THE OCCURRENCE OF MYCORRHIZAS IN PRAIRIES: APPLICATION TO ECOLOGICAL RESTORATION

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Abstract. This paper aims to summarize data on the mycorrhizal status of prairie species, provide a general knowledge of mycorrhizal fungi, and discuss the relevance and potential role of mycorrhizal fungi in ecological restoration of grasslands. Mycorrhizal associations were documented both from a field survey of prairie species and from published studies reporting the mycorrhizal status of prairie species. Only those published studies examining more than three samples of a species are reported. Plants, including members of the Poaceae, Asteraceae, Fabaceae, Plantagonaceae, Scrophulariaceae, Asclepiadaceae, Onagraceae, Malvaceae, Commelinaceae, and Cactaceae, were collected in Illinois, Kansas or Oklahoma. Of the 109 species (25 families) surveyed or reported in literature, 96% were mycorrhizal and all formed exclusively arbuscular mycorrhizal associations. No family therefore was consistently non-mycorrhizal. The role that mycorrhizas play in reclamation, restoration, and structuring of plant communities and soil, and maintaining and promoting of plant species diversity, is believed to be important. Factors which directly or indirectly determine the occurrence of mycorrhizal propagules, for example, agricultural practices, disturbances and the presence or absence of mycotrophic and non-mycotrophic species, are potentially important in subsequent plant establishment. Restoration projects should take into account soil abiotic and biotic changes, especially those associated with mycorrhizal fungi, which can influence plant population response, competition, and ultimately successional trajectories. Given the high occurrence of mycorrhizas in prairies, it is clear that mycorrhizal fungi may play an important role in these communities, and warrant detailed study and incorporation into the practice of ecological restoration.

INTRODUCTION

Mycorrhizal infections or mycorrhizas represent one example of a plant-fungal association found under a range of abiotic conditions and habitats (for recent in depth reviews on mycorrhizal fungi see Safir 1987, Allen 1991, Brundrett 1991, Allen 1992). Specifically a mycorrhiza involves a symbiotic association of a host plant root and its associated fungus. Mycorrhizal fungi are believed to be important to plants in all ecosystems, however, restoration and management practices of prairies have, in general, not been concerned about their potential role in the establishment and maintenance of plant species or soil structure. Restoration efforts, however, have provided significant insights into the functional role of mycorrhizas, such as the role these fungi play in increasing soil aggregation (Miller 1987). The lack of interest in mycorrhizal fungi is partly the result of several factors including the inconspicuous nature of soil biota and below-ground processes, the scarcity of scientific studies addressing questions directly related to mycorrhizae, the absence of detailed studies on many prairie plants, and the difficulty in working with mycorrhizas (Miller 1987, Allen 1991). This paper aims to summarize data on the mycorrhizal status of prairie species, provide a general knowledge of mycorrhizal fungi, and discuss the relevance and potential role of mycorrhizal fungi in ecological restoration of grasslands.

Mycorrhizal fungi belong to the Basidiomycetes, Zygomycetes or Ascomycetes classes of fungi, and are divided into four groups according to the external and the internal morphology of the root-fungus association. The first group, arbuscular mycorrhizal (AM) fungi (previously called vesicular-arbuscular mycorrhizal, VAM, fungi), penetrate the root forming specialized structures. These are associated mostly with herbaceous and some woody species. The second group, Ectomycorrhizae (ECM), form dense hyphal networks, called Hartig nets, outside the roots and are associated almost entirely with woody species. The third group, the Ericaceous group, form both external and internal hyphal structures associated with roots, and are associated with members of the Ericaceae. The fourth group, Orchidaceous fungi, form structures internal to the root and are generally seed-borne. These are associated with members of the Orchidaceae family. The arbuscular mycorrhizal type, the most common mycorrhizal fungi associated with herbaceous plants, will be the focus of this paper.

Arbuscular Mycorrhizal (AM) Fungi

Arbuscular mycorrhizal (AM) fungi are presumably found associated with most of the world's herbaceous species (Newman and Reddell 1987). For example, eighty-nine percent of 61 plant families surveyed in arid and semi-arid regions world-wide were found to be mycorrhizal, with 84% of these families forming exclusively AM fungal associations (Dhillion and Zak 1993). Typically non-mycorrhizal taxa include Crucifereae, Zygophylaceae, Cactaceae, Chenopodiaceae, Cyperaceae, and Junaceae, although some species belonging to these families appear on occasion to be infected by mycorrhizal fungi under certain conditions (Newman and Reddell 1987, Safir 1987). At present, only a few studies have attempted to estimate the occurrence of mycorrhizas among prairie plants (e.g. Wetta 1972, Dickman et al. 1984, Medve 1984, Zajicek et al. 1986). To document the presence of mycorrhizas in prairie plants, we surveyed published records and examined several species in Illinois, Kansas and Oklahoma.

Nearly 160 species of AM fungi within six genera are currently recognized (Schenck and Perez 1990). Mycorrhizas are highly evolved, symbiotic associations between AM fungi and plant roots. AM fungal hyphae penetrate the root epidermis and exist as specialized structures (arbuscules, pelotons, vesicles and inter- and intracellular hyphae) in the root cortex. Arbuscules are dichotomous, highly branched structures which presumably are the sites of exchange between the host and the fungus. In mutualistic associations, the host plant receives inorganic nutrients and water in exchange for carbohydrates. The host plant is generally considered the sole source of carbohydrates for the fungus. External to the root, the fungus forms hyphae and reproductive bodies called chlamydospores or azygospores, which may rarely form in the root cortex as well. AM fungi are currently best identified at the species level by their characteristic spores. The fungal hyphae extend beyond the root hair zone and exploit nutrient rich regions and thus bridge regions near the root that are relatively deficient in immobile nutrients to more nutrient-rich regions not otherwise available to the plant. Mycorrhizal hyphae, like fine roots and root hairs, have important characteristics for the uptake of nutrients such as absorbing power for ions in solution, abundance and distribution, and an effective radius. The fungi thus function as a supplemental root system for the plant and increase the volume of soil that would normally be available for nutrient extraction to the plant (Jackson and Caldwell 1989, Friese and Allen 1991a). The beneficial effects of mycorrhizae are often associated with low availability of inorganic nutrients, especially phosphorus and nitrogen. The mycorrhizal hyphal network when well ramified through the soil could be important in competing with other organisms, including non-mycorrhizal roots, for nutrients and moisture (Harley and Smith 1983). Mycorrhizal hyphal bridges can also link the circulatory system of plants of similar and different species and, therefore, may influence succession and community dynamics (Newman 1988, Friese 1991, Friese and Allen 1991a). The number of species studied is small and the ecological significance unknown, but mycorrhizal links have been reported between annuals, herbaceous perennials, and tree species as well as between different taxonomic groups (Newman 1988, Brundrett 1991, Friese and Allen 1991a). The role that mycorrhizas play in structuring plant communities is thought to be important because it operates through processes such as plant competition, phenology and interspecific nutrient transport through hyphal links both intra- and inter-specifically (Allen and Allen 1984, Newman 1988, Allen and Allen 1990, Gange et al. 1990, Brundrett 1991).

Plant Responses to AM Fungal Infection

Growth responses of temperate plants, especially grasses, to mycorrhizal infection are varied, ranging from mutualistic to parasitic (e.g. Hetrick et al. 1988, Allen et al. 1989, Anderson and Liberta 1989). In general, plants benefiting from the mycorrhizal association have greater tolerance to drought stress and higher photosynthetic rates, biomass production and inorganic nutrient uptake than non-mycorrhizal plants of the same or other species. The type of response observed in mycorrhizal plants can depend on one or several factors, including available soil moisture, inorganic nutrient availability, substrate pH, type of AM fungal species, type of host plant root system, plant host species, age of host plant, time of year, irradiance and soil associated microorganisms (e.g. Harley and Smith 1983, Fitter 1985, Anderson and Liberta 1992, Dhillion 1992a, Dhillion 1992b). Although increased biomass production has very often been used as an indicator of the nature of AM symbiosis, it is not always the best measure of the degree of host responsiveness or dependency on mycorrhizae, since physiological dependency on AM has been suggested, at least for some grasses (Allen and Allen 1986). The plants that appear to benefit from AM are those that have a rather coarse root morphology, produce few root hairs and occur in low nutrient habitats (Baylis 1976, Anderson and Liberta 1987). Baylis (1976) and Fitter (1991), for example, suggested that grasses that can persist without AM (non-mycorrhizal or facultative) generally have a well developed, fine, and highly branched topology.

Many studies on effects of mycorrhizas on plants have been done in controlled environments (green houses and growth chambers) and on crop plants. Growth habit and physiology of crop plants, however, are quite different from those of native or wild plants (Grime 1979, Chapin 1980), and most likely mycorrhizal fungi effect these plants differentially. Therefore, it is important to use care in drawing parallels between crop plants and native plants. To date little work has been conducted on non-crop forbs.

Ecological specificity

In field studies several plant species have been shown to exhibit host-endophyte preference or 'ecological specificity' when associated with indigenous mycorrhizae. The degree of plant-AM preference, measured as infection and sporulation levels and/or fungal morphology, has been related to plant dependence on native AM species (Giovannetti and Hepper 1985, Henkel et al. 1989, McGonigle and Fitter 1990, Dhillion 1992a, Dhillion 1992b, Sanders and Fitter 1992). For example, when little bluestem (*Schizachyrium scoparium*), prairie dropseed (*Sporobolus heterolepis*) and big bluestem (*Andropogon gerardii*) grasses were inoculated with each of three AM species, each formed mycorrhizas with all three AM fungal species. However, based on infection and sporulation levels there was apparently greater preference for different AM species by each plant (Dhillion 1992a, Dhillion unpublished data). These results suggest that although, mycorrhizal fungi are nonspecific in their selection of host species, it is possible that, a host exposed to a mixed selection of AM fungi could be preferentially infected by one or more of the endophytes. This specificity may affect the success of using non-native seed in restoration efforts. In a recent study, little bluestem plants from Kansas when grown in soil from Illinois experienced growth depression (Anderson and Roberts 1993). Anderson and Roberts (1993) attributed the lack of a positive mycorrhizal response for little bluestem to the lack of compatibility between Illinois sand prairie AM fungal endophytes and plants grown from Kansas seed source. The successful establishment of native seedlings thus may be determined by the presence of appropriate native mycorrhizal fungal species and *vice versa*.

Plant and Mycorrhizal Reponses

Fire

Grassland fires can directly affect the abundance of soil surface microflora (e.g. Wicklow 1975, Kapustka and Rice 1976). For mycorrhizae, however, recent studies on little bluestem grass (*Schizachyrium scoparium*) in Illinois sand prairies have shown that mycorrhizal dynamics, as well as soil microbial populations and saprophytic fungi may, in fact, be indirectly affected more by the host plant's response to fire than directly by fire (Dhillion et al. 1988, Dhillion and Anderson 1989, Dhillion and Anderson 1993a, Dhillion and Anderson 1993b, Dhillion and Anderson 1993c).

Biocides

Many management practices utilize biocides to control weeds, pests and pathogens. Although specific results differ, in conjunction with high application rates of fungicides and herbicides, both adversely affect mycorrhizal survival and function. Fungicides grouped either as substituted aromatic hydrocarbons used to control pathogens like *Alternaria* spp., *Fusarium* spp., *Rhizoctonia* spp., *Phythium* spp, [e.g., botran, lanstan and quintozene (PCNB)], or as benzimidazole fungicides such as benomyl thiophanatate, carbendazim, thiophanatate, all used as seed treatments, soil drenches, and foliage sprays, both inhibit AM fungi (Nemec 1980, Habte et al. 1990). In contrast, two anti-oomycete fungicides, fosetyl and metalaxyl, when applied at low levels are frequently known to stimulate AM colonization (Afex et al. 1991, Hetrick and Wilson 1991).

Fertilizers

Numerous studies suggest that different AM fungi may each be adapted to a specific fertility level suggesting that increased fertilization may be more deleterious to AM fungi indigenous to infertile soils than to AM fungi indigenous to fertile soils (Hayman 1982, Dehne 1987, Johnson and Pfleger 1992). Therefore, runoff from agricultural fields that reaches a prairie may have a detrimental effect on mycorrhizal infection or spore production although it may provide nutrients for prairie species.

Grazing

Both grazers and mycorrhizal fungi depend on plants for energy thus an interaction seems likely. The response of mycorrhizal plants to grazing by vertebrates and invertebrates vary from no response to stimulation in both growth and physiological conditions. Generally plants respond to moderate grazing by increasing biomass allocation to growth below the grazing zone, particularly enhanced tillerage and root growth, and to altered growth habit (Miller 1987). Heavy grazing by ungulates, however, reduced mycorrhizal activity (Bethlenfalvay et al. 1985, Wallace 1987) and altered species composition in rangeland (Bethlenfalvay et al. 1985). Alternatively, grazing increased AM fungal colonization in shortgrass prairie (Davidson and Christensen 1977) and in savanna (Wallace 1981). In addition to indirect responses to surface grazers, mycorrhizal fungi are directly affected by soil grazes. Invertebrates (e.g. amoeba, nematodes, mites, collembola and earthworms; see review by Fitter and Sanders in Allen 1992) are heavy grazers on mycorrhizal fungal hyphae. Despite the contradictions in responses to grazers, animals serve as important agents in the dispersal and migration (soil enrichment) of mycorrhizal fungi (Allen 1991, Dhillion et al. 1994, McGinley et al. 1994).

Drought

Mycorrhizal fungi can cause changes in plant water relations and can, in many cases, improve drought resistance or tolerance. Most host changes related to water relations are likely to be secondary responses due to improved nutrition. For an excellent in-depth review on drought and mycorrhizas see Safir (1987).

Soil Structure

The presence of AM hyphae can improve soil conditions. In studies of a chronosequence of restored prairie at Fermi National Laboratories, Chicago, soil aggregation was shown to be related to the presence of AM hyphae associated with roots of prairie plants (Miller and Jastrow 1990). Physical entanglement by roots and the hyphae of mycorrhizal fungi is considered to be a major mechanism in the binding of microaggregates into macroaggregates, thereby bringing about the recovery of the crumb structure of degraded agricultural soils (Miller and Jastrow 1986, Miller 1987, Miller and Jastrow 1990, Miller and Jastrow 1992). Miller and Jastrow (1990) have hypothesized that changes in the proportions of aggregates of various sizes and the amount of water-stable aggregates could be used as an index of disturbance, or recovery, in the restoration process.

Disturbance and Species Interactions

Plant communities are dynamic assemblages of species, in which all species should be viewed as potential invaders and colonists (e.g. Grubb 1977, Grime 1979, Pickett and White 1985, Gross 1987). Periodic or occasional disturbances and the type of disturbance, both large and small scale, can remove some species and allow others to become established for a certain time. In grassland and other communities, animal mounds can become sites of enhanced plant establishment because of both improved nutrient status and the presence of beneficial mycorrhizal fungi capable of initiating a mutualistic association with the invading plants (e.g. Allen, M. 1988, Dhillion et al. 1994, McGinley et al. 1994). Thus mycorrhizal plants, associated with animal disturbances, may have a better chance of establishment than nearby non-mycorrhizal individuals. Disturbance can also effect the species composition of the mycorrhizal fungus community, which can result in shifting of dominant fungal species and thereby changing host response and composition (Miller 1979). Understanding how communities develop following a small or large scale disturbance is fundamental to developing an understanding of the maintenance and restoration of diversity in plant communities (Grubb 1977, Mooney and Gordon 1983, Gross 1987, Allen E. 1988, Dhillion et al. 1994).

METHODS AND MATERIALS

Plants surveyed for this study were collected from Illinois, Kansas or Oklahoma (Table 1). Five to ten individual plants of each species were examined. Feeder roots (generally 2 mm diameter) were used for mycorrhizal evaluation. When roots could not be processed immediately they were fixed in formalin-acetic acid-alcohol (FAA; 10:35:10:5 formalin-water-ethanol-acetic acid) as soon as possible after excavation. Roots fixed in FAA were washed at least three times prior to placement for clearing in a glass vial with 10% KOH and left for about 5 days at room temperature. [Roots may be directly put in KOH if staining is to be done fairly soon, thus eliminating the FAA step. However this step can be hastened by heating root in the vial at 90°C in a water bath between 15 - 25 mins.] Cleared roots were rinsed three times with water and acidified with 1% HCl. The roots are left in 1% HCl for at least 5 mins. The HCl was decanted off and 0.5 % trypan blue stain in lactoglycerol (lactic acid:glycerol:water; 1:1:1) added to cover the roots. The roots were left in the stain for about 5 days or heated in a water bath at 90°C for about 15-30 mins. The trypan-blue-lactoglycerol solution was decanted and lactoglycerol solution added (without stain). This destaining removed excess stain, and preserved roots for up to a year. Prairie herbaceous species do not contain much lignin and thus do not require any drastic clearing processes. However, if such a requirement should arise, consult Schenck (1982) and Norris et al. (1992).

The staining procedure removes the cellular contents of the roots leaving fungal structures which appear blue when viewed under the microscope. Root fungi other than AM fungi were also stained by this process. The presence of structures characteristic of AM fungi (arbuscules, pelotons, vesicles, and coenocytic hyphae) were used to separate from other root endophytes. Percent AM colonization (% infection) was estimated using the gridline intersection method (Giovannetti and Mosse 1980).

In addition to collections made for this study, data used include those from published studies reporting on the mycorrhizal status of plant species. Only those published studies which examined at least three individuals of a species are reported in this study.

RESULTS AND DISCUSSION

Mycorrhizal Status of Prairie Plants

Like plants in other communities (Moore 1987, Dhillion and Zak 1993), prairies also consist of a large number of mycorrhizal species. Of the 109 species (25 families) surveyed in this study or reported in literature, 96% were mycorrhizal and all formed exclusively AM associations (Table 1). It should be noted that in members of families considered to be non-mycorrhizal, mycorrhizas were seen, on occasion, to form although infection levels were very low (ranging from 1-5%). No family therefore was consistently non-mycorrhizal. In this study, dominant prairies grasses, such as big bluestem, little bluestem, and Indian grass (*Sorghastrum nutans*), were found to be highly mycorrhizal. Generally plants which tend to form coarse or tap roots [e.g. rigid goldenrod (*Solidago rigida*), bull thistle (*Cirsium vulgare*), Jerusalem artichoke (*Helianthus tuberosus*), Indian grass, big bluestem] also were highly mycorrhizal. In contrast,very fine rooted plants [e.g. hairy aster (*Aster pilosus*), daisy fleabane (*Erigeron annuus*), three-awned grass (*Aristida oligantha*), grama grasses (*Bouteloua* spp.), large fescue (*Festuca arundinacea*), and foxtails (*Setaria* spp.)] had low levels of infection. These fine rooted plants may be better able to exploit soil resources then coarse rooted ones, and thereby not require a

Table 1. Mycorrhizal status and infection levels of prairie species of North America. Infection levels (% I) may be low (L, <15 %), moderate (M, 15-40 %),high (H, >40 %)[1] or absent (N).

FAMILY AND SPECIES	COMMON NAME	HABITAT	% I
APOCYNACEAE			
Apocynum cannabinum	Dogbane	oldfield	M
ASCLEPIADACEAE			
Asclepias syriaca	Prairie Milkweed	oldfield	L
Asclepias tuberosa	Green Milkweed	sand prarie, forest	M
Asclepias viridiflora	Butterfly weed	sand prairie	M
ASTERACEAE			
Ambrosia artemisiifolia	Common Ragweed	sand prairie	M
Ambrosia trifida	Giant Ragweed	sand prairie	M
Antennaria neglecta	Pussy toes	sand prairie	M
Artemisia ludoviciana	Western Mugwort	sand prairie	H
Aster drummondii	Drummond Aster	mesic prairie	M
Aster ericoides	Heath Aster	mesic prairie	M
Aster novae-angliae	New England Aster	mesic prairie	M
Aster pilosus	Hairy Aster	mesic prairie	L
Chrysanthenum leucanthemum	Ox-eye Daisy	roadside	L
Cirsium arvense	Canada Thistle	oldfield	M
Cirsium discolor	Field Thistle	oldfield	M
Cirsium undulatum	Wavyleaf Thistle	oldfield	L
Cirsium vulgare	Bull Thistle	roadside	M
Conyza canadensis	Horseweed, Muleweed	sand prairie	L
Erigeron annuus	Daisy Fleabane	mesic prairie	L
Erigeron philadelphicus	Philadelphia Fleabane	oldfield	L
Eupatorium perfoliatum	Common Boneset	oldfield	M
Helianthus annuus	Common Sunflower	roadside	H
Helianthus grosseserratus	Sawtooth Sunflower	roadside	H
Helianthus mollis	Downy Sunflower	oldfield	M
Helianthus rigidus	Prairie Sunflower	mesic prairie	M
Helianthus sempervirens		mesic prairie	H
Helianthus tuberosus	Jerusalem Artichoke	oldfield	H
Hieracium pratense	King of Devils	roadside	L
Lactuca biennis	Tall Blue Lettuce	oldfield	M
Liatris spicata	Dense Blazing Star	prairie	H
Rudbeckia hirta	Blackeyed Susan	sand prairie	M
Silphium integrifolium	Rosinweed	roadside	H
Silphium laciniatum	Compass Plant	oldfield	H
Silphium perfoliatum	Cup Plant	roadside	M
Silphium terebinthinaceum	Prairie Dock	roadside	H
Solidago altissima	Tall Goldenrod	oldfield	L
Solidago canadensis	Canada Goldenrod	oldfield	L
Solidago graminifolia	Grass-leaved Goldenrod	oldfield	N
Solidago juncea	Early Goldenrod	sand prairie	L
Solidago rigida	Rigid Goldenrod	mesic prairie	H
Solidago speciosa	Showy Goldenrod	mesic prairie	H
Sonchus asper	Spiny Sow Thistle	mesic prairie	L
Taraxacum officinale	Common Dandelion	oldfield	M

Table 1, continued.

FAMILY AND SPECIES	COMMON NAME	HABITAT	% I
Tussilago farfara	Coltsfoot	oldfield	M
Vernonia fasciculata	Ironweed	dry-mesic	M
CACTACEAE			
Opuntia humifusa	Prickly-pear Cactus	sand prairie	M
CHENOPODIACEAE			
Chenopodium album	Lamb's Quarters	roadside	L
COMMELINACEAE			
Tradescantia ohioensis	Spiderwort	mesic prairie	L
Tradescantia virginiana	Spiderwort	sand, mesic prairie	M
CORNACEAE			
Cornus racemosa	Gray Dogwood	oldfield	L
EUPHORBIACEAE			
Acalypha rhomboidea	Three-seeded Mercury	mesic prairie	M
FABACEAE			
Baptisia lactea	White Wild Indigo	dry-mesic prairie	H
Cassia fasciculata	Partridge Pea	mesic prairie	H
Lathyrus palustus	Marsh Vetching	mesic prairie	M
Tephrosia virginiana	Goat's Rue	sand prairie	M
Trifolium pratense	Red Clover	mesic prairie	L
Trifolium repens	White Clover	mesic prairie	L
LABIATAE			
Lycopus uniflorus	Northern Bugle Weed	mesic prairie	M
Prunella vulgaris	Self-heal	mesic prairie	M
LOBELIACEAE			
Lobelia inflata	Indian Tobacco	mesic prairie	M
OENOTHERACEAE			
Oenothera biennis	Evening Primrose	mesic prairie, roadside	M
OXALIDACEAE			
Oxalis stricta	Yellow Wood Sorrel	mesic prairie	M
PLANTAGINACEAE			
Plantago lanceolata	Buckhorn	mesic prairie	H
Plantago major	Common Plantain	mesic prairie	H
Plantago rugelii	Rugel's Plantain	mesic prairie	H
POACEAE			
Agropyron repens	Quack Grass	oldfield	N
Andropogon gerardii	Big Bluestem	mesic prairie	H
Aristida purpurascens	Purple Triple-awned	sand prairie	L
Aristida oligantha	Three-awned	sand prairie	L
Bouteloua curtipendula	Side-oats Grama	sand prairie	M
Bouteloua dactyloides	Buffalo Grass	dry prairie	L
Bouteloua gracilis	Blue Grama	dry prairie	L

Table 1, continued.

FAMILY AND SPECIES	COMMON NAME	HABITAT	% I
Bouteloua hirsuta	Hairy Grama	dry-mesic prairie	M
Bromus inernis	Awnless Brome	oldfield	N
Digitaria sanguinalis	Crab Grass	mesic prairie	L
Elymus canadensis	Nodding Rye	mesic prairie	M
Elymus cinerus		mesic prarie	H
Eragrostis spectabilis	Tumble Grass	sand prairie	H
Eragrostis trichodes	Sand love Grass	sand prairie	H
Festuca arundinacea	Large Fescue	oldfield	L
Koeleria pyramidata		oldfield	L
Lolium perenne	English Rye Grass	mesic prairie	L
Panicum capillare	Witch Grass	sand prairie	M
Panicum lanuginosum		sand prairie	M
Panicum virgatum	Switch Grass	sand prairie	L
Paspalum stramineum	Sand Paspalum	sand prairie	M
Phleum pratense	Timothy	mesic prairie	L
Poa pratensis	Kentucky Bluegrass	prairie	L
Schizachyrium scoparium	Little Bluestem	sand,mesic prairie	H
Setaria geniculata	Perennial Foxtail	mesic prairie	M
Setaria glauca	Yellow Foxtail	mesic prairie	L
Setaria faberii	Giant Foxtail	oldfield	M
Setaria lutescens	Yellow Foxtail	oldfield	L
Sorghastrum nutans	Indian Grass	mesic prairie	H
Spartina pectinata	Prairie Cordgrass	mesic prairie	H
Sporobolus heterolepis	Prairie Dropseed	mesic prairie	H
Stipa spartea	Porcupine Needlegrass	prairie	L
POLEMONIACEAE			
Phlox pilosa	Downy Phlox	prairie, oldfield	M
POLYGALACEAE			
Polygala senega	Senega Snakeroot	dry-mesic prairie	
Polygala verticillata	Whorled Milkwort	dry prairie	L
POLYGONACEAE			
Polygonum persicaria	Lady's Thumb	mesic prairie	N
Rumex acetosella	Sour Dock	mesic prairie	N
POLYPODIACEAE			
Onoclea sensibilis	Sensitive Fern	mesic prairie	L
MALVACEAE			
Abutilon theophrastii	Velvet Leaf	mesic prairie	M
ROSACEAE			
Potentilla simplex	Common Cinquefoil	mesic prairie	M
Prunus serotina	Wild Black Cherry	oldfield	M
Rubus allegheniensis	Common Blackberry	oldfield	M
Rubus hispidus	Swampy Dewberry	oldfield	M

Table 1, continued.

FAMILY AND SPECIES	COMMON NAME	HABITAT	% I
SCROPHULARIACEAE			
Linaria vulgaris	Butter-and-eggs	mesic prairie	L
Verbascum thapsus	Common Mullien	mesic prairie,roadside	M
SOLANACEAE			
Physalis heterophylla	Ground Cherry	mesic prairie	M
Solanum carolinense	Horse-Nettle	prairie	M
UMBELLIFERAE			
Daucus carota	Wild Carrot,Queen Ann's Lace	oldfield,roadside	N
VITACEAE			
Vitis sp.	Wild Grape	oldfield	M

[1]These data are a list of prairie species collected in either Illinois, Kansas, Oklahoma (Dhillion, period of collection 1987-91) or summarized from Anderson and Liberta 1987, Dickman et al. 1984, Ebbers et al. 1987, Hetrick et al. 1986, Hetrick et al. 1990, Medve 1984, Medve 1985 and Zajicek et al. 1986.

heavy investment in a symbiotic association. Another explanation may be that even highly mycorrhizal species can have differential responses to AM fungal infection due to soil nutrient levels, soil microbes and ecotypic variation (Hetrick et al. 1986, Cerligione et al. 1988, Hetrick et al. 1988, Anderson and Liberta 1989, Anderson and Liberta 1992, Meredith and Anderson 1992).

Relevance and Potential Role of Mycorrhizal Fungi in Restoration

Ewel (1987) stated that the success of community restoration can be judged by five criteria, sustainability, invasibility, productivity, nutrient retention and biotic interactions, all of which should be critically investigated and not simply based on whether or not a reconstituted community appears to resemble the original. Many restoration attempts are designed to establish the relatively high level of species diversity, species composition and interactions characteristic of a prairie community (Kline and Howell 1987, Dhillion et al. 1994). Successful restoration should be ecologically sustainable and repeatable. Much of what we understand today about restoration is, however, anecdotal because of the past lack of emphasis on collecting and analyzing data. This has made repeating successful restorations difficult (Allen E. 1988, Allen 1991). Thus for a prairie to be truly ecologically sustainable the need to understand interactions of its various components becomes essential. With the current rapid loss of species and deterioration of our ecosystems restoration efforts have increased. It is necessary for successful restoration to obtain appropriate data for past efforts including investigating less obvious habitat factors, such as mycorrhizal fungi, prior to the implementation of restoration, and subsequent management practices (Allen E. 1988, Allen 1991, Dhillion et al. 1994).

Species Diversity, Plant Community and Succession

There is also growing evidence from both laboratory and field data suggesting that AM fungi may be important in maintaining and promoting plant species diversity since the diversity of AM fungal communities has been correlated to diversity of plant communities (Rabatin and Stinner 1989, Allen 1991). Mycorrhizas for example can increase plant diversity in early successional communities (Gange et al. 1990). Non-mycotrophic species (those that do not form mycorrhizas) exist in early successional communities where AM fungal inoculum is low or absent and mycotrophic species predominate where AM fungal inoculum is high (Miller 1987, Allen 1989, Allen 1991). Thus a highly diverse community of AM fungi may be desirable to increase options for host-fungus combinations. Plant dependency on mycorrhizae may change with the successional stage of the system (Miller 1987, Allen 1991). For example, in shrublands of the western U.S., many pioneer herbaceous plants of early succession belong to non-mycorrhizal families, whereas late successional stages have plants belonging to mostly mycorrhizal families (Allen 1991). It appears that the earlier seral stages have facultative species that, through various means, build inoculum and nutrient levels that facilitate the establishment of obligate mycotrophs (Allen and Allen 1986, Allen 1989). In prairie restorations, Howell and Jordan (1991) argue that poor competitors should be planted first to facilitate their establishment before aggressive plants, perhaps pioneer species, are introduced. It is very likely that these 'poor competitors' or 'conservative species', which are regarded by some workers as late seral successional species

(Howell and Jordan 1991, Allen 1992, Howell personal communication), may successfully establish only when appropriate AM fungi are present. It is not surprising that some late successional species do not establish in disturbed environments where AM inoculum may be very low or absent (Janos 1980, Allen E. 1988, Allen 1992).

Numerous studies have suggested that the mycorrhizal inoculum levels (mycorrhizal propagules) of soils determine plant species establishment and persistence, and introduction of soils from late successional seres may hasten the rate of reclamation or restoration (Allen E. 1988, Allen 1991). The increasing number of species dependent on AM and larger number of mycorrhizal species in later seral stages along with growth and physiological responses of plant species from different seral stages provide support for this hypothesis (Allen E. 1988, Allen 1991). The type of mycorrhizal community found on a site, therefore, may influence the next assemblage of species through its affects on the mycorrhizal fungus population (Friese and Allen 1991b). One management strategy is to hasten the rate of succession by planting late seral species in the hope that the vegetation and associated abiotic and biotic components will continue in the same trajectory of succession as would the undisturbed system (Allen E. 1988). This approach, however, may be futile if needed AM fungi are absent from the establishment site. It is logical, therefore, to hypothesize that the introduction of AM fungi may facilitate continuity in succession and thus hasten the restoration process (Moorman and Reeves 1979, Janos 1980).

AM Fungal Inoculum

Mycorrhizal hyphae in root fragments can be more effective inoculum than spores. Recent studies show that mycorrhizal hyphae in root pieces are probably the most important source of inoculum (mycorrhizal propagules) since mycorrhizal root fragments can initiate infection faster than spores (Friese 1991, Friese and Allen 1991a, Friese and Allen 1993). Spores, however, can account for up to about 33% of the potential inoculum in sand prairies (Dhillion and Anderson 1993a, Dhillion and Anderson 1993c). The most significant contributor to mycorrhizal inoculum levels is, however, the presence of an intact mycorrhizal hyphal network and associated root system (Newman 1988, Friese and Allen 1991a). In general, mycorrhizal inoculum potential, and sporulation levels, are lowest in the middle of the growing season and highest near the end of the season (Dhillion and Anderson 1993). Seasonal patterns in sporulation can, however, vary according to the individual AM fungal or plant species. The presence of mycorrhizal propagules in recently removed soils has been shown to contain more viable mycorrhizal propagules than soils that have been stored (Miller 1984). The inoculum of AM fungi is reduced when soil is disturbed, such as during mining, biocide application, agricultural practices and erosion.

CONCLUSION

Given the high occurrence of mycorrhizas in prairies and the potential benefits of the mycorrhizal symbiosis, prairie restoration processes, plant establishment, community dynamics and soil development in prairie can be influenced by the presence or absence of mycorrhizal fungi. Factors which directly or indirectly determine the occurrence of mycorrhizal propagules, for example, agricultural practices, natural disturbances and the presence or absence of mycotrophic and non-mycotrophic species, are potentially important in subsequent plant establishment. Restoration projects should take into account soil abiotic and biotic changes, especially those associated with mycorrhizas which can influence plant population/community response, competition, and ultimately successional trajectories. Without successful establishment of appropriate mycorrhizal fungi, the plant species composition and soil characteristics of grassland communities undergoing restoration may be altered, and lead to the further degradation of these lands.

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