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Terrestrial Macrofungi Of Old-Growth Prairie Groves

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Terrestrial macrofungi of old-growth prairie groves

(TITLE)

BY

Vincent P. Hustad

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TERRESTRIAL MACROFUNGI IN OLD-GROWTH PRAIRIE GROVES

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ABSTRACT

The purpose of this study was to evaluate and contrast the communities of terrestrial macrofungi of Brownfield and Trelease Woods, Champaign Co., IL; old-growth prairie groves isolated for >120 years. This study represents the first known analysis of fungal communities in old-growth prairie grove ecosystems in the Midwestern United States, and provides an excellent opportunity to characterize the fungal biodiversity of established old-growth reference communities for comparisons with other sites, both local and distant. Fungal communities were sampled during the fall fruiting seasons of 2006 and 2007 using a plot frequency study of fungal abundance. Several estimators of species richness were utilized to estimate species richness of fungal communities and for comparison with other studies of fungal diversity. Environmental factors thought

to influence fungal communities (rainfall, humidity, air temperature, soil temperature at 10 cm depth, leaf litter composition, and woody plant communities) were surveyed and compared to fungal communities using multivariate permutational statistics. 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 having the strongest correlation to changes in community composition. Species richness indices of fungal communities at Brownfield and Trelease Woods were compared with other known studies of fungal biodiversity. Brownfield and Trelease Woods, formerly part of a contiguous prairie grove with likely identical fungal communities, are thus suggested to have developed significantly different fungal communities over a period of isolation of more than 120 years.

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Introduction and Literature Review

Fungi are integral components of terrestrial ecosystem function, responsible for much of the decomposition and recycling of nutrients, as well as carbon and nitrogen fixation. 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) conservatively estimates the number of fungi existing in nature to be greater than 1.5 million species, of which fewer than 100,000 have been described. Fungi exhibit both asexual (anamorph) and sexual (teleomorph) reproduction. Anamorphic fungi produce conidiospores genetically identical to the parent cells, whereas teleomorphic fungi, though sometimes capable of asexual reproduction, produce spores through sexual reproduction as well, allowing for genetic recombination. Spores of both anamorphic and teleomorphic fungi are adapted to aid in dispersal and survival (Dix and Webster, 1995).

The term macrofungus refers to any fungus which produces a fruiting structure (sporocarp) that is larger than 1 mm in diameter and is visible to the naked eye (Arnolds, 1992). Macrofungi are typically understood to belong to the orders Basidiomycota and Ascomycota, although certain members (those which produce conspicuous fruiting structures) of the Myxomycota, Zygomycota and Deuteromycota may also be included as they serve functionally equivalent ecological roles (Hora, 1972; Arnolds, 1992).

The field of fungal biodiversity is woefully understudied throughout North America and the rest of the world. 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 (Hawksworth, 1991), rather than on understanding fungal diversity on a local scale. In the northern hemisphere, studies of fungal diversity and species richness have been completed 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, 1991; Straatsma et al., 2001).

The majority of surveys of fungal diversity have centered exclusively around collections of macrofungal sporocarps. However, the ephemeral nature of macrofungal sporocarps proposes a unique set of challenges to studies of macrofungal diversity. At any time, many teleomorphic fungi present at a particular site will not be actively fruiting, thus results based on a single period of collection cannot be considered accurate. In order to get a good understanding of the species present at a particular site, several visits to the site must be made throughout the sampling season. Sampling intervals vary between studies, ranging from one period of collection per year (Parker-Rhodes 1950) to collections at weekly intervals (Vogt et al., 1992; Straatsma, 2001), nonetheless macrofungi were sampled several times yearly in the majority of studies. Moreover, some

species may not even fruit every year, so multiple years of sampling are required (Lodge et al., 2004).

Populations of macrofungi are particularly difficult to quantify. Individuals can rarely be distinguished in the field because an individual mycelium may produce several sporocarps or only a few. Studies have been conducted in which the number of sporocarps produced by a species or the total biomass of the dried sporocarps is quantified (Hering, 1966; Parker-Rhodes, 1950; Parker-Rhodes, 1955; Richardson, 1970), however Straatsma et al. (2001) argues that this method is appropriate only when researchers are interested in the sporocarps themselves, e.g. the sporocarps are important food sources for animal species. By quantifying populations in this method, preference is differentially given to those species which allocate larger amounts of resources to reproduction, thus the ecological significance of species may not be correctly estimated. Furthermore, the sizes, numbers, and dry weights of sporocarps vary greatly among taxa (O'Dell et al., 2004) and sporocarps represent a small fraction of the total biomass of the individual, including the vegetative mycelium (Dix and Webster, 1995).

The method of quantifying fungal abundance used in the majority of studies (Bills et al., 1986; Villenueve et al., 1989; Lodge and Cantrell, 1995) is to divide the study area into a number of subplots and then to determine fungal abundance by observing the number of subplots in which a species is found to occur. This method is not without limitations, however, as the absence or presence of a species within a subplot may not be informative. Arnolds (1992) and other authors

(Dahlberg and Stenlid, 1990; Thompson and Rayner, 1982) have pointed out that it is possible for the mycelium of a fungus to occur within the subplot but the sporocarps are produced outside of the subplot, or for the mycelium to produce sporocarps within several neighboring subplots. Despite the drawbacks, the subplot method is generally preferred (Arnolds, 1992; Straatsma et al., 2001).

Thus, approaches to studying macrofungal ecology typically follow one of two approaches: the opportunistic approach (O'Dell et al., 2004) which involves one to several collectors randomly walking an area to be sampled, collecting conspicuous specimens of select taxa and quantifying diversity based on the frequency of sporocarp production; or the plot frequency approach in which the number of subplots in which a fungus is found to occur is quantified (Wilkins et al., 1937; Ohenoja, 1984). The methods of sampling must be chosen to fit the goals of the particular study.

The opportunistic approach of sampling macrofungi is likely the easiest and least intensive method of sampling macrofungi in use today. However, the opportunistic approach does not allow for rigorous comparisons of different sites because sampling intensity is not uniform at each site. Furthermore, the likelihood of overlooking cryptic species is much higher when the opportunistic approach is used (Lodge et al., 2004).

The plot frequency approach is considered to be the best measure of species abundance at a particular site because it reflects the minimum area occupied by a species in a study site (O'Dell et al., 2004). The likelihood of overlooking cryptic

species is greatly reduced because all taxa fruiting at the time of collection are collected and scrutinized. Nonetheless some macrofungi will doubtlessly be missed, regardless of the intensity or length of sampling. For example, Straatsma et al. (2001) reported several species which fruited only once in a 21-year period during a long-term plot study in Switzerland. Taxon-effort curves of several studies (Schmit et al., 1999; Bills et al., 1986; Straatsma et al., 2001) have continued to show increases in the numbers of unique taxa several years into the study.

Other drawbacks to the plot frequency approach exist as well. Often, collections of sporocarps are identifiable only to the genus rank because collections of all developmental stages of the sporocarp cannot be made. Another drawback is that sporocarps distributed over several sampling units at a site may have originated from one large or several small mycelia (Jacobsen et al., 1993; Dahlberg and Stenlid, 1990). Thus plot frequency studies, though more accurate than opportunistic surveys of macrofungal diversity, provide only a rough estimate of the abundance and importance of terrestrial macrofungi.

Owing to the current paucity of fungal diversity studies and research into the distribution and abundances of macrofungi in North America, much work needs to be done to determine fungal diversity at the local level. In order to understand the effects of management practices and other types of environmental modifications on fungal communities, reference communities of fungal biodiversity should be established. Old-growth forests provide an excellent

opportunity to characterize the fungal biodiversity of established reference communities of fungal biodiversity for comparison with other sites, both local and distant.

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). Once part of a larger, pre-settlement prairie grove known as the Big Grove that occupied a 16 km^2 area along the Salt Fork of the Vermillion River (Telford, 1926), Brownfield and Trelease Woods are approximately 2.5 km apart and entirely disjunct, surrounded by second growth forest fragments, agricultural fields, housing developments and prairie preserves. 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 from other forest fragments, being surrounded entirely by fields and prairie preserves.

Both sites are approximately 24 ha in size (600m x 400m), 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 virgin, 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 maintained by the University of Illinois at Champaign-Urbana for more than 120 years and are used primarily as research reserves. Both sites have 50 x 50 m plots established throughout with permanent stakes at the corners of each plot and trees in the north and south direction marked by spray tagging. 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, J., 1980), and canopy tree mortality (Cortright, 1952). However, to date there have been no studies of fungal biodiversity carried out at either site.

The purpose of this study is: 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 at both sites; 5) to determine which site-specific environmental factors correspond most strongly with the fungal assemblages at both sites as well as which seasonal environmental factors are most strongly correlated with

observed changes in seasonality of fungal assemblages; and 6) to compare the fungal communities at Brownfield and Trelease woods to other known studies of fungal diversity.

Methodology

A plot frequency method of analysis was chosen for this survey to characterize the fungal communities at both sites during 2006 and 2007. Brownfield and Trelease Woods were separated into north and south divisions and within each division, five 100 m permanent transects were established. The occurrence of terrestrial macrofungal sporocarps, including fungi inhabiting wood fragments <15 cm in diameter were monitored at 10 m intervals on each transect. At each 10 m interval, a permanent center point was established and all terrestrial macrofungi within a 2 m radius of the center point were recorded. Sampling design follows 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, the sporocarps were collected, examined in the lab, and identified to the lowest identifiable taxon. In order to facilitate statistical comparison between sites, transects were grouped into four 50 x 50 m study areas within each forest division, resulting in four north and four south areas of study in each forest, for a total of 16 study areas (Figure 1). Each site was visited approximately twice monthly during the months of September, October and November of 2006 as well as June, August, October, and November of 2007.

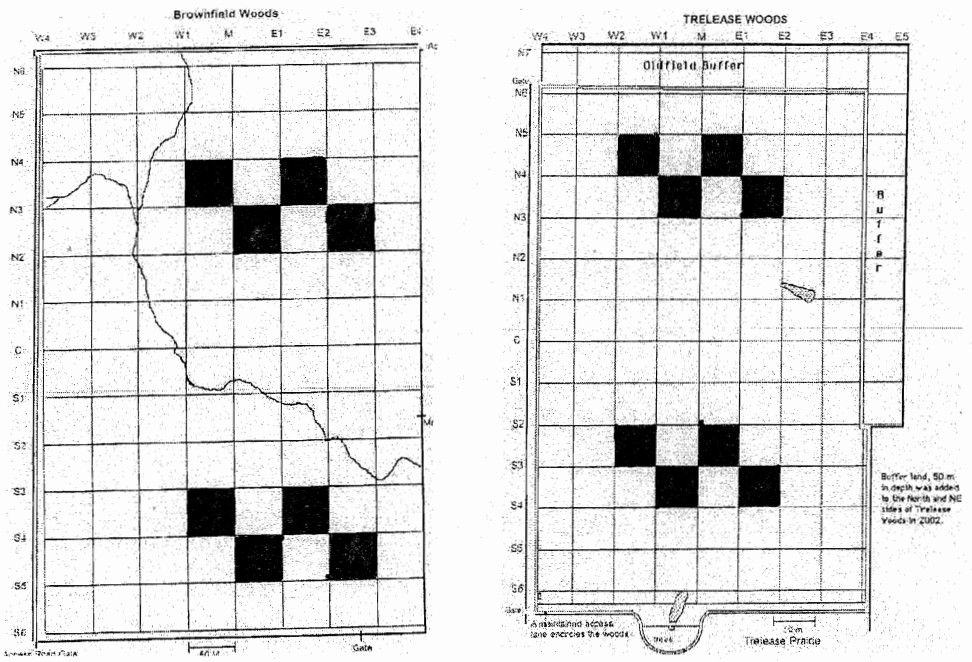

Figure 1: Location of study areas within Brownfield and Trelease Woods, each colored square represents a 50 x 50 m plot.

Statistical comparisons of the entire species set of the fungal communities at each site were performed using Primer-e., v. 6.1.6 (Primer-e, Ltd. Plymouth, UK). Taxonomic data were aggregated to the genus rank for statistical comparison in order to facilitate statistical analyses by removing singly encountered taxa (singletons). Bray-Curtis similarity matrices (Bray and Curtis, 1957) were calculated to determine the similarity of fungal species between sites. Ordination of data was performed using non-metric multidimensional scaling (MDS) (Kruskal, 1964).

Non-metric MDS is a method of ordination of samples in multidimensional space (the number of dimensions selected to generate the best stress response, defined on an individual case basis), which graphically demonstrates the absolute

similarity of samples to one another based on the values of similarity calculated through a similarity matrix. Thus the non-metric MDS constructs a configuration of the samples which attempts to satisfy all of the conditions imposed by the Bray-Curtis similarity matrix. The relative distance between two points in a non-metric MDS reflects the similarity of the two points, thus points which are compositionally similar will demonstrate higher spatial association in the MDS ordination than two points which are highly dissimilar (Clarke and Warwick, 2001).

In order to compare the fungal assemblages between Brownfield and Trelease Woods, to evaluate the effects of seasonality, and to determine correlations between fungal assemblages and environmental factors, analysis of similarity (ANOSIM) hypothesis tests were performed. ANOSIM is a non-parametric permutation procedure which is applied to the Bray-Curtis similarity matrix underlying the non-metric MDS ordination of the fungal assemblages in each site. The null hypothesis of the ANOSIM test is that there is no significant difference in the community composition between two *a priori* groups (Clarke and Warwick, 2001).

In order for an ANOSIM test to be performed, a test statistic (R) must first be calculated. The R statistic reflects the observed differences between sites contrasted with differences among replicates within sites using the Bray-Curtis similarities between samples. The value of R will always be between 0 and 1, where a value of 1 means that all replicates within sites are more similar to each

other than any replicates from different sites. An R value of 0 indicates that similarities between and within sites are approximately the same, i.e. there is no structure to the data; thus the null hypothesis is not rejected, and the test determines there are no differences in community composition between the a priori groups under consideration. R is calculated as follows:

$$R = \frac{(r_B - r_w)}{\frac{1}{2} M}$$

where r_B is the average of rank similarities determined from all pairs of replicates between sites and r_w is the average of rank similarities among replicates within sites. $M = n(n-1)^2$ where n is the total number of samples under consideration for the ANOSIM test.

After computing the R statistic for the community based on the similarity matrix, the R statistic is then recalculated under permutation of the sample labels. According the null hypothesis of the ANOSIM test, that there is no difference among a priori groups, the observed R value will not significantly differ from R values derived through permutation. The significance level of the observed R value is calculated by referring the observed R value to its permutation distribution. The null hypothesis is rejected if the observed R value is determined to be less than 5% likely to have arisen through permutational recombination. Significance is determined as follows:

Significance level = (t+1)/(T+1)

where t represents the number of simulated R values larger than the observed value and T represents the total number of R values simulated through permutation (Clarke and Green, 1988).

After determining significant associations between *a priori* groupings of fungal species, it was necessary to determine which fungal species were most informative in characterizing the differences between groupings. Similarity/distance percentage (SIMPER) analyses (Clarke and Warwick, 2001) were performed in order to determine the contribution of an individual genus to changes in fungal assemblages. SIMPER analysis examines the contribution of each genus to the resemblances between sample groups, determining the contribution of each genus to the similarity and dissimilarity between samples determined by the Bray-Curtis similarity matrix.

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. These estimates of taxon richness were then compared with published reports of taxon richness.

Sample-based rarefaction curves (Gotelli and Colwell, 2001) were calculated for each forest using the EstimateS software package to randomize the taxon abundances from samples 100 times and determine the mean number of taxa present per sample in each randomization. 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; and a rarefaction curve was chosen over an accumulation curve in order to more accurately assess the collection effort.

Several types of environmental data were collected from Brownfield and Trelease Woods in order for comparison with fungal assemblage data. Monthly measures of rainfall, minimum air temperature, maximum air temperature, mean air temperature, humidity, and soil temperature at 10 cm were recorded less than 1.5 km from each site as part of the Illinois Climate Network Water and Atmospheric Resources (WARM) program. Fungal communities were compared with data from Edgington (1991), which provided counts of trees >3cm in diameter at breast height as well as the basal area in square feet of all trees >3cm in diameter for each 50 x 50 m segment of both Brownfield and Trelease Woods. In addition to the 1991 data, a survey of woody species present in each collecting area was completed in Fall 2007.

Plant litter composition was analyzed following guidelines set forth in Facelli and Carson (1991). Five $1m^2$ quadrat samples of leaf litter and wood fragments <15cm diameter, not including organic matter integrated into the soil

(A_0 Horizon), were randomly collected in early Spring 2008 and pooled in each study area. A total of $40m^2$ of litter was collected for each forest, resulting in a total of 80 m^2 of litter collected for comparison between sites. Litter was sorted into nine groups: 1)wood fragments <15 cm in diameter; 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 hours at 85°C and weighed.

The RELATE procedure was used to determine the relatedness of the fungal communities to environmental variables. The RELATE analysis tests the null hypothesis that there is no difference between multivariate patterns from two sets of samples. The RELATE procedure determines an observed R value by comparing the rank correlation values of both samples derived from a resemblance matrix, the Bray-Curtis similarity matrix in this case, with randomly permuted samples. Similar to ANOSIM, an observed R value is compared to R values derived through random permutation of samples and the probability of the observed values occurring through random chance is determined. The null hypothesis, that no difference exists between the multivariate patterns, is then accepted or rejected based on arbitrarily determined probability distributions.

Results

Collections of terrestrial macrofungi were made during the months of September, October, and November of 2006 and June, August, September, and October of 2007. No site visits were made in July of either year due to low precipitation. 84 genera of terrestrial macrofungi were observed in Brownfield and Trelease Woods during 2006 and 2007. A total of 75 genera of terrestrial macrofungi were observed in Brownfield Woods, of which 26 (Table 1) were found only in Brownfield Woods during the sampling period. 58 genera were observed in Trelease Woods with 9 genera (Table 2) found to occur in only Trelease Woods during the sample period.

Table 1: Genera Unique to Brownfield Woods

Agaricus	*Lycogala*
Agrocybe	*Marasmiellus*
Boletus	*Panellus*
Cantharellus	*Phellinus*
Cerrena	*Pholiota*
Chlorociboria	*Pleurotus*
Cyathus	*Scleroderma*
Dadaleopsis	*Simocybe*
Daldinia	*Thelephora*
Entoloma	*Trichoderma*
Flammulina	*Tubercularia*
Geastrum	*Tyromyces*
Grifola	*Xylocoremium*

Table 2: Genera Unique to Trelease Woods

Auricularia
Bertia
Bolbitius
Coprinopsis
Cyathipodia
Ductifera
Fuligo
Gerronema
Ischnoderma

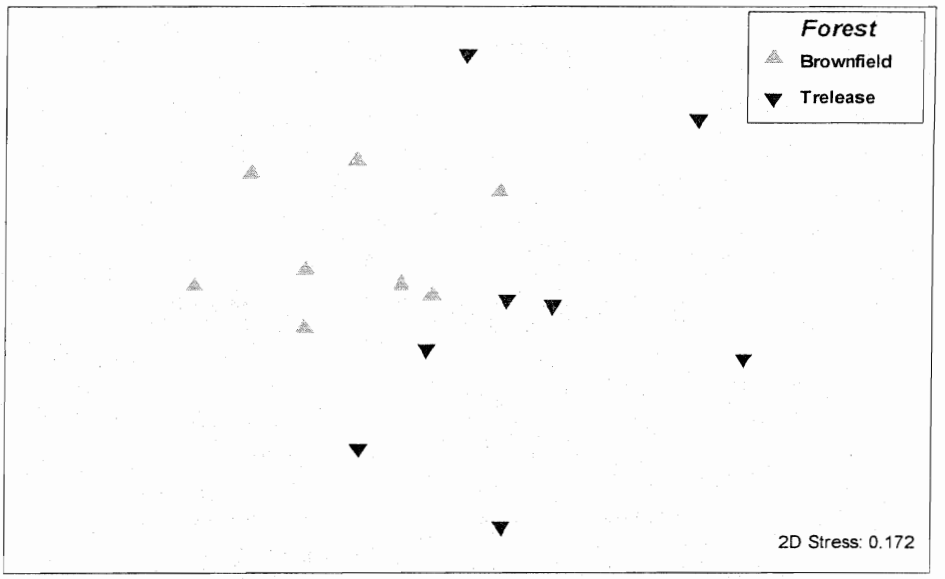

Figure 2: NMDS ordination of fungal assemblages by forest

Figure 2 is a non-metric MDS ordination of the fungal assemblages at Brownfield and Trelease Woods from 2006 and 2007. Points which are in nearer spatial association are more compositionally similar and similarity between sites decreases with distance between points. Brownfield and Trelease Woods appear to separate into two distinct groups, however a hypothesis test must be performed in order to quantify the strength of association between sites.

To test the null hypothesis that the fungal assemblages at Brownfield and Trelease Woods are not significantly different, the ANOSIM test was performed (Figure 3). The results of the ANOSIM test reject the null hypothesis and show fungal assemblages to significantly differ between Brownfield and Trelease Woods ($R=0.212$, $P=0.005$), i.e. there is less than a 0.5% chance that the fungal assemblages are identical between forests.

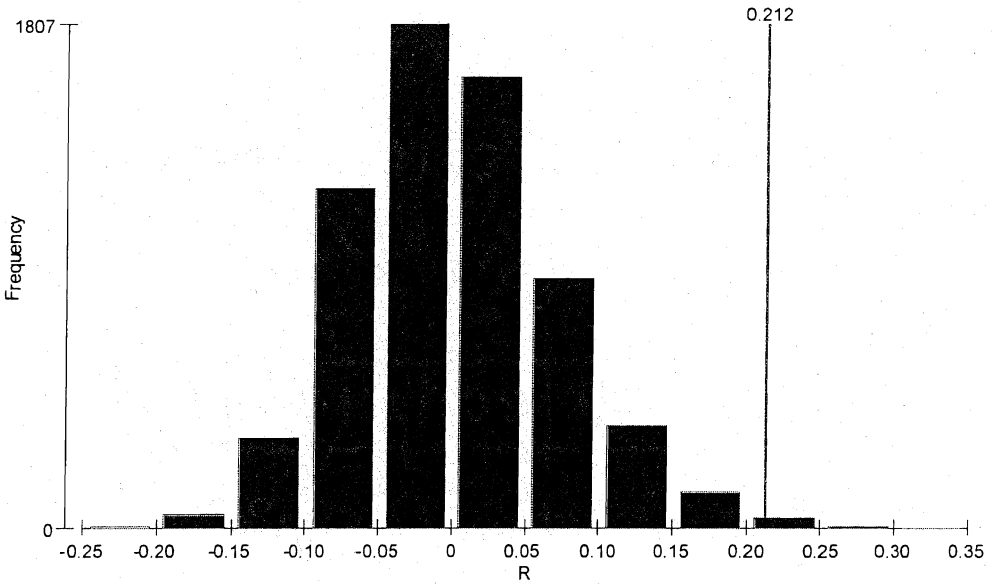

Figure 3: ANOSIM test of fungal assemblages in Brownfield and Trelease Woods. The observed R value (0.212) is compared to the R values calculated through 10,000 permutations.

Fungal assemblages were examined under NMDS ordination in order to evaluate the influence of forest division on fungal assemblages (Figure 4). Forest divisions appear to harbor separate fungal assemblages with some groups, e.g. North Brownfield, South Brownfield, and North Trelease, showing strong spatial association whereas the fungal assemblages at South Trelease are likely less compositionally similar as indicated by the lack of cohesion between points on the non-metric MDS.

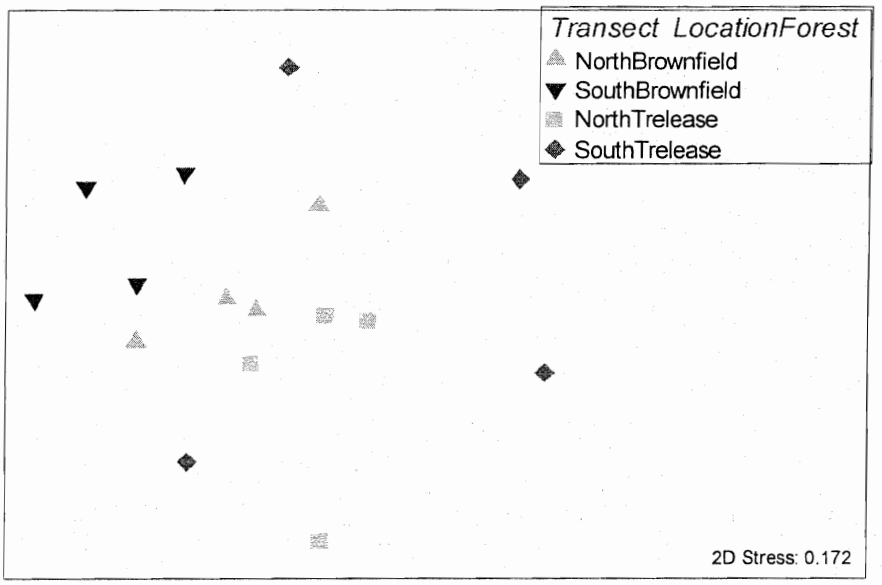

Figure 4: NMDS of macrofungal assemblages by forest division (North v South)

In order to test the null hypothesis that fungal communities do not significantly differ between forest divisions within and between Brownfield and Trelease Woods, the ANOSIM test was performed. The test rejected the null hypothesis (R=0.233, P=0.007), thus the macrofungal communities differ significantly within and between forest divisions. Pairwise tests (Table 3) demonstrated that the macrofungal community in the northern division of Brownfield Woods is 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.

Table 3: Pairwise comparisons of fungal assemblages by Forest Division. Highlighted comparisons are significant at P=0.05

Pairwise Tests Groups	R Statistic	Significance Level (P)	Actual Permutations	Number >= Observed
NorthBrownfield, SouthBrownfield	0.292	0.029	35	1
NorthBrownfield, NorthTrelease	0.063	0.229	35	8
NorthBrownfield, SouthTrelease	0.073	0.343	35	12
SouthBrownfield, NorthTrelease	0.542	0.029	35	1
SouthBrownfield, SouthTrelease	0.448	0.029	35	1
NorthTrelease, SouthTrelease	-0.042	0.629	35	22

The macrofungal communities of individual collecting areas were next compared using NMDS ordination (Figure 5).

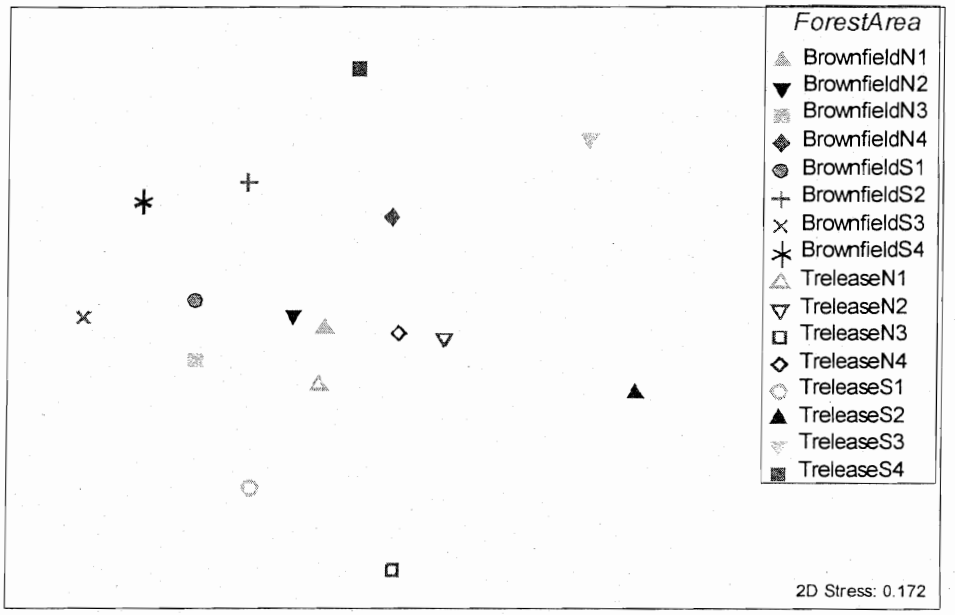

Figure 5: NMDS of macrofungal assemblages by study area

The ANOSIM test accepted the null hypothesis (R=0.132, P=0.172) that collecting areas are not significantly different from each other (Figure 6). Pairwise comparisons found no two areas to contain significantly different fungal communities over the course of the study.

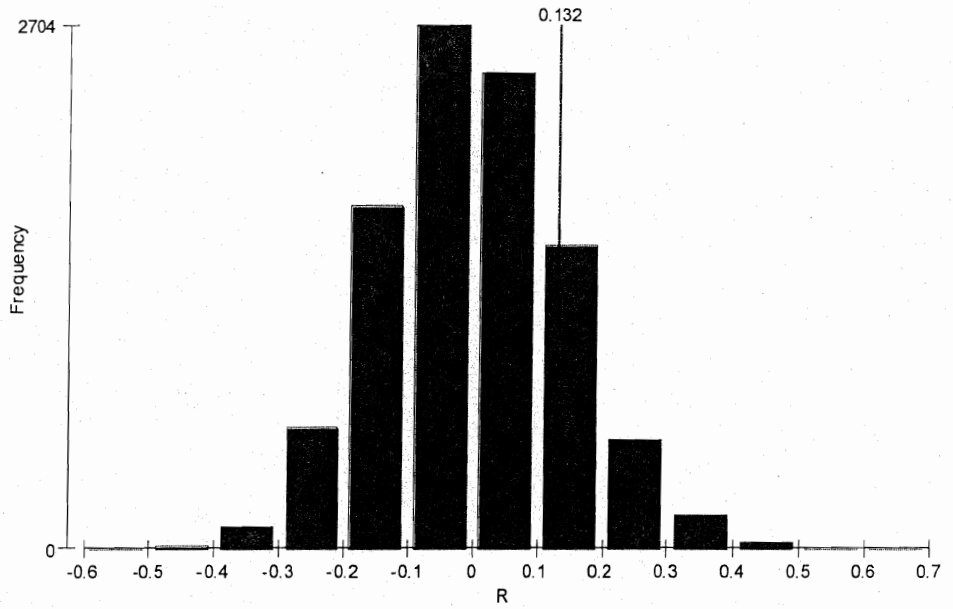

Figure 6: Results of ANOSIM tests of macrofungal assemblages between study areas at Brownfield and Trelease Woods

Thus, in order to compare fungal assemblages between sites, forest subdivisions (North or South) were determined to provide the best estimate of fungal species composition at the lowest spatial scale.

In order to determine which genera are most important in characterizing different fungal assemblages between forests and forest divisions, the SIMPER test was performed. The SIMPER test revealed 16 genera to most heavily contribute to the similarity between sites in Brownfield Woods (Table 4), with an average similarity between sites of 63.83% over the course of the study. Thirteen genera were determined to be most responsible for the similarity between sites within Trelease Woods (Table 5), 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 6).

Table 4: Results of SIMPER analysis on Brownfield Woods macrofungal community composition

Brownfield Woods Average similarity: 63.83					
Genus	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
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

Table 5: Results of SIMPER analysis on Trelease Woods macrofungal community composition

Trelease Woods Average similarity: 56.52					
Genus	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
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 6: Results of SIMPER analysis of 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

SIMPER analysis (Table 6) revealed the presence and abundance of 42 genera to be responsible for 90% of the dissimilarity between the terrestrial macrofungal communities of Brownfield and Trelease Woods. Of the 42 genera, only 3 (*Cerrena, Agaricus*, and *Grifola*) were present in only one forest. Thus, components of the complex fungal communities inhabiting Brownfield and Trelease Woods are very similar, with differences in communities the result of production of different numbers of sporocarps at each site.

The fungal communities of North Brownfield and South Brownfield (Table 7), South Brownfield and North Trelease (Table 8), and South Brownfield and South Trelease (Table 9) were analyzed using the SIMPER procedure in order to determine the significance of presence and abundance on differences between forest divisions. Within-forest comparisons yielded similar results to between-forest comparisons, however, there was greater disparity in the numbers of fungal genera collected between forests, thus the presence or absence of individual fungal genera more significantly influenced the delineation between forest divisions. Taxa which were absent in either a forest or forest division were generally genera which were rarely encountered during the course of the study, all having average abundances of less than 2 fruitings per site during the course of the study. Thus the fungal communities inhabiting Brownfield and Trelease Woods are suggested to be extremely complex, with few genera whose presence or absence alone is indicative of a particular locality.

Table 7: Results of SIMPER comparison of between North Brownfield and South Brownfield. Average Dissimilarity=37.38%

Genus	NorthBrownfield Av.Abund	SouthBrownfield Av.Abund	Av.Diss	Contrib%	Cum.%
Mycena	22.25	25.75	2.72	7.27	7.27
Hymenochaete	4.00	9.75	2.62	7.01	14.28
Irpex	10.75	15.00	2.49	6.66	20.94
Stereum	5.25	9.25	1.94	5.19	26.13
Trichaptum	2.00	5.75	1.90	5.07	31.21
Schizophyllum	5.25	4.00	1.47	3.94	35.15
Gymnopus	4.75	2.50	1.24	3.33	38.47
Marasmius	3.75	3.25	1.18	3.16	41.63
Coprinellus	3.50	1.75	1.05	2.82	44.45
Xylaria	4.25	5.50	0.90	2.42	46.87
Poria	3.50	2.50	0.88	2.34	49.21
Steccherinum	1.00	2.50	0.86	2.29	51.50
Gyrodon	0.25	1.75	0.78	2.10	53.60
Marasmiellus	0.50	1.75	0.75	2.00	55.60
Eutypa	1.75	1.75	0.73	1.96	57.56
Perenniporia	1.50	1.25	0.73	1.95	59.50
Exidia	0.50	1.75	0.69	1.83	61.34
Bisporella	1.00	1.50	0.63	1.70	63.04
Xerula	0.25	1.50	0.63	1.68	64.71
Galerina	1.25	0.50	0.60	1.60	66.31
Psathyrella	2.25	1.25	0.57	1.53	67.84
Cerrena	0	1.25	0.54	1.45	69.29
Polyporus	1.25	1.75	0.52	1.40	70.69
Crepidotus	1.25	0.25	0.52	1.38	72.07
Scutellinia	1.00	0.50	0.47	1.27	73.34
Lycoperdon	1.00	0.25	0.46	1.23	74.57
Xeromphalina	2.00	2.00	0.46	1.23	75.80
Grifola	1.00	0	0.43	1.16	76.97
Armillaria	0.75	0.75	0.41	1.09	78.06
Hymenoscyphus	0.75	1.00	0.40	1.08	79.13
Inocybe	0.75	0.50	0.35	0.95	80.08
Pluteus	0.75	0.50	0.35	0.93	81.01
Artomyces	0.50	0.50	0.34	0.91	81.91
Simocybe	0.75	0	0.33	0.90	82.81
Trametes	0	0.75	0.31	0.84	83.65
Agaricus	0.25	0.75	0.29	0.78	84.43
Coprinus	0.25	0.50	0.29	0.77	85.20
Cantharellus	0.50	0.25	0.27	0.72	85.92
Daldinia	0	0.50	0.24	0.65	86.57
Hohenbuehelia	0	0.50	0.24	0.64	87.21
Parasola	1.00	1.00	0.24	0.64	87.86
Xylocoremium	0	0.50	0.24	0.64	89.14
Tubaria	0.50	0.75	0.23	0.63	89.77
Scleroderma	0	0.50	0.23	0.62	90.39

Table 8: Results of SIMPER comparison between South Brownfield and North Trelease. Average dissimilarity=42.66%

Genus	SouthBrownfield Av.Abund	NorthTrelease Av.Abund	Av.Diss	Contrib%	Cum.%
Stereum	9.25	1.50	3.91	9.15	9.15
Mycena	25.75	19.25	3.81	8.94	18.10
Hymenochaete	9.75	3.75	3.01	7.06	25.16
Trichaptum	5.75	0.50	2.56	6.00	31.16
Irpex	15.00	12.00	2.49	5.83	37.00
Xylaria	5.50	5.75	1.68	3.93	40.92
Schizophyllum	4.00	3.25	1.47	3.45	44.37
Coprinellus	1.75	1.25	1.07	2.51	46.88
Gymnopus	2.50	3.75	1.05	2.47	49.34
Lycoperdon	0.25	2.00	1.00	2.34	51.68
Polyporus	1.75	0	0.90	2.10	53.78
Poria	2.50	1.25	0.86	2.02	55.80
Marasmiellus	1.75	0.50	0.83	1.94	57.74
Exidia	1.75	0.25	0.81	1.89	59.63
Gyrodon	1.75	0.50	0.80	1.87	61.50
Crepidotus	0.25	1.50	0.78	1.83	63.34
Marasmius	3.25	4.00	0.77	1.81	65.14
Eutypa	1.75	1.50	0.74	1.73	66.88
Bisporella	1.50	1.25	0.70	1.63	68.51
Xerula	1.50	0.25	0.69	1.61	70.12
Perenniporia	1.25	0.75	0.66	1.54	71.66
Xeromphalina	2.00	2.75	0.65	1.52	73.18
Steccherinum	2.50	1.75	0.64	1.50	74.68
Cerrena	1.25	0	0.59	1.39	76.07
Hymenoscyphus	1.00	0.50	0.50	1.17	77.24
Parasola	1.00	0	0.49	1.14	78.38
Psathyrella	1.25	0.75	0.45	1.05	79.43
Armillaria	0.75	0.75	0.44	1.03	80.46
Trametes	0.75	0.25	0.41	0.97	81.43
Agaricus	0.75	0	0.39	0.92	82.34
Scutellinia	0.50	0.75	0.38	0.90	83.24
Coprinus	0.50	0.50	0.38	0.88	84.13
Hohenbuehelia	0.50	0.50	0.38	0.88	85.01
Sarcoscypha	0.25	0.50	0.33	0.77	85.79
Artomyces	0.50	0.25	0.30	0.70	86.48
Daldinia	0.50	0	0.27	0.63	87.11
Diatrypaceae	0.50	0	0.26	0.62	87.73
Xylocoremium	0.50	0	0.26	0.62	88.35
Ciboria	0	0.50	0.26	0.62	88.97
Pluteus	0.50	0.25	0.26	0.61	89.58
Galerina	0.50	0	0.26	0.60	90.18

Table 9: Results of SIMPER comparison between South Brownfield and South Trelease. Average Dissimilarity=46.79%.

Genus	SouthBrownfield Av.Abund	SouthTrelease Av.Abund	Av.Diss	Contrib%	Cum.%
Irpex	15.00	4.25	5.71	12.20	12.20
Mycena	25.75	16.50	5.20	11.10	23.31
Stereum	9.25	3.25	3.11	6.66	29.97
Trichaptum	5.75	1.25	2.39	5.12	35.08
Xylaria	5.50	5.25	2.35	5.02	40.10
Hymenochaete	9.75	7.00	2.17	4.65	44.75
Schizophyllum	4.00	3.00	1.66	3.55	48.29
Steccherinum	2.50	1.50	1.22	2.60	50.89
Gymnopus	2.50	3.50	1.20	2.56	53.46
Poria	2.50	0.25	1.17	2.50	55.96
Exidia	1.75	0	0.91	1.95	57.90
Xeromphalina	2.00	1.50	0.91	1.94	59.85
Gyrodon	1.75	1.25	0.89	1.91	61.75
Eutypa	1.75	0.75	0.82	1.75	63.51
Marasmiellus	1.75	0.50	0.80	1.72	65.22
Bisporella	1.50	1.75	0.80	1.71	66.93
Xerula	1.50	0.25	0.71	1.52	68.46
Coprinellus	1.75	1.25	0.70	1.50	69.95
Perenniporia	1.25	0.75	0.69	1.48	71.43
Trametes	0.75	1.00	0.67	1.42	72.85
Cerrena	1.25	0	0.62	1.32	74.17
Lycoperdon	0.25	1.25	0.60	1.28	75.46
Marasmius	3.25	3.50	0.53	1.14	76.59
Hymenoscyphus	1.00	0	0.51	1.09	77.69
Crepidotus	0.25	0.75	0.48	1.03	78.72
Polyporus	1.75	1.50	0.47	1.00	79.72
Psathyrella	1.25	0.75	0.47	1.00	80.72
Parasola	1.00	0.75	0.46	0.98	81.70
Coprinus	0.50	0.75	0.45	0.97	82.67
Agaricus	0.75	0	0.41	0.88	83.55
Russula	0.50	0.5	0.41	0.87	84.41
Armillaria	0.75	0.25	0.39	0.84	85.26
Artomyces	0.50	0.50	0.39	0.84	86.09
Tubaria	0.75	0.75	0.38	0.82	86.92
Peziza	0.50	0.50	0.37	0.79	87.70
Daldinia	0.50	0	0.28	0.60	88.30
Hohenbuehelia	0.50	0	0.28	0.59	88.90
Xylocoremium	0.50	0	0.28	0.59	89.49
Scutellinia	0.50	0.25	0.28	0.59	90.08

The effects of seasonality on the fungal communities of Brownfield and Trelease Woods were next assessed with MDS ordination (Figure 7). Fungal assemblages from each forest were shown to significantly differ each month and year of study (R=0.526, P=0.0001) using the ANOSIM procedure. Fungal assemblages from each showed strong correlation by month, irregardless of year of fruiting (R=0.375, P=0.0001). When yearly and monthly changes in fungal assemblages regardless of forest were compared using the ANOSIM procedure, strong association was also exhibited (R=0.463, P=0.0001). Fungal assemblages were shown in the most liberal test, the change in assemblages between months, regardless of year of study or forest, to be significantly affected by seasonality (R = 0.392, P = 0.0001). Pairwise comparisons of monthly fungal assemblages were analyzed and fungal communities were found to be significantly different for all months of the study (Table 10).

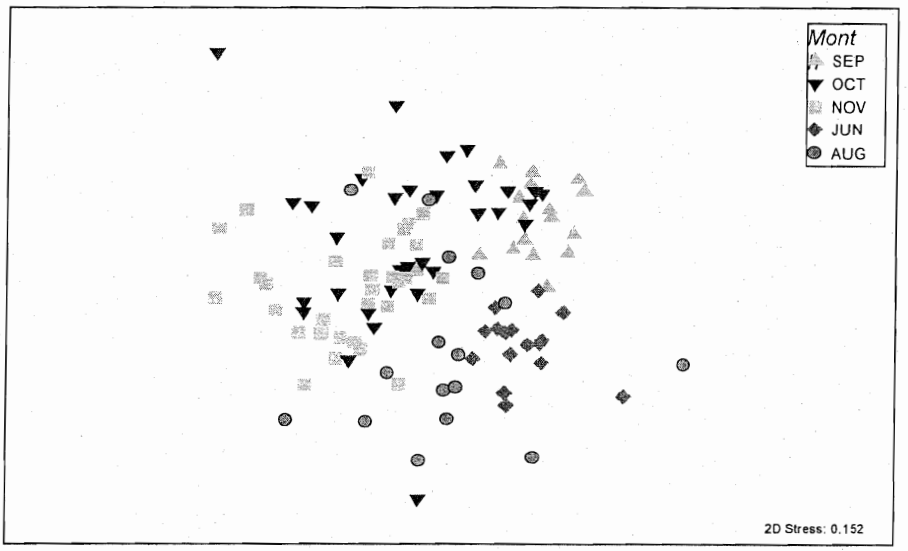

Figure 7: NMDS of macrofungal seasonality at Brownfield and Trelease Woods

Table 10: Results of pairwise ANOSIM comparisons of macrofungal communities by month

Month	R-stat	Significance
Sep, Oct	0.174	0.0006
Sep, Nov	0.672	0.0001
Sep, Jun	0.838	0.0001
Sep, Aug	0.560	0.0001
Oct, Nov	0.117	0.0020
Oct, Jun	0.453	0.0001
Oct, Aug	0.283	0.0004
Nov, Jun	0.654	0.0001
Nov, Aug	0.425	0.0001
Jun, Aug	0.468	0.0001

The SIMPER procedure was used to determine which genera were most strongly associated with changes in seasonality between sites. Table 11 and Table 12 list the within-site similarity by month (i.e. similarity of collecting areas based on presence/abundance of fungal genera) as well as which genera contribute the largest to the similarity within sites, the average abundance of genera by forest, similarity between forests, standard deviation of similarity between forests, the contribution of each species to the similarity between groups, as well as the cumulative percentage of fungal assemblage similarity for Brownfield and Trelease Woods, respectively, as determined by the SIMPER procedure.

Table 11: Results of SIMPER comparison between FOREST/MONTH/YEAR for Brownfield Woods

Year-Month (Within-site Similarity)	Genus	Av.Abund	Av.Sim	Contrib%	Cum.%
6-Sep	*Mycena*	10.63	40.00	77.46	77.46
(51.64%)	*Parasola*	1.00	3.73	7.23	84.69
	Trichaptum	1.13	1.79	3.46	88.15
	Xylaria	0.75	1.06	2.06	90.20
6-Oct	*Mycena*	1.38	18.41	67.64	67.64
(27.22%)	*Irpex*	0.50	5.60	20.56	88.19
	Cerrena	0.38	2.32	8.53	96.72
6-Nov	*Hymenochaete*	1.63	9.98	28.53	28.53
(34.97%)	*Irpex*	1.50	9.47	27.10	55.63
	Stereum	1.13	5.53	15.81	71.43
	Mycena	1.25	5.32	15.22	86.65
	Bisporella	0.50	1.05	3.00	89.64
	Eutypa	0.50	1.01	2.89	92.54
	Gymnopus	1.13	4.86	10.02	93.22
7-Jun	*Irpex*	3.75	7.53	14.29	14.29
(52.69%)	*Xylaria*	3.63	7.48	14.19	28.49
	Mycena	3.75	6.29	11.94	40.43
	Marasmius	3.13	4.39	8.33	48.75
	Gymnopus	2.63	4.35	8.26	57.01
	Xeromphalina	2.00	3.91	7.42	64.43
	Stereum	1.75	3.64	6.91	71.33
	Schizophyllum	2.38	3.58	6.80	78.13
	Eutypa	1.00	1.46	2.78	80.91
	Coprinellus	1.00	1.26	2.40	83.31
	Polyporus	1.13	1.14	2.16	85.47
	Exidia	1.13	1.14	2.16	87.63
	Trichaptum	0.88	1.11	2.11	89.74
	Steccherinum	0.75	1.04	1.97	91.71
7-Aug	*Schizophyllum*	1.00	7.35	23.17	23.17
(31.74%)	*Mycena*	1.63	5.98	18.84	42.01
	Trichaptum	0.88	4.80	15.11	57.13
	Irpex	1.00	3.03	9.56	66.68
	Stereum	0.75	2.99	9.41	76.10
	Gymnopus	0.88	2.32	7.30	83.40
	Tubaria	0.50	1.80	5.69	89.09
	Coprinellus	0.50	0.82	2.60	91.68
7-Oct	*Mycena*	2.88	19.52	37.43	37.43
(52.14%)	*Irpex*	2.88	19.33	37.08	74.51
	Hymenochaete	1.63	8.22	15.76	90.28
7-Nov	*Irpex*	2.88	17.92	34.32	34.32
(52.21%)	*Hymenochaete*	3.00	13.64	26.13	60.45
	Stereum	1.63	8.54	16.36	76.81
	Mycena	2.50	4.70	9.00	85.81
	Poria	1.38	3.44	6.59	92.39

Table 12: Results of SIMPER comparison of FOREST/MONTH/YEAR for Trelease Woods

Year-Month (Within-Site Similarity)	Genus	Av.Abund	Av.Sim	Contrib%	Cum.%
6-Sep	*Mycena*	5.25	40.36	83.19	83.19
(48.52%)	*Gymnopus*	1.13	4.86	10.02	93.22
6-Oct	*Mycena*	6.63	49.15	84.43	84.43
(58.21%)	*Stereum*	0.50	2.33	4.00	88.43
	Lycoperdon	0.63	1.78	3.05	91.48
6-Nov	*Irpex*	1.75	9.70	37.60	37.60
(25.80%)	*Hymenochaete*	1.38	8.15	31.59	69.19
	Bisporella	0.50	1.25	4.84	74.03
	Stereum	0.50	1.20	4.64	78.68
	Lycoperdon	0.38	1.16	4.49	83.16
	Eutypa	0.38	1.11	4.31	87.47
	Xylaria	0.50	0.79	3.08	90.55
7-Jun	*Marasmius*	2.25	7.79	17.91	17.91
(43.50%)	*Xylaria*	3.00	5.59	12.86	30.77
	Mycena	2.50	5.54	12.75	43.52
	Gymnopus	2.00	5.25	12.07	55.59
	Xeromphalina	2.13	4.96	11.41	67.00
	Schizophyllum	1.88	4.87	11.20	78.20
	Irpex	1.75	2.98	6.86	85.06
	Eutypa	0.63	1.55	3.57	88.64
	Steccherinum	0.88	1.27	2.93	91.57
7-Aug	*Irpex*	1.00	7.45	35.53	35.53
(20.96%)	*Xylaria*	1.00	6.16	29.38	64.91
	Marasmius	0.50	1.41	6.72	71.63
	Stereum	0.63	1.25	5.97	77.60
	Mycena	0.50	1.17	5.57	83.17
	Schizophyllum	0.50	1.17	5.57	88.74
	Artomyces	0.25	0.51	2.43	91.17
7-Oct	*Hymenochaete*	1.88	14.91	44.75	44.75
(33.32%)	*Irpex*	2.00	10.55	31.65	76.40
	Mycena	0.88	5.10	15.32	91.72
7-Nov	*Hymenochaete*	1.88	14.10	45.77	45.77
(30.81%)	*Mycena*	1.50	8.27	26.83	72.60
	Irpex	1.25	5.44	17.64	90.24

Sites in Brownfield (43.23%) and Trelease (37.30%) Woods were not significantly different in average within-site similarity of relative abundances of individual fungal species. *Mycena* was the most important component in determining within-site similarity, contributing more than 10% to the similarity between areas in 11 out of 14 periods of study.

The monthly changes in abundance of the 12 genera most strongly correlated with monthly changes in seasonality are listed in Table 13. Preference of a particular fruiting season was noted for nearly all of the most important genera, however some genera (e.g. *Mycena* and *Coprinellus*) failed to show fruiting preference but were likely heavily influenced by small scale precipitation events rather than changes in ambient conditions. Furthermore, due to preferential collection following precipitation events, the abundance data for these genera are probably inflated as a result of collection bias. The majority of genera showed preference for fruiting during the summer months (June-September) whereas relatively fewer genera showed distinct preference for fruiting during the Fall (October-November) and Winter months.

Table 13: Average monthly abundances and observed fruiting preferences of 12 seasonal genera. Column 1 indicates fruiting preference: Sp=Spring, Su=Summer, Fa=Fall, Wi=Winter, No=No Preference.

	Fungus	Jun	Aug	Sep	Oct	Nov
No	*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
No	*Coprinellus*	0.63	0.38	0.38	0.06	0.22

Several estimates of taxon richness were calculated for Brownfield and Trelease Woods using EstimateS software (Table 14). Brownfield Woods was demonstrated to possess the most taxon-rich fungal assemblage of both sites, with all estimators demonstrating nearly twice as many taxa than were present at Trelease Woods. 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. Odell 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. The results from this comparison are mostly in agreement with their assessment, with *Jacknife 2* providing the highest estimate of taxon richness. However, the values of the *Chao 2* estimate were not consistently higher

than other assessment methods. 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.

Table 14: 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

A sample-based rarefaction curve of taxon accumulation (Gotelli and Colwell, 2001) was created for each forest (Figure 8). Though neither accumulation curve assumed a definite asymptotic shape within the sampling protocol, the rarefaction curve of Trelease Woods is visibly nearer to an asymptotic shape than that of Brownfield Woods. Furthermore, the rarefaction curve of Trelease Woods is unequivocally lower than the taxon accumulation curve of Brownfield Woods. Thus, these results suggest that the macrofungal community at Brownfield Woods is substantially more diverse than what was encountered at Trelease Woods throughout the course of this study.

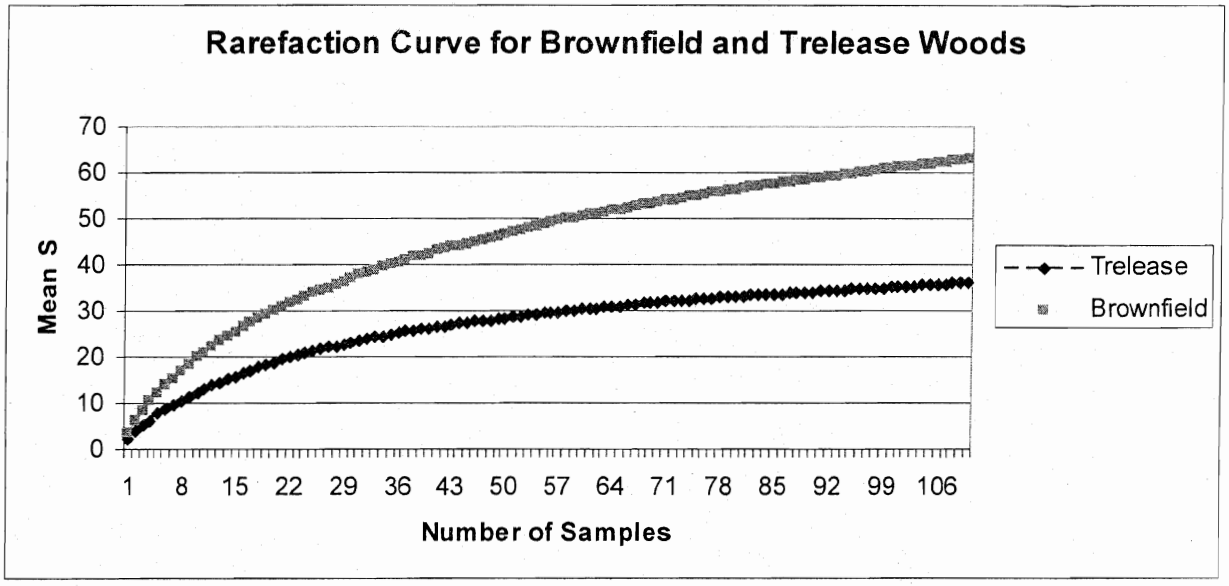

Figure 8: Mean taxon rarefaction curve for Brownfield and Trelease Woods

The tree survey completed in Fall 2007 revealed forest divisions to have significantly different vegetation communities (R=0.224, P=0.0015) (Figure 9), but significant differences were not seen in the woody vegetation communities between forests (R=0.113, P=0.3536).

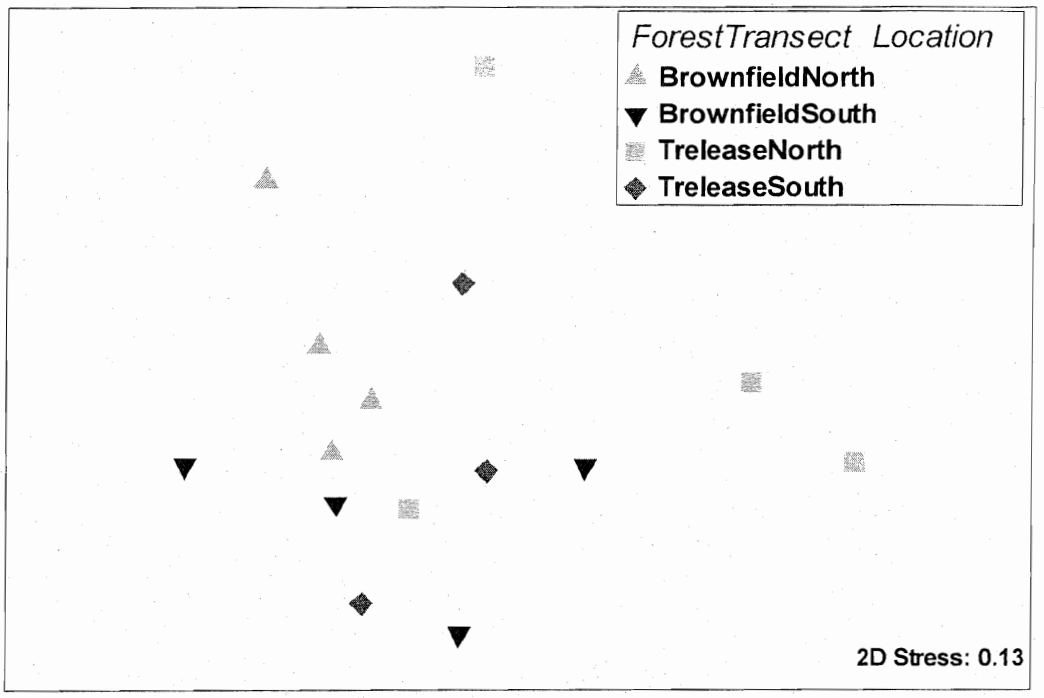

Figure 9: NMDS of woody tree vegetation surveyed Fall 2007

The tree survey data reported in Edgington (1991) were analyzed to determine the extent of correlation with fungal communities at Brownfield and Trelease Woods. Trees >3cm 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 >3cm DBH however, no significant associations were found between forest divisions (R=0.098, P=0.194).

Data from Edgington (1991) of total basal area (ft^2) occupied by trees were also examined, however no significant association was found between basal area and forests (R=0.103, P=0.084) or forest divisions (R=0.037, P=0.296). The Fall 2007 tree survey and the 1991 data were compared using the RELATE procedure

and were shown to have equivalent multivariate dispersion (R=0.058, P=0.3324), suggesting that the data sets were similar in composition.

The ANOSIM procedure was used to determine if leaf litter composition varied within and between Brownfield and Trelease Woods (Table 15). No significance of leaf litter composition between forests was observed (R=-0.78, P=0.6684), however leaf litter composition was found to vary significantly between forest division (R=0.195, P=0.031). None of the pairwise comparisons of leaf litter composition between forest divisions were found to be significant, however 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 *Quercus*, *Acer* and other leaves as well as detritus and wood fragments were obtained from each site and thus these 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 contribution of these variables was considered only when comparing the total leaf litter community between groups. Abundances of miscellaneous leaf fragments were found to significantly differ between forests (R=0.266, P=0.017).

Table 15: ANOSIM results showing association of leaf litter with forests and forest divisions. Significant (P<0.05) interactions are highlighted

Litter Type	Forest	Forest Division
Total	R=-0.780, P=0.664	R= 0.195, P=0.031
Quercus	R=-0.011, P=0.429	R= 0.170, P=0.071
Acer	R= 0.011, P=0.350	R= 0.070, P=0.181
Leaves	R= 0.266, P=0.017	R= 0.143, P=0.109
Detritus	R=-0.045, P=0.690	R=-0.068, P=0.671
Wood	R=-0.118, P=0.998	R=-0.138, P=0.889

Pairwise comparisons of the total composition of leaf litter between forest divisions yielded no significant differences (Table 16), however some marginally significant differences were observed in the distribution of *Quercus* and miscellaneous leaves.

Table 16: ANOSIM results of pairwise comparisons of leaf litter composition between forest divisions

Forest Divisions Compared	R-Stat	Significance (P)
NorthBrownfield, SouthBrownfield	0.063	0.343
NorthBrownfield, NorthTrelease	0.260	0.086
NorthBrownfield, SouthTrelease	0.323	0.114
SouthBrownfield, NorthTrelease	0.052	0.400
SouthBrownfield, SouthTrelease	0.323	0.057
NorthTrelease, SouthTrelease	0.167	0.086

All measures of woody plants by site were next combined into one model which was then evaluated for within- and between-site differences as well as comparison between the woody plant assemblage and fungal assemblages. The woody plant model, evaluated using ANOSIM, was found to be significant for delineating both forests (R=0.142, P=0.037) and forest division (R=0.256,

P=0.004). Pairwise comparisons between forest divisions revealed only North Brownfield and North Trelease to be significantly different (R=0.375, P=0.029) (Table 17) based on the combined model.

Table 17: ANOSIM results of pairwise comparisons of woody plants between forest divisions. Significant (P<0.05) interactions are highlighted.

Forest Divisions Compared	R Statistic	Significance (P)
BrownfieldNorth, BrownfieldSouth	0.156	0.086
BrownfieldNorth, TreleaseNorth	0.375	0.029
BrownfieldNorth, TreleaseSouth	0.438	0.086
BrownfieldSouth, TreleaseNorth	0.156	0.171
BrownfieldSouth, TreleaseSouth	0.125	0.229
TreleaseNorth, TreleaseSouth	0.219	0.143

The RELATE procedure was used to compare the multivariate dispersion of the woody plant environmental model with the fungal assemblages in Brownfield and Trelease Woods. No significant correlation was observed between woody plants and fungal assemblages at both sites (R=-0.04, P=0.572).

In order to evaluate the influence of environmental factors on fungal seasonality, data from the Illinois WARM program were analyzed and compared to monthly fungal assemblages using the RELATE procedure (Table 18).

Table 18: 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 T	0.261	0.001

Each monthly factor was found to demonstrate significant correlation with monthly changes in the fungal community based on the results of the RELATE procedure which demonstrated equivalent multivariate dispersion between groups. The temperature of the soil at 10 cm depth was found to demonstrate the strongest association with changes in fungal communities (R=0.261, P=0.001), whereas monthly humidity showed little association with changes in fungal communities over time.

Discussion

The results of this study suggest that significantly dissimilar fungal communities inhabit Brownfield and Trelease Woods. Furthermore, the fungal communities were found to differ within and between forests, with pairwise comparisons revealing significantly disparate fungal communities between North Brownfield and South Brownfield, South Brownfield and North Trelease, and South Brownfield and South Trelease. Several estimates of taxon richness for both sites were calculated and Brownfield Woods was demonstrated to have substantially higher richness than Trelease Woods. SIMPER analysis showed

several genera of fungi to be responsible for distinguishing fungal communities and 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 individual abundance at a particular site, rather than the presence or absence of particular genus.

However, the results of the SIMPER analysis do demonstrate which fungal taxa are most important in characterizing the fungal communities at Brownfield and Trelease Woods. Tables 4 and 5 list the genera that account for 90% of the within-site similarity at Brownfield and Trelease Woods, respectively. 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, eliminating the need for more taxonomically intensive sampling. However, by restricting the sampling of other sites to these taxa, researchers would be ignoring the rare taxa which were demonstrated to be most significant in characterizing the differences of fungal assemblages at Brownfield and Trelease Woods. Therefore, it is suggested that future studies of fungal diversity in similar sites continue to sample all taxa but pay particular attention to the taxa listed in tables 4 and 5, as these taxa were demonstrated to be most informative at these sites.

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 to note that while the fungal communities present at both sites allowed for delineation both between forests and forest divisions, woody plant communities did not always show the same disparity according to the results of ANOSIM tests.

The woody plant communities surveyed by Hustad in Fall 2007 did not significantly differ between forests but separate forest divisions were shown to have significantly different woody plant communities (R=0.224, P=0.0015). Pairwise comparisons between forest divisions found only North Brownfield and North Trelease to have significantly different woody plant communities (R=0.438, P=0.029), due largely to the absence of *Carya* and *Juglans* in North Brownfield and the greater abundance of *Tilia* in North Brownfield than in North Trelease. The forest divisions with significantly different fungal communities, North Brownfield and South Brownfield, South Brownfield and North Trelease, and South Brownfield and South Trelease, were not found to significantly differ in regards to woody vegetation communities present. *Acer*, the most abundant woody plant genus at all sites, was demonstrated to be the least important woody plant genus in delineating forest divisions due to uniformly high abundances at all sites.

Furthermore, the leaf litter composition of Brownfield and Trelease Woods did not significantly between sites, though some significant differences were noted using within-forest comparisons. Nonetheless, the degree of variation between sites may be due to chance alone. Brownfield and Trelease Woods were found to

significantly differ in regards to counts of trees with greater than 3 cm DBH, however, there was no significant difference observed when forest divisions were compared. In contrast, basal area in square feet of all trees >3cm diameter in each collecting area failed to show significant disparity between forests and forest divisions.

Thus it is evident that the values of individual categories of woody plant effects do not provide consistent delineations between forests and forest divisions. The communities of woody vegetation were found to vary significantly at narrower spatial scales but large-scale changes in vegetation communities have apparently not yet developed between the sites.

Due to the relative isolation of both forest remnants for more than 120 years, 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 tree due to isolation populations is not well studied for temperate forests, Harris and Miller (1984) suggest that changes in woody plant community structure begin within 50 years of separation of forest into disjunct fragments. The isolation of Brownfield and Trelease Woods of greater than 120 years more than satisfies this requirement and as such, divergence of woody plant communities due to isolation would be expected at both sites. 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) seem to show evidence for island biogeography theory in fungal systems.

At least at the scale of comparison used in this study, no correlation between woody plant effects and fungal communities is evident. 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 individual components of fungal communities at Brownfield and Trelease Woods were shown to vary significantly in response to changes in seasonality (Table 13). The fall fruiting period, from mid-September to early-November 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 requisition 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.

These 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 the taxa most indicative of changes in the fungal community were demonstrated. While more sampling will be needed in order to evaluate the usefulness of these taxa as indicators of monthly changes in fungal community structure, the relevance of these taxa to seasonal fungal community changes at Brownfield and Trelease Woods is established.

Changes in monthly environmental parameters were evident throughout the course of this study. Rainfall, humidity, and measures of air temperature were all found to significantly differ throughout the course of this study, whereas 10 cm soil temperature was not significantly different between years. 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 was shown to have the strongest correlation to changes in fungal communities. The correlation between ambient soil temperature and fungal fruiting has been shown by previous research (Arnolds, 1992), and the results of this study are in line with those of previous research. Terrestrial and soil-occurring macrofungi likely use changes in ambient soil temperature as a cue to begin the production of sporocarps throughout the growing

season, with large scale fruitings being produced in response to local precipitation events (Dix and Webster, 1995).

The results of SIMPER analyses performed in this study suggest that it is possible in future studies to evaluate only a subset of the macrofungal community and still maintain a large level of confidence. SIMPER analysis demonstrated that, in nearly all cases, the abundances of less than 40 genera of macrofungi represented a sufficient subset for community analysis. These results can be used in management contexts to prioritize collection efforts and can also be useful in assembling protocols of study. Collection efforts can be focused on the most informative, most abundant genera present at a site at a given time, thus reducing the taxonomic expertise needed for fungal surveys as well as the time required to carry them out.

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 two years 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 taxon accumulation curve (Figure 8) showed that the fungal communities of Brownfield and Trelease Woods demonstrate similar

accumulations of taxa to other hardwood forests, e.g. Schmit et al. (1999) and Brunner et al. (1992). The taxon accumulation curve calculated in this study reaches a more asymptotic distribution than seen in these studies however, it is important to note that the scale of comparison used in this study, the genus rank of taxonomy, is a broader concept of individual than the species rank, used in the above studies.

Because the genus rank is a broader, more encompassing concept of individuals, one would expect the taxon accumulation curve to assume a steeper, less asymptotic shape if the species rank were used instead for this study. In this study, communities were analyzed at the genus rank to minimize the probability of taxonomic inaccuracy as well as to greatly reduce the numbers of duplicated unknown taxa encountered. Prior to aggregation of all individuals to the genus rank, 209 individual taxa were recorded at the species rank which, when aggregated to the rank of genus, resulted in 102 separate genera. The total number of species-ranked taxa is more in line with other studies from hardwood forests. For example Schmit et al. (1999) recorded 177 species in 3 years of study, Brunner et al. (1992) recorded 124 species in four years of study in *Alnus* forest in Alaska, and Villenueve et al. (1989) reported 89 species in two years of study in Quebec. Likewise, if measures of taxon richness from species rank comparisons were generated in this study, the resultant estimators would be more in line with the results of other studies.

The results of this study can also be used 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 a point of comparison 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*, which have greatly changed the composition of the sites.

The continuation of this study would doubtlessly reveal new genera of macrofungi and as the number of genera increase, the resolution in differentiating forests and forest divisions would increase as well. An inherent problem of studying terrestrial macrofungal communities using sporocarp data is that sporocarp production is a relatively random event (Dix and Webster, 1995). The production of sporocarps by a single individual in a particular year may be very different from subsequent years, despite the vegetative mycelium at the site being relatively unchanged. The ethereality of sporocarps proposes significant challenges when studying fungal communities as well. As such, no study of

macrofungal sporocarps will ever provide a completely accurate representation of the fungal communities present at the particular site. It is only with the introduction of novel methods of studying fungal communities, such as using fungal DNA extracted from soil samples (Grogan et al., 2000) that an effective method of consistently analyzing terrestrial macrofungi may be discovered and avoiding the confounding variability of sporocarp production over time.

Conclusions

This study represents the first plot-based analysis of terrestrial macrofungal communities in old-growth prairie grove habitat. The fungal communities inhabiting Brownfield and Trelease Woods, separate fragments of old-growth prairie grove forest were characterized and found to differ based on the presence and abundances of several fungal species. The fungi present at Brownfield and Trelease Woods were not shown to vary in accordance with the woody vegetation communities however, a finer scale investigation of the woody vegetation communities using refined protocols would likely increase the resolution of distinction between woody plant communities and perhaps show correlation to fungal communities. Environmental variables such as soil temperature at 10 cm were found to correlate strongly with fungal seasonality, whereas others did not demonstrate strong associations. The fungal communities present at Brownfield and Trelease Woods can now be used as a benchmark for comparison with other studies of fungal community diversity as well as future restoration efforts of prairie grove habitat types.

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