, 1984). Soil studies from sites in North America indicate that species of Glomus are the most widespread, but species of Gigaspora, Acaulospora, Sclerocystis, and Entrophospora are

commonly found by using soil extraction techniques.

When species of VAM fungi from tallgrass prairie soils in Iowa are compared with those from soils in Kansas (Hetrick and Bloom, 1983), Quebec (Herskowitz and Estey, 1978), Illinois (Dickman et al., 1984), Wyoming (Stahl and Christensen, 1982), and Iowa poplar plantations (Walker et al., 1982), only Glomus mosseae was present at all six localities. Glomus fasciculatum, Glomus geosporum, Glomus microcarpum, and Gigaspora calospora were recorded in at least four of the six study areas.

Only two previous studies have examined VAM fungal populations from tallgrass prairie soils. Hetrick and Bloom (1983) reported 20 species of VAM fungi from Konza tallgrass prairie in Kansas. Nine species of Gigaspora and Glomus were common to both Iowa and Kansas soils. Eight VAM species were found in prairie soils from four Illinois sites (Dickman et al., 1984). Five of the eight species were also recorded from central Iowa soils.

Fewer VAM species appear to be present in western short grass prairie soils. Stahl and Christensen (1982) observed only 6 VAM species in Wyoming collections. Gigaspora and Sclerocystis were absent in the Wyoming soils. All four recorded species of Glomus, G. fasciculatum, G. macrocarpus, G. microcarpus, and G. mosseae, were also found in Iowa tallgrass prairie soil.

Relative spore abundance per 100 ml of soil subsample was determined for each sampling period on each prairie site (Figures 17-20). Spore counts fluctuated greatly between collections on all prairie sites.

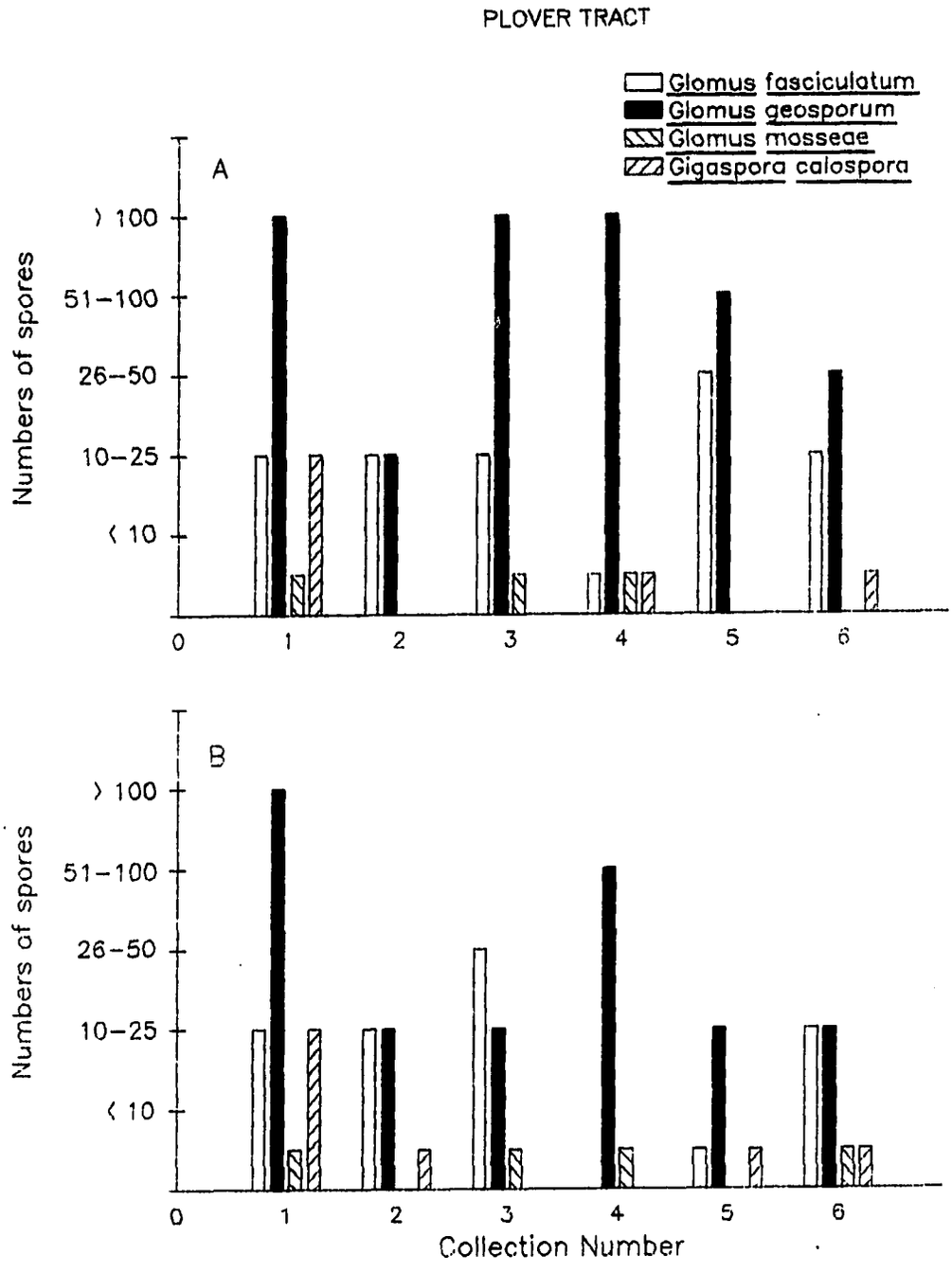


Figure 17. Relative numbers of spores of four common vesicular arbuscular mycorrhizal fungal species from unburned (A) and burned (B) plots on Plover Prairie Tract, Story County, Iowa, at preburn (1) and at postburn 2 da (2), 14 da (3), 30 da (4), 60 da (5), and 180 da (6) intervals

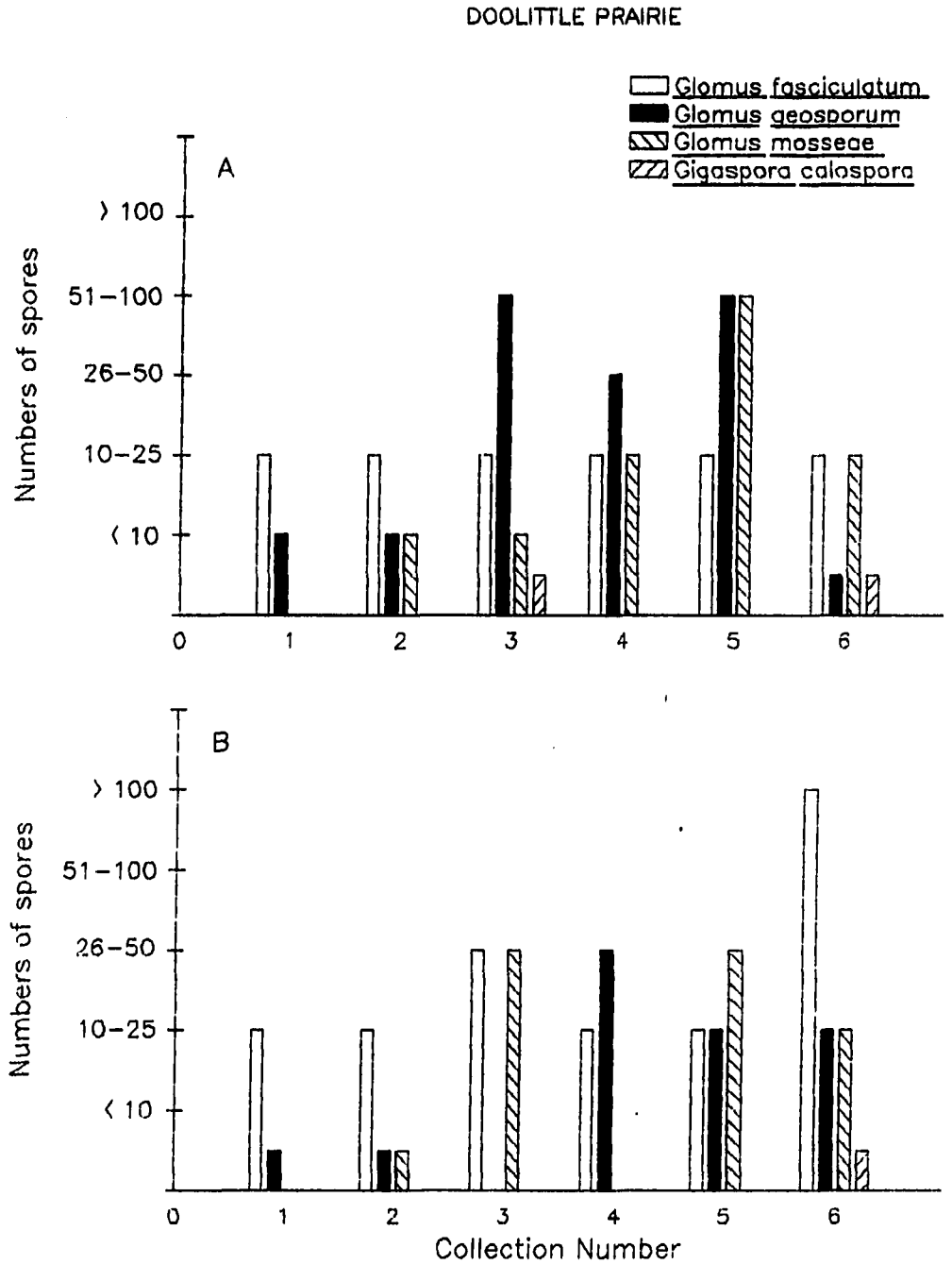


Figure 18. Relative numbers of spores of four common vesicular arbuscular mycorrhizal fungal species from unburned (A) and burned (B) plots on Doolittle Prairie, Story County, Iowa, at preburn (1) and at postburn 2 da (2), 14 da (3), 30 da (4), 60 da (5), and 180 da (6) intervals

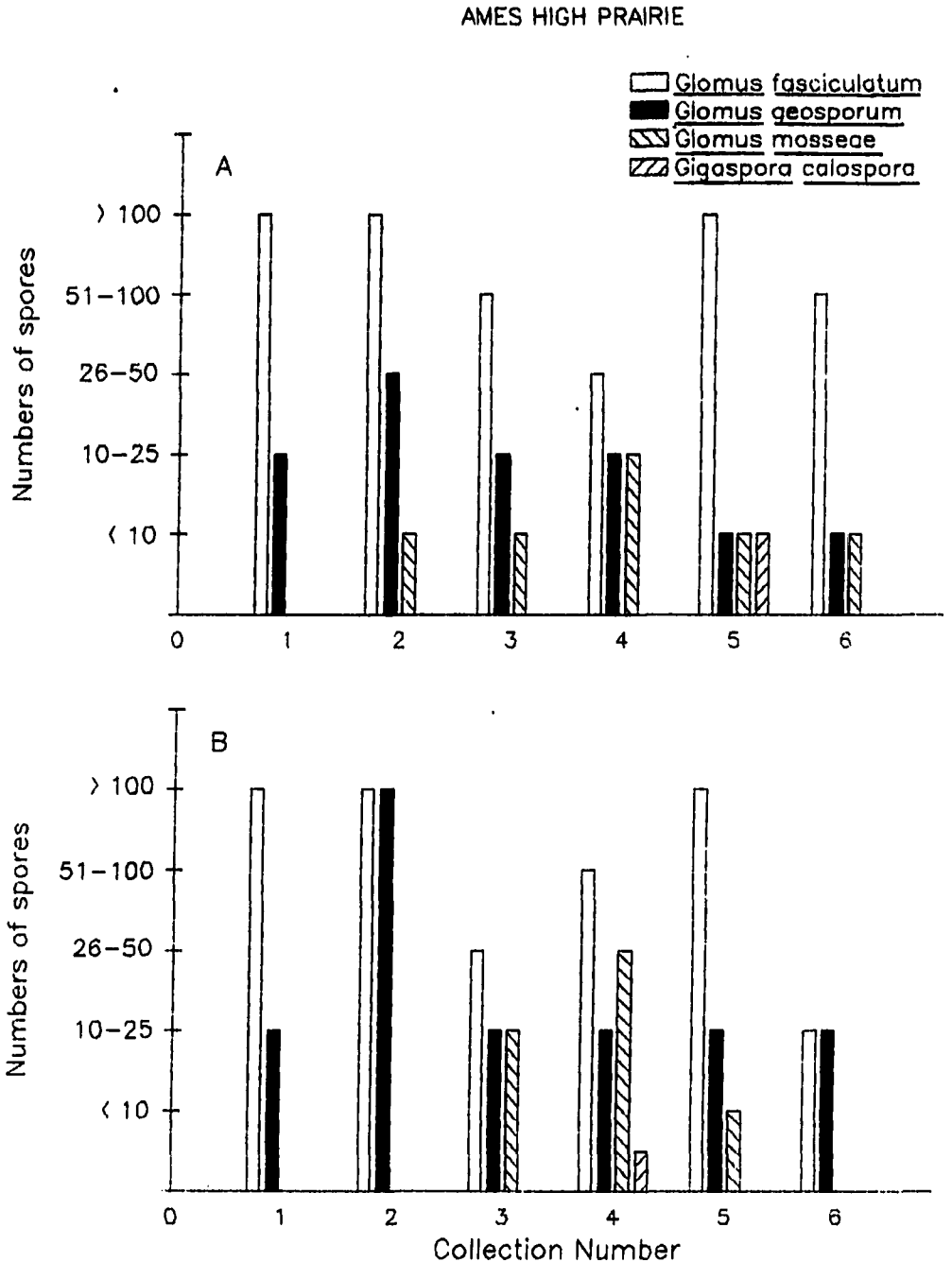


Figure 19. Relative numbers of spores of four common vesicular arbuscular mycorrhizal fungal species from unburned (A) and burned (B) plots on Ames High Prairie, Story County, Iowa, at preburn (1) and at postburn 2 da (2), 14 da (3), 30 da (4), 60 da (5), and 180 da (6) intervals

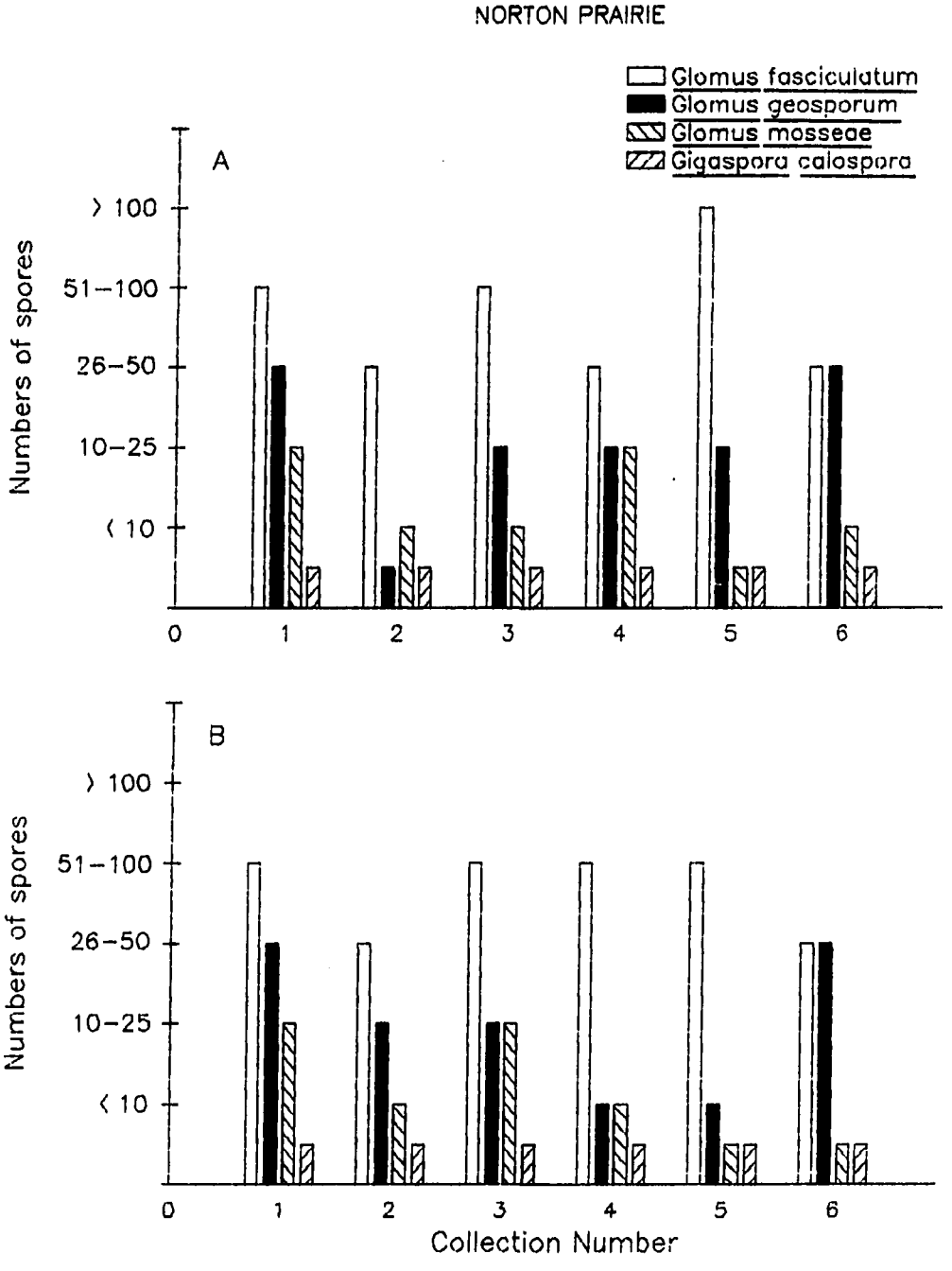


Figure 20. Relative numbers of spores of four common vesicular arbuscular mycorrhizal fungal species from unburned (A) and burned (B) plots on Norton Prairie, Story County, Iowa, at preburn (1) and at postburn 2 da (2), 14 da (3), 30 da (4), 60 da (5), and 180 da (6) intervals

Walker et al. (1982) also found high variability among spore counts from soil samples collected during successive weeks in planted poplar stands. They attributed part of the variation to insufficient sample size. While this is also a factor in the present study, the heterogeneity of soil microsites may make it extremely difficult to accurately assess VAM spore populations in prairie soils.

The relative spore numbers of Glomus fasciculatum, Glomus geosporum, Glomus mosseae, and Gigaspora calospora are presented for each prairie site in Figures 17 through 20. There was little difference in total VAM spore numbers on burned and unburned plots. Burning, although stimulatory to vascular plant growth, was not coincidentally stimulatory to increased VAM spore production.

High numbers of Glomus fasciculatum were collected at almost every sampling period in burned and unburned plots on Ames High Prairie (Figure 17) and the Norton site (Figure 20). Large populations of little bluestem, Andropogon scoparius, are present on both these prairies. A study in Illinois on the rhizosphere of little bluestem (Dickman et al., 1984) showed that G. fasciculatum had the highest mean spore number of all recorded VAM species per cubic centimeter of soil for each sampling period, May through September. G. fasciculatum also had the highest spore number of all VAM species observed in Konza prairie soils where little bluestem is one of the dominant grasses.

Andropogon scoparius is an uncommon grass species on wet-mesic Doolittle Prairie and Plover Tract. Numbers of Glomus fasciculatum were also less on these sites (Figures 18-19) than on Ames and Norton

prairies.

The most frequently observed VAM species from Doolittle and Plover prairies was Glomus geosporum. Although G. geosporum was recorded from both Illinois and Kansas, it was much less common than G. fasciculatum. It may be more closely associated with other mesic to wet-mesic prairie grasses like Andropogon gerardii, Sorghastrum nutans, Spartina pectinata, or Calamagrostis canadensis than a dry-mesic grass species like Andropogon scoparius.

Glomus mosseae and Gigaspora calospora occur with regularity on all tallgrass prairie sites in central Iowa but always in low numbers. These two species were also a component of the VAM flora of Illinois and Kansas prairie soils.

Although seasonal fall peaks of spore numbers have often been reported for VAM fungi, those trends were not evident in the Iowa study. For most sites, spore numbers were generally higher in spring, collections 1 and 2, than in fall, collection number 6 (Figures 17-20). Hetrick and Bloom (1983) obtained highest spore counts from spring collections both from virgin prairie and cultivated wheat fields.

## SUMMARY

A total of 483 species of soil inhabiting fungi were present in virgin and restored prairie soils in central Iowa. The number, though seemingly large, represents but a small portion of the total fungal community in prairie soils. Isolation media and methods are always selective for the range of taxa which develop in culture. Hyphomycetes, Zygomycetes, Ascomycetes, Coelomycetes, and Myxomycetes were successfully isolated, but Basidiomycetes, Oomycetes, and Chytridiomycetes did not develop in cultures when the modified soil plate method with extended incubation was used.

Many of the principal fungi in tallgrass prairie soils in central Iowa have been reported as principal taxa of other grassland ecosystems, both in North America and on other continents. Species of Fusarium, Penicillium, Trichoderma, Cladosporium, Alternaria, Acremonium, Aspergillus, Paecilomyces, Chrysosporium, Mucor, and Mortierella are common to Iowa and other grassland communities. Species of Ramichloridium, Staphlotrichum, Syncephalis, Piptocephalis, Arthrobotrys, and Chaetomium, included among the principal taxa in tallgrass prairie soils, are generally absent from other grassland soil fungal lists. Only additional ecological work will determine if these species are unique to tallgrass prairie soils or if they are a largely overlooked component of grassland soils worldwide.

The soil fungal communities of virgin and restored prairie soils are distinctly different. Whereas species numbers isolated were nearly

equal, composition, frequency, and density of the principal taxa differed between the two community types. Disturbance from agricultural practices was the major factor which accounted for differences between the fungi of virgin and restored prairie soils.

The fungal community of tallgrass prairie soils in Iowa are similar to those of other tallgrass prairie communities in North America. They are most similar to fungal communities of mesic prairies in Wisconsin and grasslands in Ohio. They are least similar to revegetated prairie in Wisconsin and crop fields in Iowa.

Early spring burning had little effect on fungal composition, frequency, or density in the soil ecosystem. Less than 20% of the principal taxa showed any change in density following burning. Numbers of species declined slightly in postburn samples but increased to preburn levels by fall of the same year.

Although prairie vascular plant flora have definite seasonal patterns, the soil fungi do not respond coincidentally. Most show only small fluctuations in density between collecting periods. Changes in density are more likely caused by local environmental conditions, such as moisture, than to seasonal effects.

Vesicular arbuscular mycorrhizal fungi are a common component of the mycoflora of prairie soil. Sixteen species in four genera were identified from spore suspensions following wet-sieving. Numbers of spores fluctuated between sampling periods and neither burning or seasonal patterns could be detected.

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APPENDIX A. COMMON PLANTS ON TALLGRASS PRAIRIE STUDY SITES, STORY COUNTY, IOWA

| | Doolittle Plover | Ames | Norton |
|---|---|---|---|
| **Grasses and Sedges** | | | |
| *Andropogon gerardii* Vitman | x | x | x |
| *Andropogon scoparius* Michx. | | x | x |
| *Sorghastrum nutans* (L.) Nash | x | x | x |
| *Sporobolus heterolepis* (A. Gray) A. Gray | | x | |
| *Elymus canadensis* L. | x | | |
| *Bouteloua curtipendula* (Michx.) Torr. | | x | |
| *Calamagrostis canadensis* (Michx.) Beauv. | x | | |
| *Spartina pectinata* Link | x | | |
| *Carex buxbaumii* Wahl. | x | | |
| *Carex stricta* Lam. | x | | |
| **Forbs** | | | |
| *Amorpha canescens* Pursh | | x | |
| *Artemisia ludoviciana* Nutt. | | x | |
| *Asclepias sullivantii* L. | x | | |
| *Asclepias syrica* L. | | x | x |
| *Astragalus crassicarpus* Nutt. | | x | |
| *Baptisia alba* var. *macrophylla* (Larisey) Isely | | x | |
| *Baptisia bracteata* var. *glabrescens* (Lareisey) Isely | | x | |
| *Comandra umbellata* (L.) Nutt. | | x | |
| *Dalea candida* Michx. ex Willd. | | x | |
| *Dalea purpurea* Vent. | x | x | |
| *Echinacea pallida* Nutt. | | x | |
| *Eryngium yuccifolium* Michx. | x | | |
| *Gentiana andrewsii* Griseb. | x | | |
| *Gentiana puberulenta* Pringle | | x | |
| *Helenium autumnale* L. | x | | |
| *Helianthus grosseserratus* Martens | x | | |
| *Hypoxis hirsuta* (L.) Cov. | x | | |
| *Lespedeza capitata* Michx. | | x | |
| *Liatris aspera* Michx. | | x | |
| *Liatris pycnostachya* Michx. | x | | |
| *Lithospermum canescens* (Michx.) Rehm. | x | | |
| *Lobelia spicata* Lam. | x | x | |
| *Pedicularis canadensis* L. | x | | |

| | Doolittle Plover | Ames | Norton |
|---|---|---|---|
| Phlox pilosa L. | x | | |
| Potentilla arguta Pursh | x | x | |
| Pycnanthemum virginianum Dur. & Jack. ex Robins & Fern | x | | |
| Ratibida pinnata (Vent.) Barnh. | x | x | x |
| Sisyrinchium campestre Bickn. | x | x | |
| Silphium laciniatum L. | x | | |
| Solidago canadensis L. | x | x | x |
| Solidago rigida L. | x | x | |
| Veronicastrum virginicum (L.) Farw. | x | | |
| Zizia aurea (L.) W. Koch. | x | | |

## APPENDIX B. REFERENCES USED IN THE IDENTIFICATION OF FUNGAL SPECIES IN THIS STUDY


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# APPENDIX C. FUNGAL SPECIES ISOLATED FROM TALLGRASS PRAIRIE SOIL IN STORY COUNTY, IOWA

*Absidia glauca* Hagem
*Absidia spinosa* Lendner
*Acaulopage tetraceros* Drechsler
*Acaulospora scrobiculata* Trappe
*Acremonium humicola* (Onions & Barron) W. Gams
*Acremonium implicatum* (Gilman & Abbott) W. Gams
*Acremonium kiliense* Grutz
*Acremonium rutilum* W. Gams
*Acremonium strictum* W. Gams
*Acremonium* sp.
*Acrodictys erecta* (Ellis & Everh.) M. B. Ellis
*Actinomucor elegans* (Eidam) C. R. Benjamin & Hesseltine
*Alternaria alternata* (Fr.) Keissler
*Amerosporium polynematoides* Speg.
*Anguillospora longissima* (de Wild.) Ingold
*Aphanocladium album* (Preuss.) W. Gams
*Apiosordaria verruculosa* (Jensen) V. Arx & W. Gams
*Apodus deciduus* Malloch & Cain
*Arachnomyces nitidus* Massee & Salmon
*Arnium apiculatum* (Griff.) Lundq.
*Arthrinium phaeospermum* (Corda) M. B. Ellis
*Arthrinium sphaerospermum* Fuckel
*Arthrinium* state of *Apiospora montagnei* Sacc.
*Arthrobotrys brochopaga* (Drechsler) Schenck, Kendrick & Pramer
*Arthrobotrys conoides* Drechsler
*Arthrobotrys dactyloides* Drechsler
*Arthrobotrys musiformis* Drechsler
*Arthrobotrys oligospora* Fr.
*Arthrobotrys superba* Corda
*Ascobolus furfuraceous* Pers. per Hook.
*Ascochyta* sp.
*Ascomycete* sp.
*Aspergillus flavipes* (Bain. & Sart.) Thom & Church
*Aspergillus fumigatus* Fr.
*Aspergillus niger* van Tiegham
*Aspergillus terreus* Thom
*Aspergillus ustus* (Bainier) Thom and Church
*Aureobasidium pullulans* (de Bary) Arnaud.
*Bacillospora aquatica* Nils.
*Bactrodesmium longisporum* M. B. Ellis
*Basidiomycetous mycelium* 1
*Basidiomycetous mycelium* 2
*Basidiomycetous mycelium* 3
*Basidiomycetous mycelium* with *sclerotia*

Bloxamia truncata Berk. & Br.
Botryotrichum piluliferum Sacc. & March
Boudiera walkerae Seaver
Camposporium pellucidum (Grove) Hughes
Candida spp.
Catenularia state of Chaetosphaeria myriocarpa (Fr.) Booth
Ceratocystis sp.
Cercophora coprophila (Fr.) Lundq.
Cercophora scortea (Cain) Lundq.
Cercospora sp.
Chaetomidium cephalothecoides (Malloch & Benny) v. Arx
Chaetomidium fimeti (Fuckel) Sacc.
Chaetomidium pilosum (Booth & Shipton) v. Arx
Chaetomium aureum Chivers
Chaetomium bostrychodes Zopf
Chaetomium crispatum Fuckel
Chaetomium fusispora G. Smith
Chaetomium globosum Kunze ex Steud.
Chaetomium gracile Udagawa
Chaetomium indicum Corda
Chaetomium longicollium Krzem. & Badura
Chaetomium murorum Corda
Chaetomium seminudum Ames
Chaetomium succineum Ames
Chaetomium trigonosporum (Marchal) Chivers
Chaetomium funicola Cooke
Chloridium virescens (Pers. ex Pers.) W. Gams & Hol. Jech.
Chrysosporium merdarium (Link) Carmichael
Chrysosporium sp.
Chuppia sarcinifera Deighton
Cladorrhinum foecundissimum Sacc. & Marchal
Cladosporium cladosporoides (Fr.) de Vries
Cladosporium herbarum (Pers.) Link ex Gray
Cladosporium sphaerospermum Penz.
Codinaea state of Chaetosphaeria callimorpha (Mont.) Sacc.
Coemansia aciculifera Linder
Coemansia breviramosa Linder
Coemansia erecta Bainier
Coemansia interrupta Linder
Coemansia pectinata Bainier
Colletotrichum caudatum (Sacc.) Pk.
Colletotrichum graminicola (Ces.) Wilson
Coniochaeta leucoplaca (Berk. & Rav.) Cain
Coniothyrium sporulosum (W. Gams & Domsch) van der Aa
Coniothyrium sp.
Coprinus ephemeroides (Bull. ex Fr.) Fr.
Coprinus sp.
Corynespora cassiicola (Berk. & Curt.) Wei
Cunninghamella echinulata (Thaxt.) Thaxt.

Cunninghamella elegans Lendner
Curvularia inaequalis (Shear) Boedijn
Curvularia lunata (Wakker) Boedijn
Curvularia protuberata Nelson & Hodges
Curvularia tritici Kumar & Nema
Cylindrocarpon candidum (Link) Wollemw.
Cylindrocarpon destructans (Zins.) Scholten
Cylindrocarpon didymium (Hartig) Wollenw.
Cylindrocarpon ianthothele Wollenw.
Cylindrocarpon magnusianum Wollemw.
Cylindrocarpon sp.
Cylindrocladium parvum P. J. Anderson
Cylindrocladium scoparium Morgan
Dactylaria congregata de Hoog
Dactylaria obtriangularia Mats.
Dactylaria sp.
Dactylella asthenopaga Drechsler
Dactylella haptotyla (Drechsler) de Hoog & van Oorschot
Dematiaceous mycelium 1
Dematiaceous mycelium 2
Dematiaceous orange sclerotia
Dematiacious chlamydosporous sp.
Dematiacious rhizomorph sp.
Dematiacious stroma sp.
Dendryphion nanum (Nees. ex Gray) Hughes
Dictyosporium elegans Corda
Dictyosporium heptasporum (Garov.) Damon
Dictyosporium toruloides (Corda) Gueguen
Didymella sp.
Didymium squamulosum (Alb. & Schw.) Fr.
Dinemasporium strigosum (Pers. ex Fr.) Sacc.
Diplocladiella scalaroides Arnaud
Diplococcum spicatum Grove
Diplodia sp.
Diplodina microsperma (Johnston) Sutton
Diplorhinotrichum candidulum Hohn
Doratomyces microsporus (Sacc.) Morton & G. Sm.
Doratomyces nanus (Ehrenb. ex Link) Morton & G. Sm.
Doratomyces stemonitis (Pers. ex Steud.) Morton & G. Sm.
Drechslera avenae (Eidam) Scharif.
Drechslera biseptata (Sacc. & Roum.) Richardson & Fraser
Drechslera dematioidea (Bubak & Wroblewski) Subram & Jain
Drechslera erythrospila (Drechsler) Shoemaker
Drechslera fugax (Wallr.) Shoemaker
Drechslera poae (Baudys) Shoemaker
Drechslera ravenelii (Curt.) Subram. & Jain
Drechslera state of Cochliobolus spicifer Nelson
Dreshslera state of Cochliobolus sativus
Drechslera sp.

Echinobotryum atrum Corda
Emericellopsis mirabilis (Malan) Stolk.
Emericellopsis terricola van Beyma
Epicoccum purpurascens Ehrenb. ex Schlecht.
Eurotium herbariorum (Wiggers) Link
Fimetariella rabenhorstii (Niessl.) Lundq.
Flagellospora curvula Ingold
Fusariella bizzozeriana (Sacc.) Hughes
Fusarium acuminatum Ell. & Kellerm.
Fusarium avenaceum (Fr.) Sacc.
Fusarium equiseti (Corda) Sacc.
Fusarium graminearum Schwabe
Fusarium heterosporum Nees. ex Fr.
Fusarium lateritium Nees. ex Link
Fusarium merismoides Corda
Fusarium oxysporum Schlecht.
Fusarium poae (Peck) Wollenw.
Fusarium semitectum Berk. & Rav.
Fusarium solani (Mart.) Sacc.
Fusarium sporotrichioides Sherb.
Fusarium tricinctum (Corda) Sacc.
Fusidium griseum Link
Gabarnaudia fimicola Samson & W. Gams
Gelasinospora calospora (Mouton) C. & M. Moreau
Gelasinospora cerealis Dolwding
Geomyces pannorum (Link) Sigler & Carmichael
Geotrichum candidum Link ex Leman
Gibberella zeae (Schw.) Petch
Gigaspora calospora (Nicol. & Gerd.) Gerdemann & Trappe
Gigaspora gigantea (Nicol. & Gerd.) Gerdemann & Trappe
Gigaspora sp.
Gilmaniella humicola Barron
Gliocephalis hyalina Matruchot
Gliocladium roseum Bain
Gliocladium virens Miller, Giddens & Foster
Gliocladium viride Matr.
Gliomastix murorum var. felina (Marchae) Hughes
Glomus caledonicum (Nicol. & Gerd.) Gerdemlann & Trappe.
Glomus etunicatum Becker & Gerdemann
Glomus fasciculatum (Thaxter sensu Gerd.) Gerdemann & Trappe
Glomus geosporum Tul. & Tul.
Glomus intraradices Schenck & Smith
Glomus macrocarpum Tul. & Tul.
Glomus microcarpum Tul. & Tul.
Glomus monosporum Gerdemann & Trappe
Glomus mosseae (Nicol. & Gerd.) Gerdemann & Trappe
Glomus pallidum Hall
Glomus sp.
Gonatobotrys simplex Corda

Gongronella butleri (Lendner) Peyronel & Dal Vesco
Gonytrichum macrocladium (Sacc.) Hughes
Graphium putredinis (Corda) Hughes
Gymnoascus reessii Baran.
Gyrothrix verticillata Pirozynski
Hansfordia ovalispora Hughes
Harzia acremonioides (Harz.) Cost.
Helicomyces roseus Link
Helicomyces scandens Morgan
Helicosporium phragmites Hohn.
Helicosporium state of Tubeufia helicomyces Hohnel
Helotium cyathoideum (Bull.) Karst.
Hendersonia sp.
Heteroconium chaetospira (Grove) M. B. Ellis
Heteroconium tetracoilum (Corda) M. B. Ellis
Hormiactis alba Preuss.
Humicola fuscoatra Traaen
Humicola grisea Traaen
Hyaline mycelium 1
Hyaline mycelium 2
Hyalodendron lignicola Diddens
Hyalorhinocladiella sp.
Hypocrea citrina (Pers.) Fr.
Hypocrea gelatinosa (Tode ex Fr.) Fr.
Idriella lunata P. E. Nelson & Wilhelm
Jugulospora rotula (Cooke) Lundq.
Kickxella alabastrina Coemans
Libertella sp.
Licea variabilis Schrad.
Lophotrichus ampullus Benjamin
Macrophoma graminella (Sacc.) Berl. & Vogl.
Macrophoma sp.
Marriannaea elegans (Corda) Samson
Marssonina sp.
Melanconium sp.
Melanopsamma papilla (Schw.) Ell. & Ev.
Melanospora brevirostris (Fuckel) Hohnel
Melanospora caprina (Fr. ex Hornem.) Sacc.
Melanospora damnosa (Sacc. & Berl.) Lindau
Melanospora fallax Zukal
Melanospora fusipora (Petch) Doguet
Melanospora zamiae Corda
Metarrhizium anisopliae (Metschn.) Sorok.
Micronectriella agropyri Apinis & Chesters
Microsporum sp.
Mollisia sp.
Monacrosporium cionopagum (Drechsler) Subram.
Monacrosporium ellipsosporum (Grove) Cooke & Dickinson
Monacrosporium mammilatum (Dixon) Cooke & Dickinson

Monacrosporium parvicollis (Drechsler) Cooke & Dickinson
Monilia sp.
Monochaetia karstenii (Sacc. & Syd.) Sutton
Monocillium mucidum W. Gams
Monocillium sp.
Monodictys castanae (Wallr.) Hughes
Monodictys putredinis (Wallr.) Hughes
Mortierella alpina Peyronel
Mortierella claussenii Linnemann
Mortierella elongata Linnem.
Mortierella humilis Linnem.
Mortierella hyalina (Harz) W. Gams
Mortierella parvispora Linnem.
Mortierella ramanniana (Moller) Linnem.
Mortierella vinacea Dixon-Stewart
Mortierella sp.
Mucor circinelloides van Tiegh.
Mucor hiemalis Wehmer
Mucor mucedo Mich. ex St-Am.
Mucor plumbeus Bonord.
Mucor racemosus Fr.
Murogenella terrophila Goos & Morris
Mycocentrospora acerina (Hartig) Deighton
Mycogone sp.
Myrothecium cinctum (Corda) Sacc.
Myrothecium gramineum Libert
Myrothecium leucotrichum (Peck) Tulloch
Myrothecium roridum Tode ex Steudel
Myrothecium verrucaria (Alb. & Schw.) Ditm. ex Steudel
Myxomycete sp.
Nais inornata Kohlm.
Nectria arenula (Berk. & Br.) Berk.
Nectria mammoidea Phil. & Plowr.
Nectria veuillotiana Roum. & Sacc.
Neocosmospora parva Mahoney
Nigrospora sphaerica (Sacc.) Mason
Ochroconis constricta (Abbott) de Hoog & v. Arx
Ochroconis humicola (Barron & Busch) de Hoog & v. Arx
Oidiodendron griseum Robak.
Ophiobolus erythrosporus (Riess.) Winter
Orbilia chrysocoma (Bull.) Sacc.
Orbilia curvatispora Boudier
Paecilomyces carneus (Duche & Heim)
Paecilomyces farinosus (Holm ex S. F. Gray) Brown & Smith
Paecilomyces fumosoroseus (Wize) Brown & Smith
Paecilomyces lilacinus (Thom) Samson
Paecilomyces marquandii (Massee) Hughes
Paecilomyces variotii Bainier
Papulaspora immersa Hotson

Papulaspora sp.
Penicillium brevi-compactum Dierckx.
Penicillium canescens Sopp
Penicillium chrysogenum Thom
Penicillium citrinum Thom
Penicillium expansum Link ex Gray
Penicillium frequentans Westling
Penicillium funiculosum Thom
Penicillium granulatum Bain.
Penicillium griseofulvum Dierckx.
Penicillium herquei Bain. & Sartory
Penicillium islandicum
Penicillium janthinellum Biourge
Penicillium jensenii Zaleski
Penicillium miczynskii Zaleski
Penicillium nigricans Bain. ex Thom
Penicillium ochrochloron Biourge
Penicillium oxalicum Currie & Thom
Penicillium purpurogenum Stoll.
Penicillium raistrickii G. Smith
Penicillium restrictum Gilman & Abbott
Penicillium rugulosum Thom
Penicillium sclerotiorum van Beyma
Penicillium simplicissimum (Oudem.) Thom
Penicillium spinulosum Thom
Penicillium variabile Sopp.
Penicillium verrucosum Dierckx.
Penicillium waksmanii Zaleski
Penicillium sp.
Perichaena depressa Libert
Periconia atra Corda
Periconia digitata (Cooke) Sacc.
Periconia igniaria Mason & M. B. Ellis
Periconia macrospinosa Lefebvre & A. G. Johnson
Periconia minutissima Corda
Persiciospora moreaui P. Cannon & D. Hawksw.
Petriella setifera (Schm.) Curzi.
Phaeoseptoria urvilleana (Speg.) Sprague
Phialocephala bactrospora Kendrick
Phialocephala fusca Kendrick
Phialocephala humicola Jong & Davis
Phialophora sp.
Phoma herbarum Westend.
Phoma leveillei Boerema & Bollen
Phoma medicaginis Malbr. & Roum.
Phoma sp.
Phomatospora berkeleyi Sacc.
Physarum nutans Pers.
Physarum pusillum (Berk. & Curt.) G. Lister

Physarum sp.
Pilobolus sp.
Piptocephalis cruciata van Tiegham
Piptocephalis freseniana De Bary
Piptocephalis lepidula (Marchal) Benjamin
Piptocephalis xenophila Dobbs & English
Piptocephalis sp.
Pirobasidium sarcoides Hohn.
Pithomyces chartarum (Berk. & Curt.) M. B. Ellis
Pleurophragmium simplex (Berk. & Br.) Hughes
Pleurophragmium tritici M. B. Ellis
Podospora anserina (Ces. in Rabenh.) Niessl.
Podospora araneosa (Cain) Cain
Podospora collapsa (Griff.) Cain
Podospora curvicolla (Wint.) Niessl.
Podospora dakotensis (Griff.) Mirza & Cain
Podospora decipiens (Wint. ex Fuck.) Niessl.
Podospora fimicola Ces.
Podospora glutinans (Cain) Cain
Podospora inaequalis (Cain) Cain
Podospora myriaspora (Cr. & Cr.) Niessl.
Podospora nannopodalis Cain
Podospora pauciseta (Ces.) Trav.
Podospora perplexens (Cain) Cain
Podospora setosa (Wint.) Niessl.
Podospora tarvisina (Sacc.) Mizra & Cain
Podospora tetraspora (Win.ter) Cain
Podospora unicaudata (C. Moreau & M. Moreau ex Smith) Cain
Podospora sp.
Polyscytalum berkeleyi M. B. Ellis
Preussia typharum (Sacc.) Cain
Pseudeurotium indicum Chattopadhyay & Das Gupta
Pseudeurotium multisporum (Saito & Minoura) Stolk
Pseudeurotium zonatum van Beyma
Pseudobotrytis terrestris (Timonin) Subramanian
Pseudogymnoascus roseus Raillo
Pseudohansfordia sp.
Pseudorobillarda agrostis (Sprag.) Nag Raj, Morg-Jon. & Kendrick
Pseudoseptoria donacii (Pass.) Sutton
Pseudospiropes rousselianus (Mont.) M. B. Ellis
Pseudospiropes subuliferus (Corda) M. B. Ellis
Pyrenochaeta sp.
Pyricularia grisea Sacc.
Ramichloridium schulzeri (Sacc.) de Hoog
Ramulispora andropogonis Miura
Rhizoctonia sp.
Rhizopus stolonifer (Ehrenb. ex Link) Lind.
Rhopalomyces elegans Corda
Rhynchosporium sp.

Saccobolus globuliferellus Seaver
Sartorya fumigata Vuillemin
Sclerocystis rubiformis Gardemann & Trappe
Sclerostagonospora heraclei (Sacc.) Hohn.
Scopinella solani (Zukal) Malloch
Scopinella sp.
Scytalidium liginicola Pesante
Selenophoma everhartii (Sacc. & Syd.) Sprague & Johnson
Selenosporella curvispora MacGarvie
Septocyta ruborum (Lib.) Petrak
Septoria sp.
Sigmoidea prolifera (Petersen) Crane
Solosympodiella clavata Matsushima
Sordaria fimicola (Rob.) Ces. & DeNot.
Sordaria macrospora Awd in Rab.
Spadicoides obovata (Cooke & Ellis) Hughes
Sphaerodes compressa (Udagawa & Cain) P. Cannon & D. Hawksw.
Sphaerodes fimicola (Hansen) P. Cannon & D. Hawksw.
Sphaerodes retispora (Udagawa & Cain) P. Cannon & D. Hawksw.
Sphaeropsis sp.
Spinalia tenuis (Thaxter) Zycha
Sporidesmium ehrenbergii M. B. Ellis
Sporidesmium filiferum Pirozynski
Sporidesmium parvum (Hughes) M. B. Ellis
Sporochisma mirabile Berk. & Br.
Sporodesmiella hyalinum var. novae zelandiae (Hughes) Kirk
Sporormiella bipartis (Cain) Ahmed & Cain
Sporormiella dubia Ahmed & Cain
Sporormiella lageniformis (Fuckel) Ahmed & Cain
Sporormiella leporina (Niessl.) Ahmed & Cain
Sporormiella megalospora (Auersw.) Ahmed & Cain
Sporormiella minima (Auersw.) Ahmed & Cain
Sporothrix schenckii Hektoen & Perkins
Stachybotrys chartarum (Ehrenb. ex Link) Hughes
Stachybotrys cylindrospora C. W. Jensen
Stachybotrus dichroa Grove
Stachybotrys elegans (Pidopl.) W. Gams
Stagonospora caricis (Oud.) Sacc.
Stagonospora vitensis Unam.
Stagonospora sp.
Staphylotrichum coccosporum J. Meyer & Nicot.
Stauronema cruciferum (Ell.) H. & P. Syd & Butler
Stemphylium botryosum Wallr.
Stenocarpella maydis (Berk.) Sutton
Stephanosporum cereale (Thum) Swart.
Stilbum sp.
Stylopage grandis Duddington
Syncephalastrum racemosum Cohn ex Schrot
Syncephalis cornu van Tiegham & Le Monnier

Syncephalis drechsleri Mehrota & Prasad
Syncephalis furcata van Tiegham
Syncephalis nodosa van Tiegham
Syncephalis plumigaleata Embree
Syncephalis pycnosperma Thaxter
Syncephalis sphaerica van Tiegham
Syncephalis truncata Boedijn.
Syspatospora parasitica (Tul.) P. Cannon & D. Hawksw.
Talaromyces flavus (Klocker) Stolk & Samson
Talaromyces stipitatus (Thom) C. R. Benjamin
Tetraploa aristata Berk. & Br.
Tetraploa ellisii Cooke
Thielavia basicola Zopf
Thielavia minuta (Cain) Malloch & Cain
Thielavia octospora (Natarajan) v. Arx
Thielavia terricola (Gillman & Abbott) Emmons
Thielavia tetraspora (Lodhi & Mirza) v. Arx
Thielavia sp.
Torula herbarum Pers. ex Gray
Torulomyces lagena Delitsch
Tricellula aquatica Webster
Trichocladium opacum (Corda) Hughes
Trichoderma hamatum (Bonard.) Bain.
Trichoderma harzianum Rifai
Trichoderma koningii Oudem.
Trichoderma polysporum (Link ex Pers.) Rifai
Trichophaea abundans (Karsten) Boudier
Trichophyton terrestre Durie & D. Trey
Trichurus spiralis Hasselbr.
Trichurus terrophilus Swift & Povah.
Triposporina aphanopaga Drechsler
Ulocladium atrum Preuss.
Ulocladium botrytis Preuss.
Veronaea coprophila (Subram. & Lodha) M. B. Ellis
Verticillium catenulatum (Kamyschko ex Barron & Onions) W. G.
Verticillium chlamydosporium Goddard
Verticillium psalliotae Treschow
Verticillium sp.
Verticimonosporium diffractum Matsushima
Volutella ciliata Alb. & Schw.
Volutella minima Hohn.
Zopfia rhizophila Rabenhorst.
Zopfiella latipes (Lundvquist) Malloch & Cain
Zopfiella leucotricha (Speg.) Malloch & Cain
Zygorhynchus heterogamus (Vuill.) Vuill.
Zygorhynchus moelleri Vuill.
Zythiostroma sp.