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# MYCORRHIZAL STATUS OF THE GENUS *CAREX* (CYPERACEAE)[1]

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The Cyperaceae have generally been considered nonmycorrhizal, although recent evidence suggests that mycotrophy may be considerably more widespread among sedges than was previously realized. This study surveyed 23 species of *Carex* occurring in upland and wetland habitats in northeastern Illinois. Mycorrhizal infection by arbuscular fungi was found in the roots of 16 species of *Carex* and appears to occur in response to many factors, both environmental and phylogenetic. While some species appear to be obligately nonmycorrhizal, edaphic influences may be responsible for infection in others. In five of the seven *Carex* species that were nonmycorrhizal, a novel root character, the presence of bulbous-based root hairs, was identified. The taxonomically patchy distribution of the distinctive root hair trait suggests that these structures may have evolved several times within the genus. Evidence of multiple independent origins of the root hair trait lends support to the hypothesis that root hairs represent an adaptation to nonmycotrophy. Although taxonomic position does seem to be of importance in determining the mycorrhizal dependence of sedges, the pattern may be a patchwork of both mycorrhizal clades and clades that have adapted to the nonmycorrhizal state.

**Key words:** arbuscular fungi; *Carex*; Cyperaceae; mycorrhizae; mycotrophy; root hairs.

Mycorrhizal fungi form mutualistic associations with the roots of land plants, providing the plant with phosphorus and other nutrients in exchange for photosynthate (Allen, 1991; Smith and Read, 1997). Arbuscular mycorrhizal (AM) fungi are believed to have facilitated colonization of terrestrial environments by vascular plants at the Siluro-Devonian boundary, and mycotrophy is considered the ancestral condition in vascular plants (Pirozynski and Malloch, 1975; Peterson, 1992; Taylor et al., 1995). However, it has long been held that certain families of vascular plants, including the sedges (Cyperaceae), are secondarily nonmycorrhizal (Gerdemann, 1968; Powell, 1975; Newman and Reddell, 1987; Brundrett, 1991; Peat and Fitter, 1993; Smith and Read, 1997).

In spite of the general consensus that the Cyperaceae are nonmycorrhizal, there have been numerous reports of mycorrhizal infection in certain species (e.g., Mejstrik, 1972; Read, Koucheki, and Hodgson, 1976; Haselwandter and Read, 1980; Read and Haselwandter, 1981; Gay, Grubb, and Hudson, 1982; Pendleton and Smith, 1983; Allen et al., 1987; Bellgard, 1991; Koske, Gemma, and Flynn, 1992; Meney et al., 1993; Hartnett et al., 1994; Wetzel and van der Valk, 1995; Lovera and Cuenca, 1996), and recent evidence suggests that the mycorrhizal status of sedges may need to be reevaluated. For example, in a survey of mycorrhizas of the British Isles, Harley and Harley (1987) examined 54 species of Cyperaceae, of which they found 31% to possess mycorrhizal associations. In a survey of sedges in southern India that sampled 24 species from six genera, all plants sampled had some infection, and 42% formed arbuscules (Muthukumar, Udaiyan, and Manian, 1996).

Variation in the mycorrhizal condition of sedges may be due to environmental and edaphic factors rather than a phylogenetic constraint per se (Read, Koucheki, and Hodgson, 1976; Read, 1984; Muthukumar, Udaiyan, and Manian, 1996). Because AM infection seems to be negatively correlated with soil moisture (Anderson, Liberta, and Dickman, 1984), it had been speculated that the nonmycorrhizal state of some sedges might result from their presence in marshy, anaerobic soils rather than their taxonomic position (Tester, Smith, and Smith, 1987). To complicate matters, the roots of sedges appear to be associated with several kinds of fungi, including arbuscular fungi, ectomycorrhizal fungi, or even dark septate fungi (e.g., Haselwandter and Read, 1980; Read and Haselwandter, 1981; Bledsoe, Klein, and Bliss, 1990; Kohn and Stasovski, 1990). Furthermore, the occurrence of these fungi may be restricted to brief periods of the growing season (Meney et al., 1993).

This study addresses the influence of phylogeny and environmental factors on mycorrhizal status and infection level in sedges, by focusing on the genus *Carex*. Roots of *Carex* species were collected from upland and wetland habitats of natural areas in the Chicago region and were assessed for the occurrence, amount, and type of mycorrhizal infection. In addition, the root hair morphology was determined for each of the root systems. We then

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TABLE 1. Mycorrhizal condition and taxonomic position for *Carex* species of this investigation.

| Subgenus Section | Species | Plants infected/ examined | Mean infection (%) | Infection type[a] | Bulbous root hairs[b] |
|---|---|---|---|---|---|
| Vignea | | | | | |
| Vulpinae | *C. stipata* Willd. | 7/7 | 32 | A, V, H | − |
| Multiflorae | *C. annectens* Bickn. | 2/5 | 5 | A, V, H | − |
| | *C. vulpinoidea* Michx. | 8/10 | 28 | A, V, H, S | − |
| Phaestoglochin | *C. gravida* Bailey | 2/2 | 20 | H, S | − |
| | *C. rosea* Schkuhr | 5/9 | 16 | A, V, H, D | − |
| | *C. cephalophora* Willd. | 3/8 | 8 | H | − |
| Stellulatae | *C. interior* Bailey | 0/3 | 0 | | + |
| Ovales | *C. bicknellii* Britton | 9/10 | 26 | A, V, H, S | − |
| | *C. brevior* (Dew.) Lunell | 4/5 | 27 | A. V, S | − |
| | *C. cristatella* Britton | 14/15 | 30 | A, V, H, S | − |
| | *C. scoparia* Willd. | 2/2 | 10 | V, H | − |
| | *C. tenera* Dew. | 0/2 | 0 | | + |
| Carex | | | | | |
| Phacocystis | *C. stricta* Lam. | 0/13 | 0 | | + |
| Atratae | *C. buxbaumii* Wahlenb. | 2/2 | 20 | V, H | − |
| Paniceae | *C. tetanica* Schkuhr | 1/2 | 5 | V, H | − |
| Laxiflorae | *C. blanda* Dew. | 3/9 | 5 | A, V, H | − |
| Granularis | *C. crawei* Dew. | 1/4 | 5 | H, S | − |
| | *C. granularis* Willd. | 5/10 | 16 | A, V | − |
| Griseae | *C. amphibola* Steud. | 0/2 | 0 | D | − |
| Carex | *C. pellita* Willd. | 0/16 | 0 | | + |
| Paludosae | *C. atherodes* Spreng. | 0/3 | 0 | | + |
| Hymenochlaenae | *C. sprengelii* Spreng. | 0/4 | 0 | | − |
| Acrocystis | *C. pensylvanica* Lam. | 1/8 | 4 | H, D | − |

[a] Infection types: A = arbuscules; V = vesicles; H = hyphae; S = intra-radical spores; D = dark septate hyphae.
[b] Presence (+) or absence (−) of bulbous-based root hairs.

analyzed the occurrence and pattern of fungal infection and root hair morphology as related to habitat and soil factors as well as taxonomic position.

## MATERIALS AND METHODS

The roots of 151 carices, representing 23 species from two subgenera and 15 sections, were sampled on 18–29 July 1994 (Table 1). The specimens were collected from nine sites located in DuPage and Kane Counties, Illinois. These sites consisted of remnant and restored tallgrass prairie, savanna, and wetland, encompassing a synthetic habitat/moisture gradient from xeric upland sites to lower, more mesic and hydric sites (Table 2). To the extent possible, we attempted to collect each species from at least two sites and tried to find individuals of each species in both ''characteristic'' habitats and habitats that were wetter or drier than typical for the species. The nomenclature used was that of Swink and Wilhelm (1994).

The location of each sampled individual was subjectively classified according to one of five habitat categories (wet lowland, wet mesic, mesic, dry mesic, and dry upland) on the basis of observation of microtopography and familiarity with moisture and drainage conditions at the sites. Volumetric soil moisture content was determined by time domain reflectrometry using a TRASE System 1 (Soil Moisture Equipment Corporation, Goleta, CA) with 15-cm wave guides (because of the low dielectric constants for the soils of this study we deemed it not necessary to calibrate between sites). To sample each individual, the shoot was drawn through a 5.4-cm-inside-diameter tube with a sharp cutting tip and held to one side of the tube as the tube was placed over the plant's crown and driven 15 cm into the soil with a mallet. The core with attached plant shoot was placed in a large polyethylene bag and

TABLE 2. Habitat class, and mycorrhizal and edaphic conditions for sites where *Carex* species were collected.

| Site | Samples (N) | Habitat class[a] | Organic C (%) | Total N (%) | Moisture (v/v %) | Olsen P µg/g | $pH_{(5:1)}$ | Conductivity (dS/m) |
|---|---|---|---|---|---|---|---|---|
| Argonne Natl. Lab. (ANL) | 6 | 3 | 4.31 | 0.37 | 22.9 | 17 | 6.01 | 0.120 |
| Danada Savanna (DS) | 18 | 4 | 3.62 | 0.30 | 23.8 | 11 | 6.09 | 0.080 |
| Fermilab Prairie (FNL) | 36 | 3 | 3.79 | 0.32 | 25.0 | 7 | 6.34 | 0.120 |
| Fern Meadow (FM) | 14 | 1 | 26.29 | 2.49 | 70.6 | 22 | 6.28 | 0.325 |
| Poplar Creek (PC) | 14 | 5 | 3.03 | 0.22 | 14.3 | 20 | 6.52 | 0.090 |
| Waterfall Glen | | | | | | | | |
| Floodplain (WGF) | 17 | 2 | 8.81 | 0.68 | 42.7 | 18 | 6.67 | 0.200 |
| Savanna (WGS) | 18 | 5 | 1.42 | 0.13 | 28.9 | 14 | 5.54 | 0.050 |
| West Chicago Prairie | | | | | | | | |
| Wet prairie (WCW) | 19 | 1 | 7.34 | 0.55 | 52.5 | 19 | 6.80 | 0.206 |
| Wet-mesic (WCM) | 9 | 2 | 5.46 | 0.42 | 27.6 | 22 | 6.27 | 0.128 |

[a] Dominant habitat class for the site: 1 = wet lowland; 2 = wet mesic; 3 = mesic; 4 = dry mesic; 5 = upland.

refrigerated at 4°C upon return to the laboratory. To characterize soil conditions in the vicinity of the sampled individual, a second core (5.4 × 15 cm) was collected within 5 cm of the first. Any attached aboveground plant tissue was clipped off, and the core was placed in a polyethylene bag and stored at −15°C until it was analyzed.

Within 5 d of sampling, the soil was washed from the roots of the refrigerated cores. Only fibrous roots attached to the crowns of *Carex* plants were retained. These roots were cut into 1.5-cm segments, cleared in 10% KOH for 16 h, acidified with dilute HCL, and then stained with trypan blue (0.5 g/L) in 1:2:2 lactic acid:glycerol:deionized water (by volume). Root segments were then mounted on glass slides in lactic glycerol and polyvinyl alcohol. The occurrence of fungal structures was assessed by using a compound light microscope. The mycorrhizal status of a plant (i.e., the presence or absence of colonization by mycorrhizal fungal structures) was determined, and percentage infection was calculated as the proportion of root segments infected by arbuscular fungi. The presence of vesicles, arbuscules, hyphae, and intraradical spores was recorded. The occurrence of dark septate hyphae was also noted. Observations were made of root morphology, such as the presence and morphology of root hairs.

Each of the frozen soil cores was thawed overnight in a refrigerator and bisected longitudinally. The roots were removed from one half, and the soil was air dried and gently crushed to pass a 2-mm mesh sieve. Soil carbon and nitrogen was determined by using a Carlo Erba NA 1500 CHN autoanalyser (C. E. Elantech, Lakeland, NJ). Available soil phosphorus was determined on sodium bicarbonate extracts (Olsen and Sommers, 1982). Soil pH and conductivity were measured on a 1:5 mixture of soil:deionized water after 1 h (Hendershot, Lalande, and Duquette, 1993). The other half of each soil core was used to assay relative mycorrhizal infection potential (MIP). The field-moist soil was thoroughly mixed, and a subsample of 67 $cm^3$ was combined with 33 $cm^3$ of silica sand. The soil:sand mixture was placed in a 4-cm-diameter conetainer with a sorghum seedling as the host. After 31 d, the sorghum plants were harvested, and their roots were cleared, stained, and examined for mycorrhizal infection (Moorman and Reeves, 1979).

The percentage infection data did not meet parametric assumptions because of the high heterogeneity of variance among *Carex* species. We therefore present only a categorical analysis of the presence of mycorrhizal infection. Even so, the influences of species and environmental variables on mycorrhizal infection could not be analyzed simultaneously because some species were always infected, and infection was never observed in others. Thus, we first tested for differences in the presence of infection among *Carex* species and among collection sites by using a log-likelihood test. We then removed the species that were either always infected or never infected and the species with low sample sizes from the analysis to allow the simultaneous evaluation of species and environmental influences on the presence of infection in the remaining species. In this final analysis, the abilities of *Carex* species, soil infection potential, soil phosphorus, soil moisture, and soil pH to predict the presence of infection were evaluated by logistic multiple regression using the CATMOD procedure of the SAS Version 6.11 statistical package (SAS, 1994).

## RESULTS

Of the 151 individuals assessed for mycorrhizae, arbuscular fungi were found to occur in 16 of the 23 *Carex* species sampled (Table 1). Of the 16 colonized species, five had a mean infection of ≤5%, whereas seven had a mean infection of ≥20%. Only nine of the species contained arbuscules, whereas 12 contained vesicles, and three contained only hyphae.

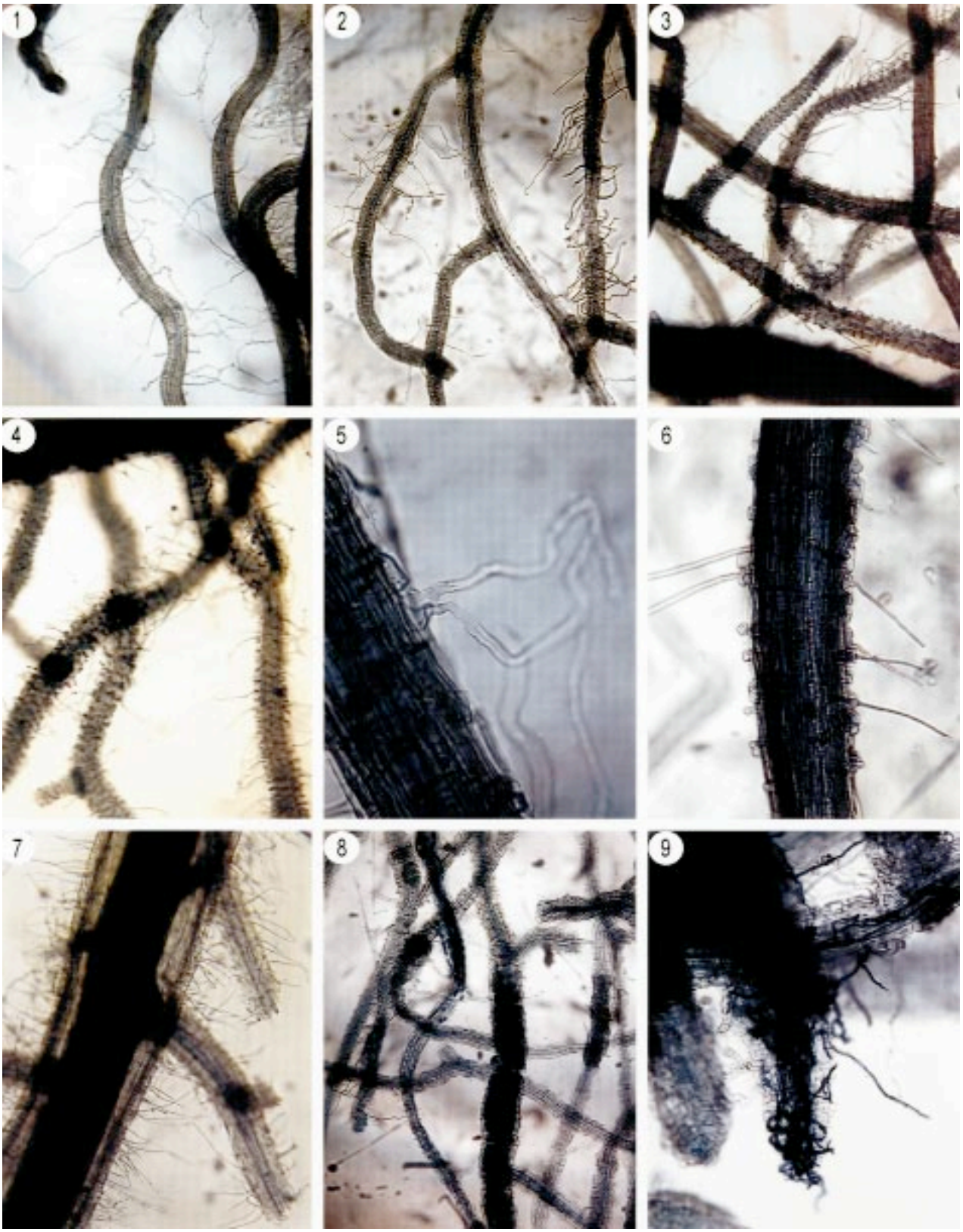
The presence of AM infection was highly dependent on the identity of the host (log-likelihood $\chi^2 = 105.72$, df = 22, $P < 0.0001$). Thus, some species were significantly more likely to be infected than others. These differences among species remained even after the nonmycorrhizal species were removed from the analysis (log-likelihood $\chi^2 = 30.809$, df = 17, $P < 0.0001$, $N = 114$).

Examination of root hairs revealed differences in morphology that were correlated with the species' mycorrhizal status. The root hairs typical for the majority of *Carex* species in this study were usually quite long (sometimes greater than 1.0 mm) and sparsely distributed (Figs. 1–2). However, the roots of some *Carex* species were covered with a fine layer of comparatively distinctive, short root hairs, ~50–250 μm in length (Figs. 3–4). Although they were somewhat variable in morphology, these structures were distinguished by bulbous swellings that were sometimes topped by a filamentous root hair (Figs. 5–6). These basal swellings form dense, homogenous mats covering every surface of the root. The presence of these bulbous root hairs was negatively associated with presence of mycorrhizal infection (log-likelihood $\chi^2 = 49.92$, df = 1, $P < 0.0001$); in fact, species with bulbous root hairs (*C. atherodes, C. interior, C. pellita, C. stricta,* and *C. tenera*) were not found to be infected with mycorrhizal fungi. In addition, although they were dissimilar in overall appearance, the roots of the other two species that consistently lacked AM infection, *C. sprengelii* (Fig. 7) and *C. amphibola,* were also covered by a dense layer of root hairs, however, without bulbous bases. In contrast, AM infection was typically associated with root morphologies similar to those presented in Figs. 1, 2, and 8.

A dark septate endophyte was also found in the cortex of several *Carex* species. The infection was characterized by loose hyphal wefts on root surfaces, cortical penetration (Fig. 9), and sporadic occurrence of intracellular sclerotia. We found this type of infection to be rather common only in *C. amphibola, C. pensylvanica,* and *C. rosea* at the Poplar Creek site.

Site-related factors also significantly influenced mycorrhizal infection (Table 2; Fig. 10). The presence of infection was significantly different among sites (log-likelihood $\chi^2 = 17.282$, df = 7, $P < 0.0001$). The MIP of the soil surrounding the sampled *Carex* species was a relatively good predictor of infection at a site. A significant linear relationship exists between site means of root infection and site MIP means (Fig. 10; $F = 6.23$, df = 7, $P < 0.041$).

Because all *Carex* species were not present at all sampled sites, we could not definitively attribute site-related effects to differences in environmental variables. However, by removing species that were either consistently nonmycorrhizal or consistently infected, we were able to test directly the effects of environmental factors. Soil infection potential (MIP), available phosphorus, and conductivity were not significant predictors of the presence of infection in species with variable mycorrhizal status. However, mycorrhizal status was predicted by soil moisture (logistic regression $\chi^2 = 9.36$, df = 1, $P < 0.0022$) and by the interactions between soil moisture and pH (logistic regression $\chi^2 = 8.70$, df = 1, $P < 0.0032$). For these species, the probability of infection was higher in areas with high soil pH and lower in areas with high soil moisture. The probability of infection was particularly low in areas with low soil pH and high moisture.




Figs. 1–9. Distinctive root hairs and endophytic fungi associated with of roots of *Carex* species. Magnification ×63 (1 cm = 330 μm), except for ×160 in Fig. 6 (1 cm = 82 μm) and ×250 in Figs. 5 and 9 (1 cm = 58 μm). Fig. 1 (*C. vulpinoidea*) and Fig. 2. (*C. bicknellii*) show root and root hair morphology typical for *Carex* species possessing mycorrhizae. Figs. 3–6 show the characteristic bulbous-based root hair morphology associated with nonmycotrophy. Fig. 3 (*C. tenera*) and Fig. 4 (*C. pellita*) show general morphology of roots and bulbous-based root hairs. Fig. 5 (*C. atherodes*) and Fig. 6 (*C. stricta*) show root hairs attached to a bulbous-based epidermal cell. These bulbous base cells appear to remain after

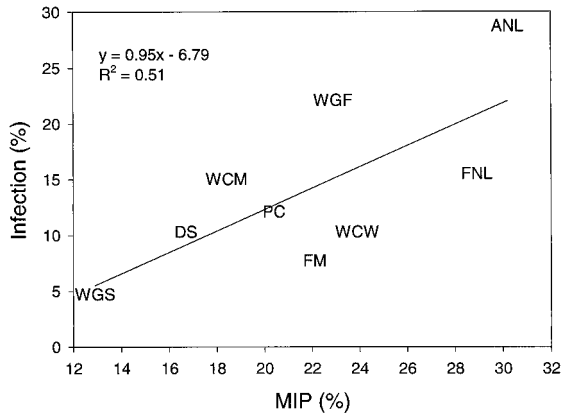



Fig. 10. The relationship between sampling site mean mycorrhizal infection for *Carex* species roots and mycorrhizal infection potential (MIP) of associated soil. Sampling site abbreviations are defined in Table 2.

## DISCUSSION

***Occurrence of mycorrhizal fungi in Carex species***—The data presented in this and other recent studies indicate that the extent of mycotrophy in the genus *Carex* is much greater than may have been realized previously. Moreover, the data suggest that both taxonomic and environmental factors contribute to the determination of mycorrhizal status. Specifically, certain species appear to be typically mycorrhizal, other species are usually nonmycorrhizal, and the mycorrhizal status of a third group of species depends upon the environment. The environmental dependence observed in the last group supports previous reports that wetland habitats are not conducive to mycorrhizal infection. Although moisture per se does not completely account for variation in infection, we found that infection is lowest in soils with high moisture and low pH, conditions typical of many of the wetland habitats in the region.

One aspect of the interspecific variation we observe with mycorrhizal infection that merits further scrutiny is the apparent connection between the morphology of root hairs and the nonmycorrhizal condition. Some *Carex* species in the tribes Cariceae and Rhynchosporeae produce swollen dauciform roots with long root hairs when growing in nutrient deficient and poorly drained soils (Davies, Briarty, and Rieley, 1973; Lamont, 1974). It is believed that these hairy cluster roots and the morphologically similar proteoid roots may be a morphological adaptation to the nonmycorrhizal condition (Lamont, 1993).

The occurrence of root hairs increases nutrient uptake (Föshe, Claassen, and Jungk, 1991), and the abundance of root hairs has been shown to increase under low-nutrient conditions (Föshe and Jungk, 1983). In addition, root hair length and abundance are negatively correlated with mycorrhizal dependence or benefit (Baylis, 1975; Manjunath and Habte, 1991; Schweiger, Robson, and Barrow, 1995). In this study, we identify a unique root hair morphology, with bulbous swellings, which is associated with the nonmycorrhizal condition. This character gives the root a fuzzy appearance. The apparent ''fuzziness'' of *Carex* roots was described previously and has been used as a tool in the description and identification of some *Carex* species (Reznicek, 1986). The distinctive root hairs may represent an adaptation for nonmycorrhizal growth. The development of these root hair modifications may have freed the individuals possessing them from dependence on mycorrhizae for nutrient uptake. Such a preadaptation to nonmycorrhizal conditions might have allowed these species to colonize wetland soils, where a lack of mycorrhizal fungal propagules could have excluded other plants (Anderson, Liberta, and Dickman, 1984).

Alternatively, the association between the bulbous root hairs and the nonmycorrhizal state may be coincidental. Root hair production in *Carex* has been shown to increase under soil anoxia (Moog and Janiesh, 1990). In the present study, bulbous root hairs are associated with growth in wetland habitats, as the abundance of root hairs was correlated with soil moisture content ($r = 0.10$, $P < 0.0001$), and four of the five species with bulbous root hairs are considered obligate wetland species (*C. atherodes, C. interior, C. pellita,* and *C. stricta*). Therefore, the occurrence of distinctive root hairs and a lack of mycorrhizal colonization could both result from growth in waterlogged soils. Frequent inundation might have eliminated the population of mycorrhizal fungi and promoted root hair growth. This hypothesis, however, seems unlikely for several reasons. First, the root hair trait described above appears to be consistently expressed in species possessing it, even in individuals collected at more upland sites. Second, this trait is not consistently present in any of the other species of *Carex,* even among plants growing in wetland areas. Finally, although past studies have documented fewer spores in wetland soils (Anderson, Liberta, and Dickman, 1984), the mycorrhizal infection potentials of the soils sampled in this study were, in fact, somewhat higher in wetland habitats than in upland habitats, and habitat class was not significantly correlated with either mycorrhizal status or percent infection. It is therefore doubtful that the absence of colonization in species with root hairs is due to a lack of fungal propagules.

Although a dark septate endophyte has been identified with other *Carex* species (e.g., Haselwandter and Read, 1982), this is the first report of an occurrence in a prairie savanna community. For this study, the only variable that appears to be associated with the occurrence of the endophyte is the low moisture content and the sandy nature of soils at the Poplar Creek site (Table 2).

***Phylogeny and the distribution of mycotrophy***—Hypotheses of functional adaptation should account for phylogenetic distribution of the character. Unfortunately, the phylogeny of *Carex* is poorly understood (Reznicek,

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the root hair has been sloughed. Fig. 7 shows the nonmycotrophic species *C. sprengelii,* characterized by a dense layer of fine root hairs covering the majority of the fibrous roots. Fig. 8 shows arbuscular colonization in roots of *C. pensylvanica,* represented by the intensely stained blue regions of the fibrous roots. Fig. 9 shows dark septate fungus associated with the cortical tissue in *C. rosea* roots.

1990), so a rigorous phylogenetic analysis is not possible. However, if we assume that the existing taxonomy is reasonably reflective of the underlying evolutionary history, we can at least draw some preliminary inferences regarding the distribution of characters and the extent to which mycotrophy is tied to common ancestry.

Table 1 depicts the mycorrhizal state of the species included in this study. The species are grouped into sections and subgenera based upon the current understanding of patterns or relatedness within the genus (A. A. Reznicek, personal communication, University of Michigan). Where the correct order is unknown, taxa are listed alphabetically. The taxonomically patchy distribution of the distinctive root hairs described in this study seems to indicate that these structures may have evolved several times within the genus. This evidence of multiple independent origins lends supports to the hypothesis that root hairs represent an adaptation to nonmycotrophy.

A preliminary examination of the distribution of mycotrophy within the genus seems to indicate a phylogenetic influence on the mycorrhizal condition; mycorrhizal status appears generally consistent within the section at least. A larger pattern might exist across sections as well. However, the limited sample size, coupled with the uncertainty in current *Carex* taxonomy, means that this larger trend must be considered provisional at best. Moreover, as information about the phylogeny of the genus accumulates, and particularly as molecular techniques are brought to bear on this large and challenging group, it will be interesting to see how mycorrhizal condition relates with phylogenetic history and whether a pattern can be resolved.

Mycorrhizal infection among sedges appears to occur in response to many factors, both environmental and phylogenetic. While some species appear to be obligately nonmycorrhizal, edaphic influences may be responsible for infection in others. Although taxonomic position does seem to be of importance in determining the mycorrhizal dependence of sedges, the pattern may be a patchwork of both mycorrhizal clades and clades that have adapted to the nonmycorrhizal state. Clearly, however, the evidence presented here and in other recent publications indicates that the conventional wisdom regarding the mycorrhizal condition of the Cyperaceae must be reevaluated.

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