January 2011

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Terrestrial Macrofungi of Illinois Old-Growth Prairie Groves

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ABSTRACT.—Macrofungi from two old-growth prairie grove remnants in the Midwestern United States (Brownfield and Trelease Woods, Champaign Co., IL) were surveyed over two summer and fall fruiting periods. Communities of Ascomycetes, Basidiomycetes and Myxomycetes were sampled and compared using multivariate statistical analyses. Standard estimations of species richness were calculated for comparison with other studies of fungal diversity. Environmental factors (rainfall, humidity, air temperature and soil temperature at 10 cm depth) as well as leaf litter composition, and woody plant communities were surveyed to assess their impact on fungal communities. Fungal community structure was found to differ significantly both between and within Brownfield and Trelease Woods. Communities of terrestrial macrofungi were determined to be strongly influenced by seasonality, with soil temperature at 10 cm depth showing the strongest correlation to changes in community composition. Brownfield and Trelease Woods, formerly part of a contiguous prairie grove with likely a single fungal community, are shown to have developed significantly different fungal communities over a period of separation of more than 120 y.

INTRODUCTION

Fungi are integral components of terrestrial ecosystem function, responsible for much of the decomposition and recycling of nutrients. Fungi further influence terrestrial ecosystems through mycorrhizal and endophytic associations with vascular plants and by serving as parasites, food sources and natural biological controls (Dix and Webster, 1995; Wicklow and Carroll, 1992).

Hawksworth (1991, 2001) conservatively estimated the number of fungi existing in nature to be greater than 1.5 million species, of which fewer than 10% have been described. While interest in fungal biodiversity has grown in recent years, much of this interest has been centered on estimating the total number of fungal species in the world, rather than on understanding fungal diversity on a local scale (Schmit *et al.*, 1999). In the northern hemisphere, studies of macrofungal diversity and species richness have been conducted in both Europe (Straatsma *et al.*, 2001; Hering, 1966; Richardson, 1970; Ohenoja, 1984) and the United States (Bills *et al.*, 1986; Brunner and Petrini, 1992; Palmer *et al.*, 1994; Schmit *et al.*, 1999); however, the paucity of studies is widely recognized (Hawksworth, 2001; Straatsma *et al.*, 2001).

Owing to the current paucity of fungal diversity studies in North America and elsewhere Hawksworth (2001) argues for increased sampling of fungal diversity at local levels and the establishment of reference communities. Accessible old-growth forests with protected status are excellent choices for the establishment of fungal biodiversity reference communities. Such reference communities can be compared with other sites and for studies of community and ecosystem changes in response to local, regional and global impacts.

Fungi are highly integrated into the old-growth forest environment, playing key roles in food chains (Komonen *et al.*, 2000), and nutrient cycling (Lindahl *et al.*, 2002).

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Furthermore, fungi play an important role in the balance of the global carbon cycle and are the primary group driving CO_2 release in old-growth forests (Rygiewicz and Andersen, 1994).

The purpose of this study was: (1) to provide initial characterization of fungal biodiversity at both Brownfield and Trelease Woods, including estimates of taxon richness; (2) to determine if fungal assemblages present both within and between Brownfield and Trelease Woods are significantly different; (3) to determine which taxa of macrofungi are most informative in characterizing macrofungal assemblages at both sites; (4) to evaluate the effects of seasonality on the fungal communities; (5) to determine which site-specific biotic factors correspond most strongly with the fungal assemblages at both sites; and (6) to compare the fungal communities at Brownfield and Trelease woods to other known studies of fungal diversity.

METHODS

STUDY AREA

Brownfield and Trelease Woods, located approximately 5 km northeast of Urbana in Champaign County, Illinois (40°09′N, 88°10′W) are old-growth prairie grove forest remnants dominated by oak (*Quercus* spp.), ash (*Fraxinus* spp.), hickory (*Carya* spp.) and sugar maple (*Acer saccharum* Marshall). These sites are ideal for studying community divergence as they are remnants of a single 16 km^2 pre-settlement prairie grove known as the "Big Grove" along the Salt Fork of the Vermillion River (Telford, 1926). The Brownfield and Trelease Woods remnants are now entirely disjunct (approximately 2.5 km apart) and are surrounded by second growth forest fragments, agricultural fields, housing developments and prairie restoration. Brownfield Woods is in closer proximity to second growth forest fragments, with second growth forest adjacent to the southern end of the preserve, whereas Trelease is more isolated, surrounded entirely by agricultural fields and prairie plantings.

Both sites are approximately 24 ha in size (600 m × 400 m), though Brownfield Woods has more topographic relief and a small stream running through from northwest to southeast (Gelhausen *et al.*, 2000). Brownfield and Trelease Woods have existed as separate islands of forest remnants since the late 1870s (Telford, 1926). Although initially old-growth, deciduous, upland forests with a high, closed canopy and fairly open (Brownfield Woods) to moderately dense (Trelease Woods) understory, sugar maple (*Acer saccharum* Marshall) has rapidly become the dominant tree species in both forests (Boggess, 1964).

Brownfield and Trelease Woods have been owned and managed by the University of Illinois at Champaign-Urbana for more than 120 y and are used primarily as research reserves. Both sites have been extensively studied regarding edge effects on plant communities (Gehlhausen *et al.*, 2000), changes in woody vegetation (Telford, 1926; Boggess, 1964; Miceli *et al.*, 1977), neighbor-related demography of rare plant species (Lin and Augspurger, 2006), forest herb colonization of treefall gaps (Thompson, 1980) and canopy tree mortality (Cortright, 1952). To date, fungal biodiversity has not been studied at either site.

FUNGAL SAMPLING AND ANALYSIS

Brownfield and Trelease Woods were arbitrarily separated into north and south halves with four 50 × 50 m study plots established within each half, for a total of 16 study plots (Fig. 1). Two 50 m transects were established within each study plot and the occurrence of terrestrial macrofungal sporocarps, including fungi inhabiting wood fragments <15 cm in

Locations of Brownfield and Trelease Woods
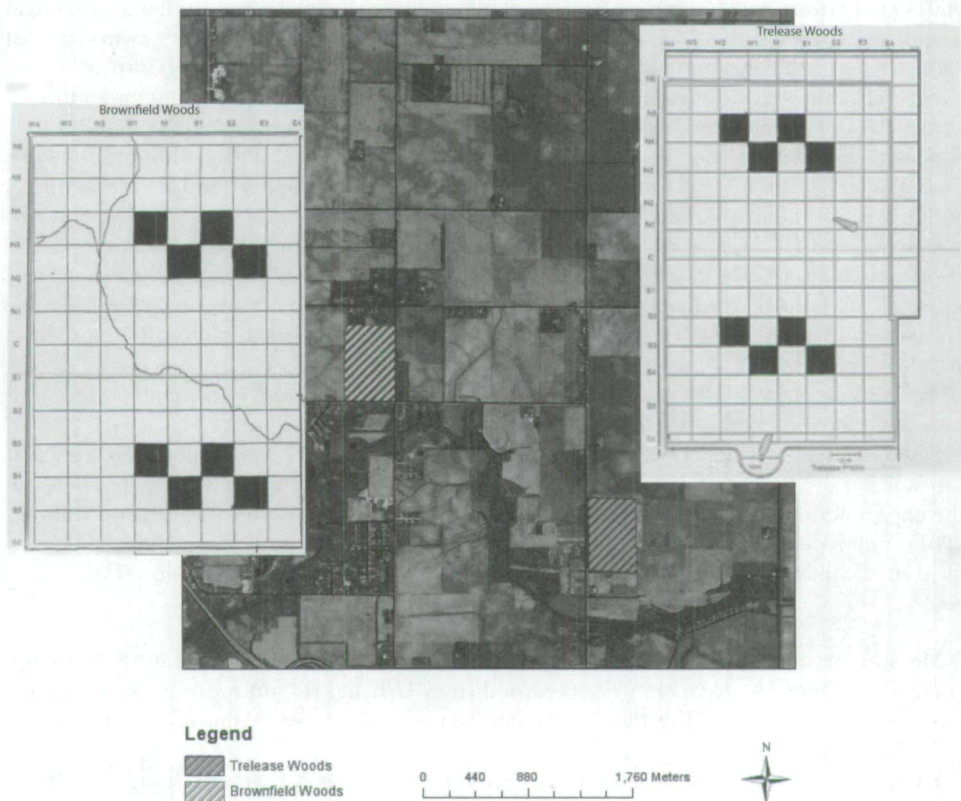## Northeast of Champaign-Urbana, Illinois

FIG. 1.—Locations of Brownfield and Trelease Woods relative to each other and surrounding environment. Location of study areas within Brownfield and Trelease Woods, each colored square represents a 50 × 50 m plot

diameter, were monitored in circle plots at 10 m intervals along each transect. At each 10 m interval, a permanent center point for 2 m radius circle plot was established and all terrestrial macrofungi within the circle were recorded. Thus, each sample plot contained 10 circle plots, resulting in 80 circle plots/forest resulting in a total of over 1000 m^2 sampled in each forest during each collection event. Sampling design followed guidelines set forth in Mueller *et al.* (2004).

When possible, macrofungi were identified to the species rank in the field; however, when species could not be determined, sporocarps were collected and identified to the lowest identifiable taxon rank. Each site was visited approximately twice monthly during the months of Sept., Oct. and Nov. of 2006 as well as Jun., Aug., Oct. and Nov. of 2007. No site visits were made in Sept. 2007 and Jul. of either year due to low precipitation.

Statistical analyses were performed using Primer-e., v. 6.1.6 (Primer-e, Ltd. Plymouth, UK). Taxonomic data were aggregated at the genus rank in order to facilitate statistical analyses by decreasing singly encountered taxa (singletons). Ordination of data was performed using non-

metric multidimensional scaling (NMDS) (Kruskal, 1964), using Bray-Curtis Distances (Bray and Curtis, 1957). Analysis of similarity (ANOSIM) (Clarke and Warwick, 2001) hypothesis tests were performed. Similarity/distance percentage (SIMPER) analysis (Clarke and Warwick, 2001) was performed to determine the contribution of an individual genus to changes in fungal assemblages. Lastly, the RELATE procedure, which assesses the effect of environmental variables on observed sample distribution (Clarke and Warwick, 2001), was performed.

Several parameters of taxon richness were utilized to compare the fungal communities present at Brownfield and Trelease Woods. The EstimateS software package (Colwell, 1997) was used to calculate the *Chao 1* (Chao, 1984), *Chao 2* (Colwell and Coddington, 1994), *Jacknife 1* and *Jacknife 2* (Burnham and Overton, 1978, 1979), *Bootstrap* (Smith and van Belle, 1984), *Chao 3* (Chao and Lee, 1992), as well as the Individual-based Coverage Estimator of taxon richness (ICE), and Abundance-based Coverage Estimator of taxon richness (ACE) (Chazdon *et al.*, 1998) estimates at both sites. Schmit *et al.* (1999) consider all estimators of taxon richness to be overly conservative in approximating diversity and regard the *Chao 2* and *Jacknife 2* estimators as the most accurate, principally due to the higher values of species richness predicted by these estimators. O'Dell *et al.* (2004) also regard the *Jacknife 2* and *Chao 2* estimators as highly reliable, especially when sample numbers are small and when a preponderance of rare taxa are present, as is often the case with fungi.

Sample-based rarefaction curves (Gotelli and Colwell, 2001) were calculated for each forest using the EstimateS software package. A sample-based assessment was chosen because the experimental design, plot-based accumulative comparisons of sites (Gotelli and Colwell, 2001), follows the statistical assumptions of this assessment. A rarefaction curve was chosen over an accumulation curve in order to more accurately assess the collection effort.

ENVIRONMENTAL DATA AND ANALYSIS

Measurements of monthly rainfall, minimum and maximum air temperature, humidity and soil temperature at 10 cm were recorded from Urbana, IL and mean air temperature was calculated as part of the Illinois Climate Network Water and Atmospheric Resources (WARM) program.

Fungal communities were related to tree composition using data from Edgington (1991), which provided counts of trees >3 cm in diameter at breast height as well as the basal area in square feet of all trees >3 cm in diameter for each 50×50 m segment of both Brownfield and Trelease Woods. In addition to the 1991 data, a relative abundance survey of woody species present in each sample plot was completed in fall 2007.

Plant litter composition was analyzed following Facelli and Carson (1991). Five 1 m^2 quadrat samples of leaf litter and wood fragments <15 cm diameter, not including organic matter integrated into the soil (A_0 Horizon), were randomly collected in early spring 2008 and pooled from each study plot. A total of 40 m^2 of litter was collected for each forest. Litter was sorted into nine groups: (1) wood fragments; (2) herbaceous material; (3) fruits of woody tree species; (4) detritus; leaves of (5) *Quercus*, (6) *Acer*, (7) *Tilia* and (8) *Platanus*; and (9) leaf remnants not identified (*Fraxinus, Aesculus, Juglans* etc. leaflets). After sorting, litter was placed into paper bags and oven dried for >72 h at 85 C and weighed. The RELATE procedure was performed to determine the influence of environmental variables as well as tree composition on fungal communities.

RESULTS

A total of 209 species (Appendix) representing 102 genera of terrestrial macrofungi were observed in Brownfield and Trelease Woods during 2006 and 2007. A total of 93 genera of
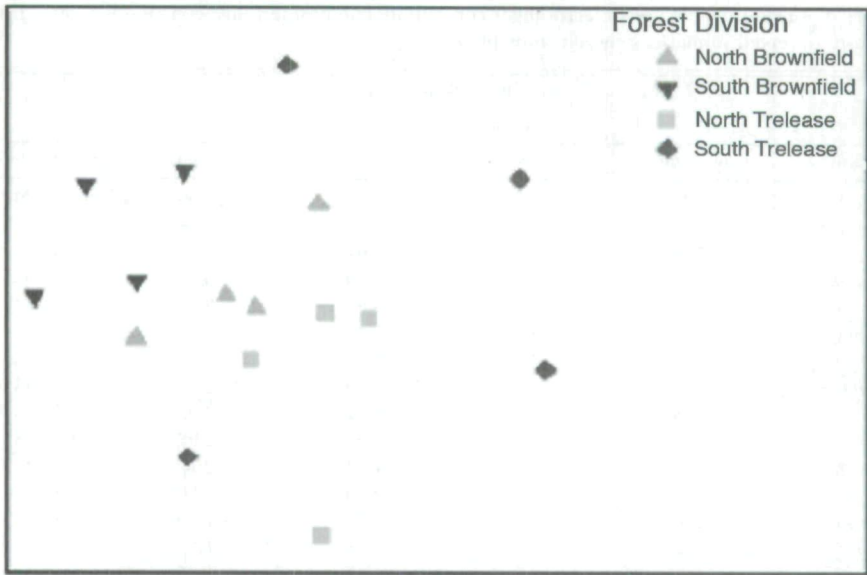
FIG. 2.—NMDS of macrofungal assemblages by forest divisions (North v South halves)

terrestrial macrofungi were observed in Brownfield Woods, of which 26 were unique to Brownfield. Of the 76 genera observed in Trelease Woods, 9 genera were exclusively in Trelease Woods.

Figure 2 is a NMDS ordination (3D stress = 0.172) of the fungal assemblages at Brownfield and Trelease Woods from 2006 and 2007. Significantly different fungal assemblages were observed between Brownfield and Trelease Woods (R = 0.212, P = 0.005). Forest divisions also harbored significantly different fungal assemblages (R = 0.233, P = 0.007), with some divisions (*e.g.,* North Brownfield, South Brownfield and North Trelease) showing strong spatial association whereas the fungal assemblages at South Trelease were less compositionally similar.

Pairwise ANOSIM tests demonstrate that the macrofungal community in the northern division of Brownfield Woods was significantly different from that in the southern division (R = 0.292, P = 0.029); however, Trelease Woods failed to show significant within-site differences in fungal communities (R = −0.042, P = 0.629). Between-site differences in forest division were significant for South Brownfield and North Trelease (R = 0.542, P = 0.029), as well as South Brownfield and South Trelease (R = 0.448, P = 0.029).

The macrofungal communities of individual study areas were not significantly different (R = 0.132, P = 0.172). Thus, fungal communities were found to differ most significantly between Brownfield and Trelease Woods at the 10,000 m^2 scale of forest subdivisions (North vs. South).

16 genera were identified that contribute most intensely to the similarity between sites in Brownfield Woods (Table 1), with an average similarity between sites of 63.83% over the course of the study. Thirteen genera were determined to contribute most to the similarity between sites within Trelease Woods (Table 2), which exhibited an average similarity of 56.52% between sites. Brownfield and Trelease Woods were determined to be 42.44% dissimilar in fungal community composition, determined by the differences in abundances in 42 genera between sites (Table 3).

TABLE 1.—Brownfield Woods macrofungal community composition and contribution of individual genera to observed similarity between study plots

Genus	Av. Abund	Av. Sim	Sim/SD	% Contrib	Cumulative %
		Brownfield Woods			
		Average similarity: 63.83			
Mycena	24.00	19.14	7.66	29.99	29.99
Irpex	12.88	9.43	3.64	14.78	44.77
Stereum	7.25	4.83	5.61	7.57	52.34
Hymenochaete	6.88	4.31	2.59	6.74	59.08
Xylaria	4.88	3.55	3.85	5.56	64.64
Schizophyllum	4.63	2.83	1.48	4.43	69.07
Gymnopus	3.63	2.19	1.42	3.43	72.50
Trichaptum	3.88	1.87	1.50	2.94	75.43
Poria	3.00	1.87	2.02	2.93	78.36
Marasmius	3.50	1.87	1.56	2.92	81.28
Coprinellus	2.63	1.35	1.14	2.12	83.40
Xeromphalina	2.00	1.34	2.29	2.10	85.50
Psathyrella	1.75	1.01	1.37	1.59	87.09
Eutypa	1.75	0.88	1.38	1.37	88.46
Polyporus	1.50	0.86	1.41	1.35	89.82
Steccherinum	1.75	0.80	0.82	1.26	91.07

Forty-two genera were found to be responsible for 90% of the dissimilarity between the terrestrial macrofungal communities of Brownfield and Trelease Woods (Table 3). Of these 42 genera, only three (*Cerrena*, *Agaricus* and *Grifola*) were present in only one of the forests, indicating differences between forests results from differences in abundance of genera between sites rather than presence or absence of genera.

The effects of seasonality on the fungal communities of Brownfield and Trelease Woods were also assessed (Fig. 3) (3D stress = 0.152). Fungal assemblages within each forest were

TABLE 2.—Trelease Woods macrofungal community composition and contribution of individual genera to observed similarity between study plots

Genus	Av. Abund	Av. Sim	Sim/SD	% Contrib	Cumulative %
		Trelease Woods			
		Average similarity: 56.52			
Mycena	17.88	19.84	5.21	35.10	35.10
Irpex	8.13	6.75	1.66	11.95	47.04
Hymenochaete	5.38	4.64	2.34	8.21	55.25
Marasmius	3.75	4.29	3.43	7.59	62.84
Xylaria	5.50	3.55	1.52	6.28	69.12
Gymnopus	3.63	3.09	1.67	5.47	74.59
Schizophyllum	3.13	2.74	1.70	4.85	79.44
Stereum	2.38	1.74	1.04	3.08	82.52
Xeromphalina	2.13	1.56	1.00	2.75	85.27
Steccherinum	1.63	0.88	0.87	1.55	86.82
Eutypa	1.13	0.85	0.89	1.50	88.32
Bisporella	1.50	0.79	0.65	1.40	89.72
Psathyrella	0.75	0.71	1.04	1.26	90.97

TABLE 3.—Contribution of individual genera toward dissimilarity between forests Average Dissimilarity = 42.44%

Genus	Brownfield Av. abundance	Trelease Av. abundance	Av. Diss	% Contrib	Cum. %
Mycena	24.00	17.88	4.16	9.80	9.80
Irpex	12.88	8.13	3.61	8.50	18.30
Stereum	7.25	2.38	2.63	6.19	24.49
Hymenochaete	6.88	5.38	2.05	4.82	29.31
Xylaria	4.88	5.50	2.02	4.75	34.06
Trichaptum	3.88	0.88	1.60	3.78	37.84
Schizophyllum	4.63	3.13	1.50	3.54	41.38
Poria	3.00	0.75	1.38	3.26	44.64
Gymnopus	3.63	3.63	1.28	3.02	47.65
Coprinellus	2.63	1.25	1.23	2.91	50.56
Marasmius	3.50	3.75	1.11	2.62	53.18
Steccherinum	1.75	1.63	0.93	2.19	55.37
Lycoperdon	0.63	1.63	0.90	2.11	57.49
Bisporella	1.25	1.50	0.81	1.92	59.40
Crepidotus	0.75	1.13	0.78	1.83	61.23
Xeromphalina	2.00	2.13	0.77	1.82	63.06
Perenniporia	1.38	0.75	0.70	1.64	64.69
Gyrodon	1.00	0.88	0.68	1.61	66.30
Polyporus	1.50	0.75	0.66	1.56	67.85
Psathyrella	1.75	0.75	0.65	1.54	69.39
Marasmiellus	1.13	0.50	0.63	1.49	70.88
Eutypa	1.75	1.13	0.63	1.49	72.37
Exidia	1.13	0.13	0.57	1.34	73.71
Galerina	0.88	0.13	0.51	1.21	74.92
Scutellinia	0.75	0.50	0.49	1.15	76.08
Parasola	1.00	0.38	0.49	1.15	77.23
Hymenoscyphus	0.88	0.25	0.48	1.13	78.36
Trametes	0.38	0.63	0.47	1.10	79.46
Xerula	0.88	0.25	0.46	1.09	80.55
Armillaria	0.75	0.50	0.45	1.06	81.60
Coprinus	0.38	0.63	0.39	0.92	82.52
Artomyces	0.50	0.38	0.38	0.89	83.42
Pluteus	0.63	0.25	0.36	0.85	84.26
Inocybe	0.63	0.38	0.36	0.84	85.10
Tubaria	0.63	0.63	0.34	0.79	85.89
Cerrena	0.63	0	0.30	0.71	86.61
Russula	0.38	0.25	0.29	0.69	87.30
Agaricus	0.50	0	0.28	0.65	87.95
Grifola	0.50	0	0.27	0.64	88.59
Peziza	0.38	0.25	0.27	0.64	89.23
Hypoxylon	0.38	0.38	0.25	0.59	89.82
Sarcoscypha	0.13	0.38	0.25	0.58	90.40

shown to significantly differ each month and year of the study (R = 0.526, P = 0.0001). In addition, fungal assemblages within each forest showed strong correlation by month, regardless of year of fruiting (R = 0.375, P = 0.0001). When yearly and monthly changes in fungal assemblages were compared without regard to forest, strong association was also exhibited (R = 0.463, P = 0.0001). Fungal assemblages were found to shift in composition
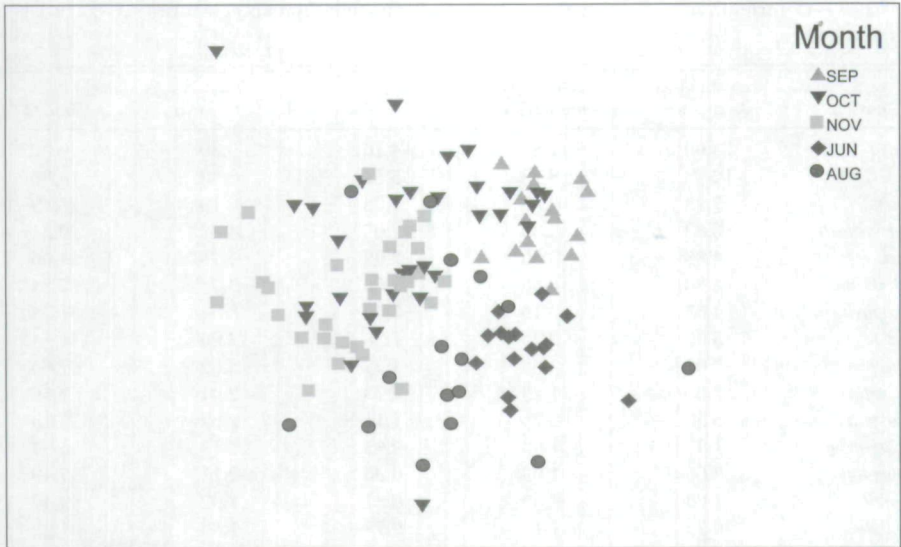
FIG. 3.—NMDS of Macrofungal seasonality at Brownfield and Trelease Woods

between months, regardless of year of study or forest (R = 0.392, P = 0.0001). Pairwise ANOSIM comparisons of monthly fungal assemblages were analyzed and fungal communities were found to be significantly different for all months of the study.

Peak fruiting seasons were noted for nearly all of the most important genera (Table 4). However some genera (*e.g.*, *Mycena* and *Coprinellus*) did not display peak fruiting and were likely heavily influenced by small-scale precipitation events rather than changes in temperature. Due to targeted collection following precipitation events, the abundance data for these genera are potentially inflated. The majority of genera had peak fruiting

TABLE 4.—Average monthly study plot abundances and observed fruiting preferences of 12 seasonal genera. Column 1 indicates fruiting preference: Sp = Spring, Su = Summer, Fa = Fall, Wi = Winter, – = No Preference

Seasonal preference	Fungus	Jun.	Aug.	Sept.	Oct.	Nov.
—	*Mycena*	3.13	1.06	7.94	2.94	1.47
Wi	*Irpex*	2.75	1.00	0.31	1.38	1.84
Fa	*Hymenochaete*	0.25	0.13	0.00	0.91	1.97
Su	*Xylaria*	3.31	0.63	0.56	0.16	0.19
Su	*Schizophyllum*	2.13	0.75	0.19	0.16	0.25
Wi	*Poria*	0.31	0.25	0.00	0.15	0.50
Su	*Gymnopus*	2.31	0.69	0.63	0.00	0.00
Su	*Marasmius*	2.61	0.25	0.19	0.16	0.09
Su	*Xeromphalina*	2.06	0.00	0.00	0.00	0.00
Su	*Psathyrella*	0.75	0.13	0.13	0.13	0.13
Fa	*Bisporella*	0.00	0.06	0.25	0.19	0.34
—	*Coprinellus*	0.63	0.38	0.38	0.06	0.22

TABLE 5.—Parameters of taxon richness calculated by Estimates

Forest	Chao 1	Chao 2	Jacknife 1	Jacknife 2	Bootstrap	ICE	ACE
Brownfield	84.11	83.81	83.81	95.67	72.45	82.59	79.21
Trelease	40.00	41.95	44.92	48.89	40.24	41.90	41.34

during the summer months (Jun.–Sept.) whereas relatively fewer genera had peak fruiting during the fall (Oct.–Nov.) and winter months.

Brownfield Woods was the richer site, with all estimators indicating nearly twice as many taxa as in Trelease Woods (Table 5). *Jacknife 2* provided the highest estimate of taxon richness at both sites whereas *Chao 1* provided the lowest estimate at Trelease Woods and *Bootstrap* provided the lowest estimate for Brownfield Woods. In comparing the utility of these estimators of taxon richness in macrofungal communities, Schmit *et al.* (1999) found none of the estimators to accurately and predictably apply to their data.

A sample-based rarefaction curve of taxon accumulation (Gotelli and Colwell, 2001) was created for each forest (Fig. 4). Though neither accumulation curve was clearly asymptotic, the rarefaction curve of Trelease Woods is visibly nearer to an asymptote than that of Brownfield Woods. Furthermore, the rarefaction curve of Trelease Woods is lower than the taxon accumulation curve of Brownfield Woods. Thus, these results suggest that the macrofungal community at Brownfield Woods was substantially more diverse than what was encountered at Trelease Woods.

A fall 2007 woody tree survey revealed the forest divisions had significantly different vegetation communities (R = 0.224, P = 0.0015), but significant differences were not seen in the woody vegetation communities between forests (R = 0.113, P = 0.3536). *Acer*, the most abundant woody plant genus, was the least important woody plant genus in delineating forest divisions due to uniformly high abundances at all sites.

The tree survey data reported in Edgington (1991) were related to fungal communities at Brownfield and Trelease Woods. Number of trees >3 cm diameter at breast height were found to differ significantly between forests (R = 0.203, P = 0.044), with Trelease Woods having larger numbers of trees >3 cm DBH; however, no significant associations were found between forest divisions (R = 0.098, P = 0.194). Total basal area (ft^2) occupied by trees was also examined, but only marginal significance was found between forests (R = 0.103, P =
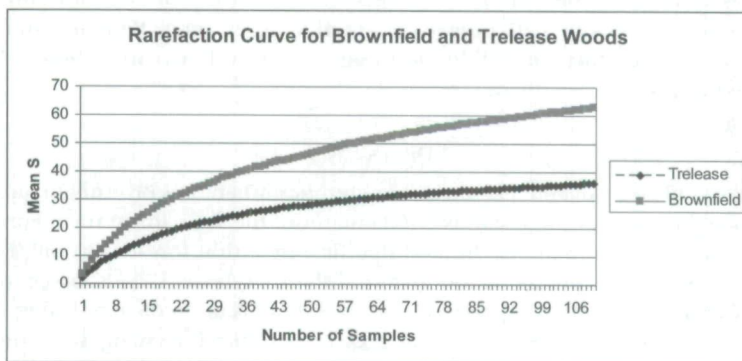

FIG. 4.—Mean taxon rarefaction curve for Brownfield and Trelease Woods

TABLE 6.—Relate results of correlation between monthly environmental variables and changes in the fungal community

Factor	R	P
Monthly rainfall	0.185	0.001
Monthly humidity	0.134	0.001
Air min	0.249	0.001
Air max	0.243	0.001
Air mean	0.244	0.001
10 cm Soil Temp	0.261	0.001

0.084) and no significant association was found between forest divisions (R = 0.037, P = 0.296).

Leaf litter composition did not significantly differ between forests (R = −0.78, P = 0.6684) but did vary significantly between forest divisions (R = 0.195, P = 0.031). None of the pairwise comparisons of leaf litter composition between forest divisions were found to be significant, though marginal significance was observed between South Brownfield and South Trelease (R = 0.323, P = 0.057), North Trelease and South Trelease (R = 0.167, P = 0.086) and North Brownfield and North Trelease (R = 0.260, P = 0.087). Of the marginally significant comparisons above, only South Brownfield and South Trelease were found to have significantly disparate fungal communities.

Measurable quantities of leaves *Quercus, Acer,* unidentified leaflets, as well as detritus and wood fragments were obtained from each area and thus these leaf litter components were considered appropriate for comparison singly. *Platanus* and *Tilia* leaves, as well as herbaceous material and fruits of woody species were not obtained in measurable amounts from all study areas; therefore, the influence of these variables on fungal communities was considered only when comparing the total leaf litter composition between groups. Miscellaneous leaf fragment composition was found to significantly differ between forests (R = 0.266, P = 0.017). Pairwise comparisons of the total composition of leaf litter between forest divisions yielded no significant differences.

Data from the Illinois WARM program were compared to monthly fungal assemblages (Table 6). Each factor was significantly correlated with monthly changes in the fungal community based on equivalent multivariate dispersion between factors and fungal communities. The temperature of the soil at 10 cm depth showed the strongest association with changes in fungal communities (R = 0.261, P = 0.001), whereas monthly humidity correlated least with changes in fungal communities over time. Rainfall, humidity and measures of air temperature were all found to significantly differ yearly, whereas 10 cm soil temperature was no significantly different.

DISCUSSION

We found significantly dissimilar fungal communities inhabiting Brownfield and Trelease Woods despite the fact that these stands are remnants of the same forest tract. Furthermore, the fungal and plant communities differed significantly within forests. Overall, Brownfield Woods had substantially higher taxon richness than Trelease Woods based on several estimators. Certain genera of fungi were found to be important in distinguishing the fungal communities and the wide array of fungal taxa responsible for changes in communities demonstrated the complexity of the fungal communities at Brownfield and Trelease Woods. SIMPER analysis showed within- and between-site differences to be primarily the

consequence of differences in relative abundances at a particular site, rather than the presence or absence of a particular fungal taxon.

The SIMPER analyses showed that the following fungal taxa were most important in characterizing the fungal communities at Brownfield and Trelease Woods: *Mycena, Irpex* and *Hymenochaete.* The results of this analysis suggest that by narrowing the sampling requirements to these few taxa, the fungal communities of old-growth prairie groves may be more easily characterized, reducing the need for intensive taxonomic training. However, by restricting the sampling of other sites to these taxa, researchers would be ignoring the rare and unique taxa. Therefore, it is suggested that future studies of fungal diversity in similar sites continue to sample all taxa but pay particular attention to the abundances of characteristic taxa.

The forest divisions with significantly different fungal communities were not found to significantly differ in regards to woody vegetation communities present. This may indicate that fall fruiting fungi are not as strongly correlated with woody plant communities as previous research indicated (Wilkins *et al.*, 1937; Liang *et al.*, 2007). Other measures of woody plant effects, such as canopy cover, dominance and proportion of ectomycorrhizal species should be considered for future studies as the addition of these variables would likely bring higher resolution to the delineations between sites and may serve to demonstrate which measures of woody plant effects exhibit the greatest influence on fungal communities.

The correlation between fungal diversity and woody plant diversity is well established (Bills *et al.*, 1986; Hawksworth, 1991; O'Dell *et al.*, 2004); consequently, the patterns of fungal community diversity are expected to correlate strongly with communities of woody plants. It is, thus, interesting that while the fungal communities present at both sites differed significantly enough to allow for delineation both between forests and within forests, woody plant communities did not always show the same disparity. The communities of woody vegetation at Brownfield and Trelease Woods were found to vary significantly at narrower spatial scales, but large-scale differences in vegetation communities have apparently not yet developed between the forests or the woody plant communities of both forests have been forced to develop along similar successional pathways due to the increasing dominance of *Acer saccharum.*

Due to the relative isolation of both forest remnants for more than 120 y, changes in the woody plant communities and fungal community composition would be expected according to the theory of island biogeography (MacArthur and Wilson, 1967). Though the rate of expected divergence of woody trees due to isolation of populations is not well studied for temperate forests, Harris and Miller (1984) suggest that changes in woody plant community structure begin within 50 y of separation of forest into disjunct fragments. The isolation period of Brownfield and Trelease Woods more than satisfies this requirement. At present, island biogeography theory has not been applied to terrestrial macrofungi; but studies of fungal colonization of leaves (Andrews *et al.*, 1987), hypogeous fungi on islands (Weden *et al.*, 2004) and resource utilization in soil (Wildman, 1987) indicate island biogeography theory applies in fungal systems.

The individual components of fungal communities at Brownfield and Trelease Woods were shown to vary significantly in response to changes in season (Table 4). The fall fruiting period, from mid-Sept. to early-Nov. is typically a highly active period of reproduction for many temperate macrofungi (Dix and Webster, 1995). As deciduous trees mobilize nutrients from the canopy and sequester them into the roots in preparation for leaf senescence, mycorrhizal associates respond with a late season flush of sporocarp

production. Nonetheless, the expected flushes of sporocarp production may not occur due to drought, fire or other stressors on forest communities (Dix and Webster, 1995). The rainfall levels for 2007 were lower than were measured rainfall in 2006, which may have influenced observed patterns in fungal diversity.

Our results indicate a predictability of occurrence for several fungal taxa. The fungal communities of Brownfield and Trelease Woods were shown to change significantly between months and *Mycena, Irpex* and *Hymenochaete* were most indicative of changes in the fungal community. Sampling at additional sites wouldbe needed in order to evaluate whether the indicators of fungal fruiting phenology from Brownfield and Trelease Woods are more broadly applicable.

Composition of fungal communities differed between years and this likely corresponds to inter-annual variations in humidity, rainfall and air temperature between 2006 and 2007. Additional years of study would be helpful in assessing the annual variation of fungal taxa to determine if the observed differences between years were the result of random inter-annual variation or if a stronger association with yearly weather patterns exists.

Soil temperature at 10 cm and ambient air temperature were the two environmental variables most strongly correlated with changes in fungal communities. The correlation between ambient soil temperature and fungal fruiting has been previously observed (Arnolds, 1992). Previous authors (Dix and Webster, 1995) have suggested that terrestrial macrofungi likely use changes in ambient soil temperature as a cue to initiate production of sporocarps, with peak fruitings in response to local precipitation events. Our results support this conclusion as well: all measures of temperature were found to be more important in predicting macrofungal fruiting patterns than measures of humidity and rainfall.

The parameters of taxon richness calculated for this study can be compared to published studies of fungal communities to determine how fungal community diversity of prairie groves compares to that of other sites. During the first 3 y of their study investigating macrofungi on the Indiana Dunes National Lake Shore, Schmit *et al.* (1999) calculated higher diversity values for each taxon richness parameter. However, the estimates of taxon richness employed in that study were based on species rank comparisons rather than genus rank comparisons used here.

The total number of species-ranked taxa (209) encountered during this study is similar to observed values from previous studies from hardwood forests. For example Schmit *et al.* (1999) recorded 177 species in 3 y of study, Brunner *et al.* (1992) recorded 124 species in 4 y of study in *Alnus* forest in Alaska, and Villenueve *et al.* (1989) reported 89 species in 2 y of study in Quebec. The continuation of this study would doubtlessly reveal new occurrences of macrofungi due to the relatively random production of terrestrial macrofungal sporocarps despite the presence of mycelium (Dix and Webster, 1995) and lead to increased resolution in differentiating forests. Thus, estimators of species richness and taxon accumulation curves are essential tools for comparing macrofungal communities from different habitats. The taxon accumulation curve (Fig. 4) showed that the fungal communities of Brownfield and Trelease Woods were similar to other hardwood forests (*e.g.,* Brunner *et al.,* 1992; Schmit *et al.,* 1999).

The results of this study may be useful for comparison during habitat restoration projects in order to gauge the effectiveness of restoration efforts. The prairie grove habitat type was one of the first to be settled and modified for agricultural production by European settlers in Illinois and the Midwest (Peattie, 1938) and as a result, is now one of the rarest habitats in the state. Several projects are in place to restore prairie grove habitats in Illinois, the Somme Prairie Grove in Cook County and Baber's Woods in Edgar County (McClain and Ebinger,

1968) are examples, and these results may be useful by providing points of comparison to the restoration efforts of those studies. However, it should be noted that even Brownfield and Trelease Woods no longer exist in their natural states due to the extirpation of species such as *Ulmus americana* and the emergent domination of shade-tolerant *Acer saccharum*, among other influences which have greatly changed the composition of fungal communities at these sites. The continued long-term alteration of prairie ecosystem processes and successional pathways by fire suppression will change macrofungal communities at these sites. The isolation and fragmentation of prairie grove habitats is influential in reducing fungal community diversity and will doubtlessly lead to accelerated loss of diversity in some of the most accessible and unique ecosystems in the Midwestern United States.

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APPENDIX.—List of all species encountered at Brownfield and Trelease Woods during this study

Agaricus campestris	Ceratiomyxa fruticulosa	Cyathipodia villosa
Agaricus sp. 1	Ceratiomyxa sp.	Cyathus striatus
Agaricus sp. 2	Cerrena unicolor	Dadaleopsis confragosa
Agaricus sp. 3	Cheimonophyllum	Daldinia concentrica
Agrocybe pediades	candidissimum	Diatrypaceae sp.
Agrocybe sp. 1	Chlorociboria aerugenescens	Ductifera pululahuana
Agrocybe sp. 2	Chlorosplenium versiforme	Entoloma sp. 1
Aleuria aurantia	Ciboria peckiana	Entoloma sp. 2
Arcyria cinerea	Comatricha aequalis	Entoloma sp. 3
Armillaria gallica	Coprinellus disseminatus	Eutypa spinosa
Armillaria mellea	Coprinellus micaceus	Exidia glandulosa
Armillaria rhizomorphs	Coprinellus radians	Exidia recisa
Armillaria sp. 1	Coprinellus radians ozonium	Exidia sp.
Armillaria sp. 2	Coprinelluus domesticus	Flammulina velutipes
Armillaria tabescens	Coprinus atramentarius	Fuligo septica
Artomyces pyxidatus	Coprinus sp. 1	Galerina marginata
Auricularia auricula	Coprinus sp. 2	Galerina sp. 1
Bertia moriformis	Coprinus variegatus	Galerina sp. 2
Bisporella citrina	Cordyceps variabilis	Ganoderma applanatum
Bjerkandera adusta	Cortinarius hinnuleus	Geastrum saccatum
Bolbitius reticulatus	Cortinarius iodes	Gerronema strombodes
Boletus bicolor	Cortinarius sp.	Grifola frondosa
Boletus sp. 1	Creopus gelatinosus	Gymnopus dryophilus
Boletus sp. 2	Crepidotus applanatus	Gymnopus subnudus
Cantharellus lateritius	Crepidotus crocophyllus	Gyrodon merulioides
Cantharellus sp.	Crepidotus sp.	Hohenbuehelia petaloides

APPENDIX.—Continued

Hydnochaete olivaceum	Perenniporia ohiensis	Russula densifolia
Hymenochaete sp. 1	Peziza badioconfusa	Russula silvicola
Hymenochaete sp. 2	Peziza sp.	Russula sp.
Hymenochaete tabacina	Phanerochate chrysorhiza	Sarcoscypha dudleyi
Hymenoscyphus calyculus	Phellinus gilvus	Sarcoscypha occidentalis
Hymenoscyphus fructigenus	Pheogenea fagicola	Schizophyllum commune
Hymenoscyphus sp.	Phlebia incarnata	Scleroderma sp.
Hypoxylon fragiforme	Phlebia radians	Scutellinia scutellata
Hypoxylon multiforme	Phlebia tremellosa	Simocybe centunculus
Hypoxylon sp.	Pholiota sp.	Spinellus fusiger
Inocybe calospora	Pleurotus pulmonarius	Spongipellis pachydon
Inocybe fastigiella	Pluteus admirabilis	Steccherinum ochracium
Inocybe sp. 1	Pluteus cervinus	Stereum complicatum
Inocybe sp. 2	Pluteus longistriatus	Stereum ostrea
Irpex lactius	Pluteus seticeps	Thelephora terrestris
Ischnoderma resinosum	Pluteus sp. 1	Trametes conchifer
Laetiporus cincinnatus	Pluteus sp. 2	Trametes elegans
Laetiporus sulphureus	Pluteus tomentosulus	Trametes hirsuta
Lepiota americana	Polyporus alveolaris	Trametes versicolor
Lepiota cristata	Polyporus arcularius	Trichaptum biforme
Lepiota sp. 1	Polyporus badius	Trichoderma sp.
Lepiota sp. 2	Polyporus brumalis	Tubaria sp. 1
Lycogala epidendron	Polyporus elegans	Tubaria sp. 2
Lycoperdon perlatum	Polyporus picipes	Tubercularia vulgaris
Lycoperdon pyriforme	Polyporus sp. 1	Tubifera ferruginosa
Marasmiellus nigripes	Polyporus sp. 2	Tyromyces chioneus
Marasmiellus opacus	Polyporus squamosus	Xeromphalina tenuipes
Marasmiellus sp.	Poria latitans	Xerula furfuracea
Mycena laeana	Poria sp.	Xerula megalospora
Mycena luteopallens	Poria spissa	Xerula sp. 1
Mycena niveipes	Psathyrella candolleana	Xerula sp. 2
Mycena sp. 1	Psathyrella sp. 1	Xylaria acuta
Mycena sp. 2	Psathyrella sp. 2	Xylaria hypoxylon
Mycena sp. 3	Psathyrella sp. 3	Xylaria immature
Mycena sp. 4	Psathyrella sp. 4	Xylaria longiana
Mycena sp. 5	Psathyrella sp. 5	Xylaria polymorpha
Panellus stipticus	Psathyrella sp. 6	Xylaria sp.
Panus conchatus	Psathyrella velutina	Xylobolus frustulatus
Parasola plicatilis	Resinomycena rhododendri	Xylocoremium sp.