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Microhabitat Affinities of Missouri Ozarks Lichens

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Abstract. *The lichen communities of nine mixed-hardwood sites in the southeastern Missouri Ozarks were characterized from sampling of the ground layer, tree-bases, midboles, and canopy branches. Of the 181 lichen taxa documented, the majority were crustose (55%) or foliose (32%) lichens. Only a quarter (26%) of all species occurred across all four microhabitats, with the majority of dominant taxa demonstrating apparent preferences for a single (38%) or multiple (27%) microhabitat, a given host tree species (17%), or a particular ground substrate (12%). High diversity of ground substrates and a large amount of presumed litterfall in the ground layer were of particular note. Relative species composition and abundance of lichen communities differed in stands with overstories dominated by red oak species as opposed to white oak species, but showed only suggestive variation with aspect class, geology, bedrock, landform, and soil type. Lichen diversity measures were also weakly associated with the presence of individual white or red oak species in the overstory, but no clear patterns appeared with respect to white or red oak subgroups. Stratification by microhabitat and host species would be necessary in future experimental studies in this region.*

Keywords. Community, host, microhabitat, MOFEP, oak forest, Ozark lichens, substrate.

Lichens fall into the category of poorly known organismal groups in Missouri (Ladd 1991a) and perhaps the entirety of midcontinental North America. Progress has been made in recent decades to characterize the state lichen flora, but systemic conservation (as opposed to species-targeted conservation) requires a broader understanding of lichen ecology (Ladd 1993). Although some ecological functions have been documented in this and other regions [e.g., material for birds' nests and nutrient cycling sinks (Ladd 1998), food for birds (Pettersson et al. 1995), and wildlife (Sharnoff 1994; Stevenson 1978)], the relative importance of lichens in these functions, as well as other possible functions, remains unknown. Throughout the country, lichens are gaining attention as indicators of air quality (de Wit 1983; McCune et al. 1997a; Showman 1975),

vegetation classifications, or other groups of rare organisms (e.g., Nilsson et al. 1995), as important contributors to nutrient cycling (e.g., Knops et al. 1996; Pike 1978), and as rare species that require protection (e.g., Ladd 1991a). With the exception of Ladd (1996), sufficient data to evaluate the potential contributions of lichen communities in the Ozarks have hitherto been lacking. Because any or all of these functions may be relevant in the Ozarks region of Missouri, lichen community sampling was incorporated into the Missouri Ozark Forest Ecosystem Project (MOFEP) in 1996. This long term (ca 90 year) experiment to assess the impacts of forest management practices on organisms and ecosystem attributes in Missouri Ozark woodlands (MOFEP, Shifley & Brookshire 2000) has provided the framework for a range of ecological projects, from those addressing the impacts of forest management alternatives to studies deriving baseline information about poorly known organismal groups.

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We report here on findings gleaned from pre-treatment baseline data collection of the lichen communities in these sites (Ladd & Grabner 1996).

Lacking sufficient data for the Missouri Ozarks ecosystem, sampling stratification in the current study was based primarily on results from other parts of the country. Lichen communities found in the canopy generally differ from those found on tree-bases or boles (e.g., Hale 1965; Hoffman & Kazmierski 1969; McCune et al. 2000; Pike et al. 1975). In particular, lichen communities have been seen to vary along a gradient from tree-bases to midboles to the canopy (Ladd 1996; Lang et al. 1980; McCune 1993; McCune et al. 1997b), presumably due to gradients in photosynthetic activity and humidity (Hosokawa et al. 1964; Szczawinski 1953). Variability has also been recorded among host tree species (Jesberger & Sheard 1973; McCune & Antos 1982; Schmitt & Slack 1990) and branch size in the canopy (Esseen et al. 1996; Hilmo 1994).

We wished to answer the following questions: 1) what is the species composition of the lichen communities in this portion of the Ozarks on the ground layer, tree-bases, tree midboles, and canopy branches; 2) do these communities vary consistently with respect to classifications that can be used to stratify future sampling toward the goal of evaluating the experimental treatment effects on these lichen communities, and 3) what, if any, association exists between the relative species composition and abundance and diversity of the observed lichens and the available environmental characteristics.

METHODS

Sites and data collection.—Each of the nine MOFEP sites (~36°50'–37°15'N, 91°00'–91°15'W) are contiguous 285+ ha forested tracks in the southeastern Missouri Ozarks, largely free of manipulation for at least the 45 years prior to initiation of the MOFEP experiment in 1996 (Shifley & Brookshire 2000). Most overstory trees in these second growth mixed hardwood stands (white oak-*Quercus alba* basal area 5–7 m²/ha, black oak-*Quercus velutina* 5–6 m²/ha, and scarlet oak-*Quercus coccinea* 3–7 m²/ha, with scattered other hardwoods and shortleaf pine-*Pinus echinata*) were 50–70 years old in 1996. The lichen sampling reported here occurred prior to the application of the MOFEP treatments, which are described in detail in Shiff (2002).

Most lichen community data were collected in six plots at each site from March–May 1996 using the standard MOFEP vegetation plot design (Jensen 1993). Plots were selected to ensure homogeneity of parent material, aspect, and major vegetation groups and all were on shoulder or backslope positions (10–60% slope; Ladd & Grabner 1996). Tree sampling was conducted in the northern 0.02 ha (15.78 m diameter) subplot of each 0.20 ha (49.6 m diameter) MOFEP vegetation plot and included all trees greater than 11.43 cm in diameter at breast height [thus a variable number (ranging from 32 to 68) of microplots for tree-bases and midboles per six plots at each of nine sites].

The bases and midboles (centered at breast height) of each tree were sampled using a 0.25 m² variable length cylindrical microplot. Ground sampling was conducted along four 24.8 m permanent line transects dissecting the entire 0.20 ha vegetation plot. Along each transect, five 0.25 m² microplots were placed at random points within five meter intervals and centered on the transect line (thus 20 per six plots at each of nine sites = 1,080 ground microplots total). Canopy sampling was enabled in six of the nine sites when trees were harvested in October 1996 as part of the larger MOFEP experiment. Canopy sampling was conducted in three plots at each of these six sites, which were randomly selected from those measured for tree and ground sampling. Two dominant or co-dominant trees were sampled in each plot, each providing two separate branches, typically from opposite sides of the tree, immediately after tree fall. Four 30.48 cm (12") samples were cut from each branch, representing four size classes on the basis of diameter of the largest end (1.27 cm, 3.81 cm, 7.62 cm, and 10.16 cm) (thus 16 per three plots at each of six sites = 288 microplots total). All analyses were conducted on microplots containing at least one lichen taxon (i.e., not empty); one midbole, 81 ground, and five canopy microplots were thus excluded prior to analysis.

In all cases, within each microplot all lichen taxa were recorded (nomenclature follows Ladd 2002) and a cover value assigned. Cover values were as follows: 1 = <1% cover; 2 = 1–5% cover; 3 = 6–25% cover; 4 = 26–50% cover; 5 = >50% cover. Data analyzed here are cover class midpoints (0.5%, 3%, 15.5%, 37.5%, 75%) either at the microplot level or averaged across microplots to the site level. Voucher specimens of MOFEP lichens are deposited in the herbarium of the New York Botanical Garden (NY); the Missouri Department of Conservation in Columbia, Missouri has a duplicate set of most vouchers.

For ground microplots, note was also taken of the substrate upon which the lichen was found, including: soil, rock (by type), and downed woody debris [twigs = diameter < 0.5" (1.3 cm), branches = diameter > 0.5" (1.3 cm), logs = diameter > 2" (5.1 cm), or lignum = loose fragments]. Downed woody debris with diameters greater than 2" (5.1 cm) were also assigned a MOFEP decay class [1–5, least to most decayed, Appendix A in Shifley & Brookshire (2000)].

At the site level, environmental variables included in the analyses were two tree attributes: basal area and density for both individual oak species and composite values for the white oak (*Quercus* subgenus *Lepidobalanus*) and red oak subgroups (*Quercus* subgenus *Erythrobalanus*). At these sites, the white oak subgroup included white oak (*Q. alba*) and post oak (*Q. stellata*) while the red oak subgroup included scarlet oak (*Q. coccinea*), black-jack oak (*Q. marilandica*), northern red oak (*Q. rubra*), shumard oak (*Q. shumardii*), and black oak (*Q. velutina*).

At the microplot level, environmental variables included in the analyses were the categorical variables of ecological land type (Meinert et al. 1997), geology and bedrock type, aspect class (1 = exposed, 2 = neutral, 3 = protected), landform and soil type, and slope angle. All environmental variables are reported in Shifley and Brookshire (2000).

Analysis of microhabitat and substrate relations.—Variation in the lichen community among microhabitats was evaluated at the site level (i.e., the average across all microplots from a given site) on the basis of all observed lichen taxa after species occurring in fewer than two sites were deleted and data were relativized to species totals (i.e., by the sum of mean cover class midpoints for a given

species across all sites) and arcsine-squareroot transformed, which has been shown to improve the statistical properties of proportion data (Sokal & Rohlf 1981). Contrasts of relative species composition and abundance were made at the site level using multi-response permutation procedures (MRPP in PC-ORD v. 4.01, McCune & Mefford 1999). MRPP contrasts the within-group variation in the species space distance matrix among *a priori* groups [i.e., species were coded as to their group membership (e.g., microhabitat) and these groups were then contrasted on the basis of their homogeneity; see Mielke et al. 1981]. For all analyses, the Sørensen coefficient (also known as the Bray & Curtis or Czekanowski coefficient) was used as the measure of dissimilarity (Sørensen 1948).

Significant contrasts at the site level were further evaluated with a calculation of indicator values (IV, Dufrene & Legendre 1997; McCune & Mefford 1999). Indicator values are the product of the relative frequency and abundance of a species across the groups of interest, and provide a simple and objective way of gauging the tendency for a species to occur in a particular set of samples. As a relative measure, no standard cutoff IV was used to determine microhabitat affinity. Two criteria were used for interpretation. First, only taxa with significant IVs (based on a $p = 0.05$ cutoff from a Monte Carlo procedure) were considered. Secondly, since with such a large number of species some would be significant simply by chance, only differences in IV among groups greater than 30 were taken to indicate a greater frequency and abundance of a given species in a given microhabitat. Similar contrasts were made among the sizes of canopy branches at the site level as well.

Analysis of environmental relations.—The association between the lichen community and the measured environmental variables was analyzed at the site level for all of the sampled lichen taxa after species occurring in fewer than two sites were deleted and data were relativized to species totals and arcsin-squareroot transformed. Overlays of the tree attributes onto nonmetric multidimensional scaling ordination diagrams were visually examined (NMS in PC-ORD v. 4.01, McCune & Mefford 1999). When strong, consistent patterns were observed, correlations with the ordination axes were calculated for both environmental variables and lichen species. Only associations with $r > 0.45$ are reported here.

Microplot-level analysis was also conducted for all nine sites together, to evaluate host species, and for each site separately, to evaluate the association between the observed lichen community and the measured environmental characteristics, including host tree species, using the same procedures as for the site level analysis above with the exception that data transformations were deemed unnecessary. MRPPs and IVs were also calculated for all categorical variables at the microplot level. Because of the low percentage of variance explained by all ordinations (both site and microplot levels), regression analysis of ordination scores on environmental characteristics was not deemed appropriate.

Analysis of diversity.—Both gamma and mean alpha diversity were calculated at both the site and microplot level (using PC-ORD v. 4.01, McCune & Mefford 1999). Across a given unit of measurement (e.g., microplots within a site), gamma (γ) diversity was defined as the total number of species (Whittaker 1972), and mean alpha (α) diversity as the average number of species (Whittaker 1972). These measures were regressed (PROC GLM, SAS 6.12 1996) on the available environmental characteristics at the site and microplot levels after checking for normality. Lichen diversity was also contrasted among vari-

ous site level groupings, including across sites, microhabitats, and canopy branch sizes using analysis of variance (PROC GLM, SAS 6.12 1996) with Tukey's Studentized Range Test for multiple comparisons. Although the total surface area in ground, tree-base, midbole, and canopy microplots varied, we believe that such comparisons are valid on the basis of the fact that in all cases species area curves at the site level demonstrated that these communities had been amply sampled. In order to contrast canopy branch segments to one another, surface areas for each branch were estimated by assuming that the smallest size class was equivalent to a circular cone and the larger classes were equivalent to truncated cones

$$\text{circular cone: } SA = \pi r \sqrt{r^2 + h^2} \quad (1)$$

truncated cone = parallelogram:

$$SA = \frac{h}{2(a + b)} \quad (2)$$

where "r" is the radius of the circle at the base, "h" is the height of the cone or parallelogram, and "a" and "b" are the lengths of the sides of the parallelogram. Species richness was then standardized by surface area prior to analysis.

RESULTS

Species composition.—A total of 181 lichen taxa were sampled across the four microhabitat classes on these nine sites (Table 1). Forty-eight taxa (26%) occurred in all four microhabitat classes and 80 (44%) in at least two, while 61 (34%) were found in only one. There were 100 (55%) crustose, 59 (32%) non-gelatinous foliose, 15 (8%) fruticose, and 7 (4%) gelatinous foliose lichen taxa. Ten (5%) species were found to have nitrogen-fixation capabilities. Although none of the observed taxa are rare, threatened, or endangered in the state of Missouri, one species, *Tuckermannopsis ciliaris*, has been placed on a "watch list" to reflect the restricted distribution of this species in the state (Ladd 1991a). Typically found in old growth *Pinus echinata* stands, the single occurrence of this species in this study was at the base of a *P. echinata* in Site 6.

A total of 107 taxa were collected from ground sampling. Of these, 25 taxa (23%) occurred in all nine MOFEP sites, while 48 (45%) occurred in two-thirds of the sites. *Lecanora strobilina* actually occurred in over 75% of microplots (almost exclusively as the result of litterfall), but 91 taxa (85%) occurred in fewer than 10% of microplots. The ground sampling was composed of 57 (53%) crustose, 41 (38%) foliose, 7 (7%) fruticose, and 2 (2%) gelatinous lichens. *Punctelia rudecta*, *Lecanora hybocarpa*, and *Usnea strigosa* were also commonly found in ground sampling.

A total of 122 taxa were collected from tree-base sampling. Of these, 20 (16%) occurred in all sites, while 38 (31%) occurred in two-thirds of the sites. *Cladonia* was the most common lichen on tree-bases at the microplot level, occurring in over 50%

TABLE 1. Percent frequency of lichen species found in nine MOFEP sites at the site-level and the microplot (Mp) level by microhabitat class. The P column indicates physiognomy; c = crustose, f = foliose, fr = fruticose, and g = gelatinous. Nitrogen-fixing species are indicated by N, while W denotes species on the watch list for the state of Missouri (Ladd 1991a). Common/representative corticolous species (indicated by frequency $\geq 70\%$ in at least one habitat and similar overall prevalence in wooded sites throughout the Missouri Ozarks based on personal observation) are shown in bold. Nomenclature follows Ladd 2002.

Species	P	Ground		Tree-base		Midbole		Canopy	
		Site n = 9	Mp n = 999	Site n = 9	Mp n = 435	Site n = 9	Mp n = 434	Site n = 6	Mp n = 283
<i>Acarospora fuscata</i>	c	44	1	0	0	0	0	0	0
<i>Agonimia</i> sp. #1	c	0	0	56	2	11	0	0	0
<i>Amandinea dakotensis</i>	c	0	0	0	0	0	0	17	0
<i>Amandinea polyspora</i>	c	88	5	22	1	22	1	100	19
<i>Amandinea punctata</i>	c	0	0	44	4	44	2	0	0
<i>Anaptychia palmulata</i>	f	0	0	22	1	0	0	0	0
<i>Anisomeridium polypori</i>	c	0	0	78	4	56	2	17	0
<i>Arthonia caesia</i>	c	100	14	56	2	89	5	100	16
<i>Arthonia dispersa</i>	c	0	0	11	1	22	1	0	0
<i>Arthonia punctiformis</i>	c	55	1	0	0	0	0	100	42
<i>Arthonia pyrrhuliza</i>	c	0	0	22	1	89	6	50	2
<i>Arthonia radiata/pyrrhuliza</i>	c	0	0	11	0	0	0	0	0
<i>Arthonia</i> sp.	c	22	0	0	0	11	0	0	0
<i>Arthothelium spectabile</i>	c	11	1	0	0	0	0	17	0
<i>Arthothelium taediosum</i>	c	100	2	44	1	100	16	100	44
<i>Aspicilia caesiocinerea</i>	c	55	1	0	0	0	0	0	0
<i>Aspicilia</i> sp.	c	55	2	0	0	0	0	0	0
<i>Bacidia circumspecta</i>	c	0	0	11	0	0	0	0	0
<i>Bacidia diffracta</i>	c	0	0	11	0	0	0	0	0
<i>Bacidia laurocerasi</i>	c	0	0	0	0	11	0	0	0
<i>Bacidia polychroa</i>	c	66	1	100	6	89	8	0	0
<i>Bacidia schweinetzii</i>	c	77	1	100	16	100	14	17	0
<i>Bacidia suffusa</i>	c	11	0	22	1	44	2	17	0
<i>Bacidia</i> sp.	c	33	1	0	0	0	0	0	0
<i>Buellia spuria</i>	c	88	7	0	0	0	0	0	0
<i>Buellia stillingiana</i>	c	100	16	78	4	100	22	100	50
<i>Buellia</i> sp.	c	44	1	0	0	0	0	0	0
<i>Caloplaca brunneola</i>	c	0	0	11	0	11	0	50	1
<i>Caloplaca campitida</i>	c	67	1	89	4	100	14	33	1
<i>Caloplaca cerina</i>	c	67	1	33	1	78	5	17	1
<i>Caloplaca flavorubescens</i>	c	22	0	0	0	0	0	0	0
<i>Caloplaca flavovirescens</i>	c	0	0	0	0	0	0	17	0
<i>Caloplaca pollinii</i>	c	33	0	0	0	56	2	0	0
<i>Caloplaca</i> sp.	c	11	0	0	0	0	0	0	0
<i>Candelaria concolor</i>	f	100	5	100	18	100	46	67	4
<i>Candelaria fibrosa</i>	f	11	0	0	0	0	0	0	0
<i>Candelariella reflexa</i>	c	11	0	0	0	22	1	83	6
<i>Candelariella xanthostigma</i>	c	78	3	44	1	100	6	0	0
<i>Canoparmelia caroliniana</i>	f	0	0	22	1	11	0	0	0
<i>Canoparmelia subtinctoria</i>	f	33	1	100	6	89	8	0	0
<i>Canoparmelia texana</i>	f	22	0	44	3	44	3	100	10
<i>Canoparmelia</i> sp.	f	56	1	0	0	0	0	0	0
<i>Catillaria nigroclavata</i>	c	0	0	0	0	11	0	0	0
<i>Chaenothecopsis nana</i>	c	0	0	44	3	44	5	0	0
<i>Chaenothecopsis rubescens</i>	c	0	0	0	0	11	0	0	0
<i>Cladina subtenuis</i>	fr	11	0	0	0	0	0	0	0
<i>Cladonia apodocarpa</i>	fr	0	0	11	0	0	0	0	0
<i>Cladonia cristatella</i>	fr	0	0	11	0	0	0	0	0
<i>Cladonia cylindrica</i>	fr	0	0	11	0	0	0	0	0
<i>Cladonia grayi</i>	fr	0	0	89	5	0	0	0	0
<i>Cladonia macilenta bacillaris</i>	fr	11	0	44	4	22	1	0	0
<i>Cladonia parasitica</i>	fr	0	0	11	0	0	0	0	0
<i>Cladonia peziziformis</i>	fr	0	0	89	3	0	0	0	0
<i>Cladonia polycarpoides</i>	fr	11	0	0	0	0	0	0	0
<i>Cladonia</i> sp. <i>squamules</i>	fr	100	21	100	50	100	21	0	0
<i>Coccocarpia palmicola</i> ^N	f	22	0	33	1	0	0	0	0
<i>Collema conglomeratum</i> ^N	g	0	0	22	1	22	1	0	0
<i>Collema furfuraceum</i> ^N	g	0	0	100	11	89	6	0	0
<i>Dendrococaulon intricatum</i> ^N	fr	0	0	11	1	11	0	0	0

TABLE 1. Continued.

Species	P	Ground		Tree-base		Midbole		Canopy	
		Site n = 9	Mp n = 999	Site n = 9	Mp n = 435	Site n = 9	Mp n = 434	Site n = 6	Mp n = 283
<i>Dimerella pineti</i>	c	0	0	0	0	11	0	0	0
<i>Dimerella</i> sp. #1	c	0	0	22	1	22	1	0	0
<i>Endocarpon pusillum</i>	c	11	0	22	1	0	0	0	0
<i>Flavoparmelia baltimorensis</i>	f	89	11	22	1	0	0	0	0
<i>Flavoparmelia caperata</i>	f	100	19	100	32	100	36	100	42
<i>Graphis scripta</i>	c	100	4	67	4	100	23	17	0
<i>Gyalideopsis</i> sp. #1	c	0	0	0	0	0	0	17	0
<i>Heterodermia granulifera</i>	f	11	0	22	1	22	1	17	0
<i>Heterodermia hypoleuca</i>	f	0	0	11	0	33	1	17	0
<i>Heterodermia obscurata</i>	f	11	0	100	15	100	29	33	2
<i>Heterodermia speciosa</i>	f	89	1	100	32	100	14	17	0
<i>Hypotrachyna livida</i>	f	100	13	33	1	78	6	100	33
<i>Hyperphyscia syncolla</i>	f	0	0	0	0	0	0	17	0
<i>Julella fallaciosus</i>	c	0	0	56	1	78	3	50	1
<i>Lecanora caesiurubella prolif.</i>	c	78	4	33	1	100	12	100	23
<i>Lecanora dispersa</i>	c	11	0	0	0	0	0	0	0
<i>Lecanora hybocarpa</i>	c	100	23	89	7	100	33	100	52
<i>Lecanora imshaugii</i>	c	0	0	0	0	22	1	0	0
<i>Lecanora minutella</i>	c	0	0	0	0	22	1	0	0
<i>Lecanora strobilina</i>	c	100	78	100	14	100	28	100	81
<i>Lecanora thysanophora</i>	c	0	0	11	0	11	0	0	0
<i>Lecanora</i> sp.	c	11	0	33	1	0	0	0	0
<i>Lecanora</i> sp. [usnic acid, zeorin]	c	0	0	0	0	11	0	0	0
<i>Lecidea varians</i>	c	89	8	0	0	56	4	100	42
<i>Lepraria lobificans</i>	c	56	2	100	29	100	9	0	0
<i>Lepraria</i> sp.	c	11	0	0	0	0	0	0	0
<i>Lepraria</i> sp. #1	c	33	0	89	26	100	25	50	3
<i>Leptogium austroamericanum</i> ^N	g	0	0	78	2	22	1	0	0
<i>Leptogium cyanescens</i> ^N	g	0	0	89	9	56	3	0	0
<i>Leptogium dactylinum</i> ^N	g	0	0	44	2	0	0	0	0
<i>Leptogium milligranum</i> ^N	g	11	0	89	4	89	6	0	0
<i>Loxospora pustulata</i>	c	100	5	100	18	100	35	50	4
<i>Maronea polyphaea</i>	c	100	13	44	2	89	10	100	39
<i>Mycocalicium albonigrum</i>	c	22	0	0	0	0	0	0	0
<i>Mycocalicium subtile</i>	c	0	0	0	0	11	0	0	0
<i>Mycoglaena quercicola</i>	c	0	0	0	0	0	0	83	6
<i>Mycoporum pycnocarpoides</i>	c	22	0	0	0	56	2	50	2
<i>Myelochroa aurulenta</i>	f	100	12	100	47	100	41	100	4
<i>Myelochroa galbina</i>	f	100	10	33	1	89	7	100	47
<i>Nadvornikia sorediata</i>	c	0	0	11	0	11	0	0	0
<i>Nectria parmeliae</i>	c	0	0	11	0	0	0	0	0
<i>Ochrolechia africana</i>	c	33	0	0	0	44	2	50	1
<i>Opegrapha varia</i>	c	11	0	56	2	67	3	0	0
<i>Opegrapha vulgata</i>	c	0	0	0	0	22	1	0	0
<i>Pannaria lurida</i> ^N	f	0	0	11	0	11	0	0	0
<i>Parmelinopsis minarum</i>	f	33	1	78	5	56	3	17	0
<i>Parmotrema austrosinense</i>	f	22	0	0	0	0	0	0	0
<i>Parmotrema euryzacum/despectum</i>	f	100	6	44	1	89	4	17	0
<i>Parmotrema gardneri</i>	f	0	0	11	0	0	0	17	0
<i>Parmotrema hypotropum</i>	f	100	6	100	14	100	13	83	11
<i>Parmotrema michauxianum</i>	f	22	0	11	0	11	0	17	0
<i>Parmotrema perforatum</i>	f	56	1	0	0	0	0	100	10
<i>Parmotrema</i> [hypt/perf]	f	0	0	11	0	11	0	100	16
<i>Peltigera</i> sp. ^N	f	11	0	0	0	0	0	0	0
<i>Pertusaria amara</i>	c	33	0	44	3	100	10	33	1
<i>Pertusaria hypothamnolica</i>	c	0	0	11	0	56	2	33	1
<i>Pertusaria macounii</i>	c	0	0	0	0	22	1	0	0
<i>Pertusaria neoscotica</i>	c	11	0	11	0	0	0	0	0
<i>Pertusaria ostiolata</i>	c	0	0	100	5	89	6	17	0
<i>Pertusaria paratuberculifera</i>	c	78	1	100	29	100	22	67	5
<i>Pertusaria propinqua</i>	c	0	0	11	0	67	3	67	2

TABLE 1. Continued.

Species	P	Ground		Tree-base		Midbole		Canopy	
		Site <i>n</i> = 9	Mp <i>n</i> = 999	Site <i>n</i> = 9	Mp <i>n</i> = 435	Site <i>n</i> = 9	Mp <i>n</i> = 434	Site <i>n</i> = 6	Mp <i>n</i> = 283
<i>Pertusaria pustulata</i>	c	89	3	67	2	100	13	100	29
<i>Pertusaria subpertusa</i>	c	0	0	11	0	78	5	50	3
<i>Pertusaria tetralthalmia</i>	c	11	0	44	1	67	2	17	0
<i>Pertusaria texana</i>	c	22	0	56	1	100	12	67	5
<i>Pertusaria trachythallina</i>	c	0	0	11	0	44	1	100	7
<i>Pertusaria valliculata</i>	c	0	0	33	1	44	1	0	0
<i>Pertusaria velata</i>	c	11	0	67	2	89	6	33	1
<i>Pertusaria</i> sp.	c	89	3	0	0	0	0	0	0
<i>Phaeocalicium polyporaenum</i>	c	11	0	22	1	22	1	0	0
<i>Phaeophyscia adiaetola</i>	f	11	0	11	1	0	0	0	0
<i>Phaeophyscia cernohorskyi</i>	f	0	0	0	0	33	1	0	0
<i>Phaeophyscia ciliata</i>	f	0	0	0	0	11	1	0	0
<i>Phaeophyscia hirsuta</i>	f	11	0	0	0	0	0	0	0
<i>Phaeophyscia pusilloides</i>	f	100	5	100	27	100	31	50	1
<i>Phaeophyscia rubropulchra</i>	f	100	3	100	35	100	19	33	1
<i>Phaeophyscia squarrosa</i>	f	11	0	33	1	0	0	0	0
<i>Phlyctis argena</i>	c	22	0	0	0	0	0	0	0
<i>Phyllopsora corallina</i>	c	0	0	22	1	0	0	0	0
<i>Physcia americana</i>	f	100	6	100	37	100	57	17	1
<i>Physcia millegrana</i>	f	89	4	56	2	89	12	67	5
<i>Physcia pumilior</i>	f	11	0	22	1	44	2	83	3
<i>Physcia stellaris</i>	f	100	19	56	1	100	5	100	25
<i>Physcia subtilis</i>	f	78	3	0	0	0	0	0	0
<i>Physcia</i> sp.	f	56	3	0	0	0	0	0	0
<i>Physciella chloantha</i>	f	0	0	0	0	11	0	17	1
<i>Physciella melanchra</i>	f	0	0	11	1	22	1	0	0
<i>Physconia detersa</i>	f	0	0	56	2	67	3	0	0
<i>Placidium tuckermanii</i>	c	0	0	44	2	56	2	0	0
<i>Punctelia missouriensis</i>	f	0	0	11	0	0	0	0	0
<i>Punctelia rudecta</i>	f	100	36	100	46	100	53	100	38
<i>Punctelia subrudecta</i>	f	0	0	11	0	0	0	33	1
<i>Pyrenula caryae</i>	c	0	0	0	0	0	0	33	2
<i>Pyrenula pseudobufonia</i>	c	56	1	33	1	100	18	33	1
<i>Pyxine soredata</i>	f	67	2	89	12	100	20	67	3
<i>Pyxine subcinerea</i>	f	78	2	89	7	100	23	100	30
<i>Ramalina americana</i>	fr	22	0	0	0	44	2	0	0
<i>Ramalina culbersoniiorum</i>	fr	0	0	0	0	0	0	33	1
<i>Rimelia cetrata</i>	f	11	0	0	0	22	1	33	1
<i>Rimelia reticulata</i>	f	100	3	89	11	100	15	67	5
<i>Rimelia subsidiosa</i>	f	67	1	11	0	11	0	17	0
<i>Rinodina applanata</i>	c	0	0	11	0	11	1	33	1
<i>Rinodina subminuta</i>	c	0	0	44	1	22	1	17	1
<i>Rinodina tephraspis</i>	c	11	0	0	0	0	0	0	0
<i>Rinodina</i> sp.	c	11	0	0	0	0	0	0	0
<i>Robergea pupula</i>	c	0	0	11	0	33	1	0	0
<i>Schismatomma glaucescens</i>	c	0	0	11	0	33	1	0	0
<i>Strigula jamesii</i>	c	0	0	33	1	0	0	0	0
<i>Thelopsis flaveola</i>	c	0	0	22	1	56	1	0	0
<i>Trapeliopsis flexuosa</i>	c	89	2	22	1	11	1	0	0
<i>Tuckermannopsis ciliaris</i> ^W	f	0	0	11	0	0	0	0	0
<i>Tuckermannopsis fendleri</i>	f	89	5	0	0	0	0	17	0
<i>Usnea mutabilis</i>	fr	0	0	11	1	11	1	0	0
<i>Usnea strigosa</i>	fr	100	21	33	2	89	6	100	53
<i>Vulpicidia viridis</i>	f	100	18	0	0	33	1	100	35
<i>Xanthoparmelia subramigera</i>	f	22	0	0	0	0	0	0	0
<i>Xanthoria fulva</i>	f	0	0	0	0	11	0	0	0
unknown crust 1	c	100	13	78	7	100	6	67	13
unknown crust 2	c	0	0	22	1	33	1	17	0
unknown foliose	f	11	0	22	1	0	0	0	0
unknown gelatinous	g	11	0	0	0	0	0	0	0
unknown pyrenocarp	c	78	2	33	1	11	1	0	0

of microplots, but 102 (84%) species occurred in fewer than 10% of microplots. The tree-base sampling was composed of 63 (52%) crustose, 41 (34%) foliose, 12 (10%) fruticose, and 6 (5%) gelatinous lichens. *Myelochroa aurulenta*, *Punctelia rudecta*, and *Physcia americana* were also commonly found in tree-base sampling.

A total of 118 taxa were collected from midbole sampling. Of these, 33 (28%) were found in all sites, while 54 (46%) occurred in two-thirds of the sites. *Physcia americana* and *Punctelia rudecta* were the most prevalent species at the microplot level, occurring in over 50% of microplots, but 88 (75%) taxa occurred in fewer than 10% of microplots. The midbole sampling was composed of 70 (59%) crustose, 37 (31%) foliose, 6 (5%) fruticose, and 5 (4%) gelatinous lichens. *Candelaria concolor* was also commonly found in midbole sampling.

A total of 84 taxa were collected from canopy sampling. Of these, 23 taxa (27%) were found on all six sampled MOFEP sites, while 35 (42%) occurred in two-thirds of the sites. *Lecanora strobilina* occurred in over 80% of microplots, but 58 (70%) taxa occurred in fewer than 10% of microplots. The canopy sampling was composed of 48 (57%) crustose, 34 (40%) foliose, and 2 (2%) fruticose lichens. *Usnea strigosa*, *Lecanora hybocarpa*, and *Buellia stillingiana* were also commonly found in canopy sampling.

Stratification potential.—Significant variation in relative species composition and abundance of the lichen community was observed among the four microhabitat classes (MRPP $p < 0.001$), including among ground and tree lichens despite the overlap of some species through litterfall. This variation is attributable to a large number of taxa (139) demonstrating preferences for a given microhabitat (Table 2). Although nearly 70 species were most common and abundant in a single microhabitat, more than 20 species had high indicator values (IV) for both the base and the midbole tree microhabitat. Ten additional species showed a preference for both midboles and canopies, while a handful of species were found only as epiphytes (i.e., somewhere on a tree), but did not demonstrate a preference for a particular tree microhabitat.

Ground substrates.—Ground specimens occurred predominantly on undecayed twigs and pine cones or were unattached (50% of specimens, 69 taxa); on undecayed wood larger than twigs (33%, 80 taxa); and on stone (12%, 49 taxa). [Note: very little decayed wood was present in these sites (see Shifley & Brookshire 2000).] Fully 54% of ground specimens were thought to have possibly originated as recent (i.e., not re-established) litterfall, involving 69 of the 181 lichen taxa. However, 39 ground

taxa never appeared as potential litterfall, while only 16 taxa only appeared as potential litterfall.

Although sampling was not stratified by ground substrate (and hence unequal sampling probabilities reduce our confidence in statistical tests comparing these groups), a quick look at apparent substrate patterns may help guide future sampling efforts. Relative species composition and abundance varied by substrate (MRPP $p < 0.01$). No species showed a preference (i.e., IV's ~ 30 higher than for other groups) for soil, while rock substrates were the most typical (or exclusive) host for six taxa (*Acarospora fuscata*, *Aspicilia* sp., *Aspicilia caesiocinerea*, *Buellia spuria*, *Flavoparmelia baltimorensis*, and *Physcia subtilis*). Downed woody debris was the preferred substrate for another six taxa (*Bacidia* sp., *Canoparmelia* sp., *Pertusaria* sp., *Physcia* sp., *Trapeliopsis flexuosa*, and *Tuckermannopsis fendleri*). Notable differences were observed among ground substrate groups (MRPP all $p < 0.01$), including among stone vs. logs/branches/twigs/unattached specimens, among soil/stone/lignum vs. fresh logs/branches/twigs, and between specimens thought to have originated as litterfall and non-litterfall. Similarly, the size and decay class of downed woody debris also affected lichen community composition (MRPP both $p < 0.05$), with various species occurring to a greater extent on twigs vs. branches vs. logs (detailed results can be found in Peck et al. 2002).

Host tree species.—Samples were collected from 13 tree species on tree-bases and midboles and from seven tree species in the canopy. Again, despite unequal sampling probabilities, examining apparent patterns in host specificity may help guide future sampling efforts. Relative species composition and abundance varied significantly (MRPP $p < 0.001$) among groups of host species, particularly with regard to shortleaf pine (Fig. 1), although less so in the canopy than on tree-bases and midboles. Across all habitats, *Heterodermia speciosa*, *Pertusaria paratuberculifera*, and *Punctelia rudecta* were more frequent and abundant (i.e., IV's ~ 30 higher than for other groups) on trees in the red oak subgroup, while no species showed a preference for the white oak subgroup. Shortleaf pine (*Pinus echinata*), however, was consistently dominated by *Amandinea punctata*, *Canoparmelia caroliniana*, *C. texana*, *Cladonia macilenta bacillarlis*, *Cladonia squamules*, *Chaenothecopsis nana*, *Lecanora strobilina*, and *Parmotrema hypotropum*. Hickory (*Carya*) was the preferred host for *Arthonia caesia*, *A. dispersa*, *Bacidia schweinitzii*, *Graphis scripta*, *Candelaria concolor*, *Lecanora strobilina*, *Lepraria lobificans*, *Leptogium milligranum*, *Myelochroa aurulenta*, *Opegrapha varia*, *Pertusaria tetrathalamia*, *Phaeophyscia pusilloides*, *P. rubropulchra*,

TABLE 2. Indicator Values for lichen taxa across the four microhabitat classes (G = ground, Tb = tree bases, M = midboles, C = canopy) for taxa occurring in more than two sites, from data aggregated to the site level ($n = 9$; 6 for canopy). Indicator Values are the product of the relative frequency and abundance of a species in a given group and suggest the degree of indication of the species for that group. Values ~ 30 higher than for other groups suggest group preference. p -values test the significance of a strong preference for a single group. Taxonomic names are abbreviated using the first three letters of the genus followed by the first three letters of the specific epithet. Species with significant p -values demonstrating preference for one or more groups are shown in bold.

Species	G	Tb	M	C	p	Species	G	Tb	M	C	p
Acafus	44	0	0	0	0.01	Ochafra	2	0	21	24	0.34
Ago #1	0	55	0	0	0.00	Schglia	0	6	17	0	0.39
Amapol	11	0	1	84	0.00	Opevar	0	28	33	0	0.21
Amapun	0	23	21	0	0.26	Paraus	22	0	0	0	0.21
Anipol	0	71	4	0	0.00	Pare/d	33	2	48	1	0.09
Artcae	22	2	25	47	0.05	Pargar	0	5	0	10	0.57
Artdis	0	6	10	0	0.73	Parhyp	5	37	11	38	0.69
Artpun	0	0	0	100	0.00	Parmic	4	3	1	8	0.90
Artpyr	0	0	78	5	0.00	Parmin	1	47	16	1	0.05
Artspe	7	0	0	6	1.00	Parh/p	0	0	0	99	0.00
Art sp.	5	0	9	0	0.81	Parper	1	0	0	98	0.00
Arttae	1	0	27	72	0.00	Perama	0	3	80	4	0.00
Aspcae	56	0	0	0	0.00	Perhyp	0	0	9	27	0.27
Asp sp.	56	0	0	0	0.00	Perneo	1	10	0	0	0.85
Bacpol	2	66	27	0	0.04	Perost	0	68	28	0	0.00
Bacsch	1	61	38	0	0.01	Perpar	0	65	32	2	0.00
Bac sp.	33	0	0	0	0.05	Perpro	0	0	44	21	0.02
Bacsuf	0	11	17	1	0.59	Perpus	2	2	41	53	0.06
Buespu	89	0	0	0	0.00	Per sp.	89	0	0	0	0.00
Bue sp.	44	0	0	0	0.02	Persub	0	1	56	10	0.01
Buesti	6	2	36	55	0.01	Pertet	0	8	54	0	0.01
Calbru	0	2	2	35	0.06	Pertex	0	5	76	10	0.00
Calcam	1	17	76	1	0.00	Pertra	0	0	4	91	0.00
Calcer	10	3	54	1	0.01	Perval	0	11	30	0	0.15
Cal sp.	22	0	0	0	0.23	Perverl	0	5	73	3	0.00
Calpol	5	0	47	0	0.01	Phaadi	0	11	0	0	0.84
Cancar	0	22	0	0	0.19	Phacer	0	0	33	0	0.05
Cancon	2	14	81	1	0.00	Phahir	11	0	0	0	1.00
Canref	0	0	1	78	0.00	Phapol	1	9	11	0	0.61
Cantex	0	5	11	63	0.00	Phapus	3	31	60	3	0.00
Canxan	15	3	75	0	0.00	Pharub	2	58	39	0	0.02
Can sp.	0	89	0	0	0.00	Phasqu	0	33	0	0	0.04
Clamaba	0	41	1	0	0.03	Phlarg	22	0	0	0	0.25
Cansub	0	89	0	0	0.00	Phyame	1	28	70	0	0.00
Clasqu	6	78	16	0	0.00	Phychl	0	0	3	13	0.38
Chanan	0	23	21	0	0.21	Phydet	0	17	46	0	0.02
Can sp.	56	0	0	0	0.00	Phymel	0	1	21	0	0.40
Cocpal	4	28	0	0	0.11	Phymil	11	2	58	12	0.02
Colcon	0	13	9	0	0.56	Phypum	0	1	8	63	0.00
Colfur	0	86	13	0	0.00	Phy sp.	56	0	0	0	0.00
Dim #1	0	17	5	0	0.40	Physte	30	1	10	59	0.00
Endpus	2	19	0	0	0.23	Physub	78	0	0	0	0.00
Flabal	76	3	0	0	0.00	Platuc	0	23	26	0	0.24
Flacap	5	21	40	35	0.09	Punrud	4	25	51	19	0.00
Grascr	7	3	89	0	0.00	Punsub	0	3	0	23	0.11
Hetgra	0	21	1	0	0.30	Pyrca	0	0	0	33	0.03
Hethyp	0	1	27	2	0.09	Pyrpse	1	0	97	0	0.00
Hetobs	0	28	70	0	0.00	Pyxsor	1	23	62	7	0.00
Hetsps	0	83	17	0	0.00	Pyxsob	3	5	44	47	0.03
Hypliv	9	0	9	79	0.00	Ramame	2	0	40	0	0.02
Julfal	0	2	71	3	0.00	Ramcul	0	0	0	33	0.03
Lecpro	5	1	23	69	0.00	Rimcet	1	0	12	14	0.47
Lechyb	6	3	32	59	0.00	Rimret	2	31	36	18	0.51
Lec sp.	0	33	0	0	0.05	Rimsub	12	0	9	0	0.91
Lecstr	14	5	11	70	0.00	Cansub	0	63	31	0	0.01
Lecvar	2	0	1	96	0.00	Rinapp	0	1	1	25	0.20
Lepaus	0	72	2	0	0.00	Rinsub	0	18	7	5	0.33
Lepcya	0	82	5	0	0.00	Robpup	0	0	33	0	0.08
Lepdac	0	44	0	0	0.01	Strjam	0	33	0	0	0.05

TABLE 2. Continued.

Species	G	Tb	M	C	<i>p</i>	Species	G	Tb	M	C	<i>p</i>
Leplob	1	80	17	0	0.00	Thefla	0	17	14	0	0.67
Lepmil	0	44	45	0	0.06	Trafle	40	7	3	0	0.06
Lep #1	0	46	45	1	0.04	Tucfen	64	0	0	5	0.00
Lep sp.	11	0	0	0	1.00	unknn cr 1	16	15	18	31	0.68
Loxpus	2	17	73	4	0.00	unknn cr 2	0	1	30	1	0.28
Marpol	11	1	18	68	0.00	unknn fol	2	18	0	0	0.21
Mycalb	22	0	0	0	0.22	unknn pyr	64	4	1	0	0.00
Mycpyc	0	0	20	31	0.17	Usnstr	14	1	5	78	0.00
Mycque	0	0	0	83	0.00	Vulvir	17	0	0	82	0.00
Myeaur	2	43	54	1	0.00	Xansub	22	0	0	0	0.22
Myegal	8	0	8	81	0.00						

Physciella melanchra, *Physcia americana*, *P. millegrana*, and *Placidium tuckermanii*. Only *Lecanora caesiorubella prolifera* and *Pertusaria paratuberculifera* showed a preference for dogwood (*Cornus*).

Canopy branches.—Relative species composition of lichens was compared across the four size classes of canopy branches and found to differ significantly (MRPP $p < 0.001$), particularly among the largest and smallest classes (presence/absence transformed to minimize the fact that larger branches tended to be colonized by larger specimens). Species most associated (IV's ~30 higher than for other groups) with the smallest branch class were *Arthonia punctiformis*, *Mycoglaena quercicola*, and an unknown sterile crustose taxon. Species associated with the next smallest size class were *Lecidea varians*, *Maronea polyphaea*, *Physcia stellaris*, and *Vulpicida viridis*. The second to largest class was associated with *Flavoparmelia caperata*, *Hypotrachyna livida*, *Lecanora caesiorubella prolifera*, *L. hybocarpa*, *Maronea polyphaea*, *Parmotrema hypotropum*, *Punctelia rудecta*, and *Pyxine subcinerea*. The largest branches were colonized by *Buellia stillingiana*, *Canoparmelia texana*, *Flavoparmelia caperata*, *Lecanora hybocarpa*, *Maronea polyphaea*, *Parmotrema perforatum*, *Pertusaria pustulata*, *Punctelia rудecta*, and *Pyxine subcinerea*.

The pattern in branch sizes is most clearly seen in the ordination diagram in Figure 2, where axis one captures the size gradient. A positive association ($r > 0.45$) with this axis (i.e., greater frequency and abundance on larger branches) was seen for *Flavoparmelia caperata* and *Punctelia rудecta* and a negative gradient (i.e., more on smaller branches) was seen for *Arthonia punctiformis* and *Lecanora strobilina*. Occasionally, species typically found in the canopy were also found in abundance on the ground due to litterfall. These included *Amandinea polyspora*, *Lecanora strobilina*, *Myelochroa galbina*, *Usnea strigosa*, and *Vulpicida viridis*.

Site level environmental relations.—The lichen communities of all four microhabitats were asso-

ciated with the relative abundance of various oak species, and subgroups of oak species, in the overstory (Table 3). Although tempting to characterize these associations as patterns of contrast among members of the red and white oak subgroups, they are in fact more complex. There was a general trend for the white oak group to contrast with the red oak group (all Fig. 3), but northern red oak (Fig. 3a), black oak (Fig. 3b), and schumard oak (Fig. 3a,d) often showed differing patterns from their associate groups.

Microplot level environmental relations.—No association with lichen assemblages was seen with ecological land type in the ground microhabitat, and mostly weak associations in sites 8 and 9 for tree-bases, in sites one and 8 for midboles, and in sites 3 (Fig. 4) and 7 for canopy lichens. However, relatively consistent associations were seen for aspect class, geology, bedrock, landform, and soil for all four microhabitats, although not always demonstrating the same pattern. In all microhabitats, bedrock depth, aspect class and slope were associated with the lichen assemblages (e.g., Fig. 4). In some canopy sites, landform was also important. These patterns, however, are all too weak to regress and produce a predictive model. In the case of ground lichens, it is possible that these environmental patterns are diluted by the presence of litterfall from tree microhabitats. Further, strong host specificity may obscure weaker environmental gradients in these naturally variably mixed stands. However, data are lacking upon which to base the exclusion of any given species prior to analysis. Future measurements of ground lichens in the Missouri Ozarks will need to pay special attention to the distinction of true litterfall, while analyses of tree microplots will be best conducted stratified by host species.

Lichen diversity.—Substantial differences in mean alpha and gamma diversity were observed for different microhabitats (Table 4). At the site level, no significant patterns of association were seen between canopy lichen diversity measures and the

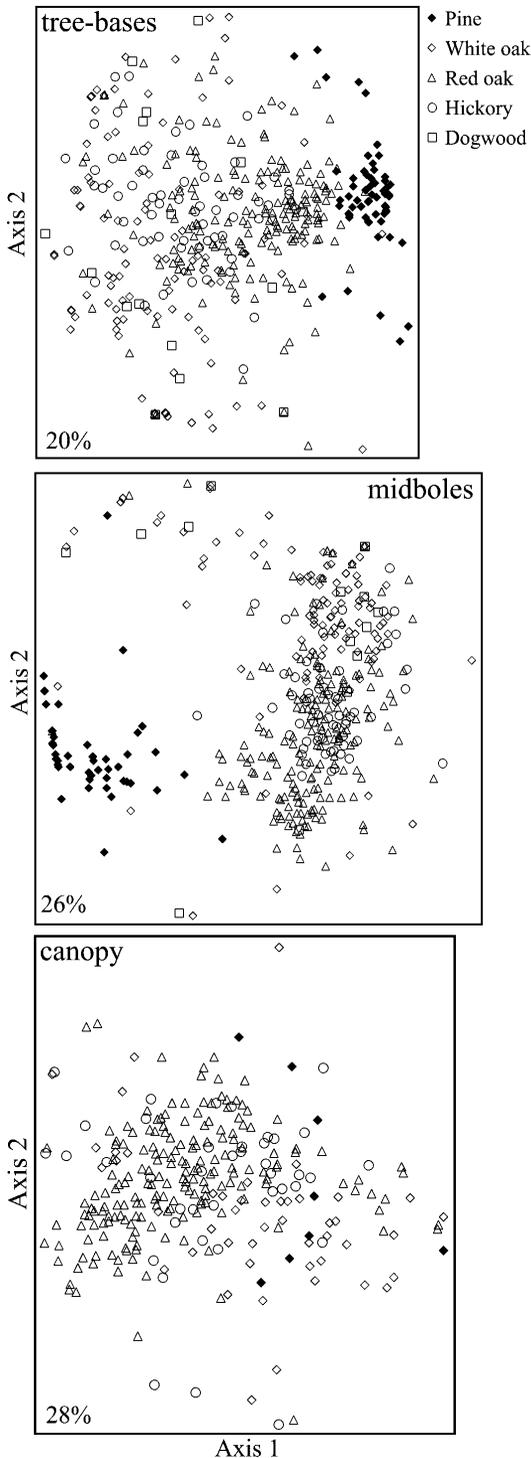


FIGURE 1. Microplot level NMS ordination diagrams of all sites combined showing separation of lichen communities on the occasional short-leaf pine (*Pinus echinata*; filled diamond) from the white oak subgroup (*Quercus* subgenus *Lepidobalanus*), red oak subgroup (*Quercus* subgenus *Erythrobalanus*), hickory (*Carya*), and dogwood (*Cornus*) on tree-bases (top), midboles (middle), and canopy branches (bottom).

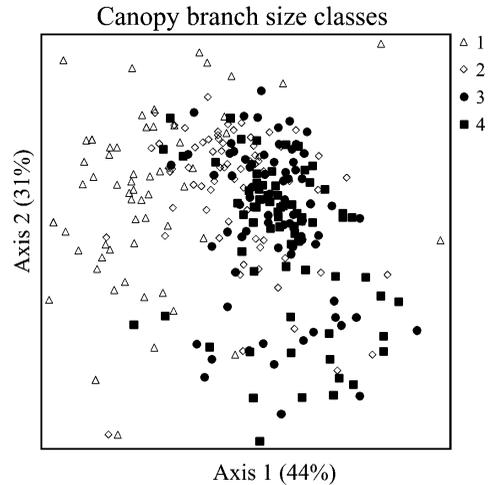


FIGURE 2. Microplot level NMS ordination diagram of all six canopy sites combined showing separation of the lichen community by canopy branch size (smallest 1 to largest 4). Variation in branch size is most strongly expressed across axis 1, with the greatest distinction between the two largest and two smallest size classes.

measured tree attributes. In addition, no associations were seen between lichen diversity measures and the white oak subgroup variables for any microhabitat. However, strong patterns of association with lichen diversity were seen with the red oak subgroup variables and individual white and red oak species. Gamma diversity in the ground microhabitat was positively associated with white oak density ($r = 0.48$), while on tree-bases the positive association was with scarlet oak ($r = 0.45$) and black oak ($r = 0.48$) density. Midbole gamma diversity was positively associated with black oak density ($r = 0.47$) but negatively associated with post-oak density ($r = 0.48$). Mean alpha diversity in the ground microhabitat showed a negative association with white oak basal area ($r = 0.56$), but positive associations with the red oak subgroup basal area and density (both $r = 0.64$), due in large part to scarlet oak basal area and density (both $r = 0.55$). Tree-base mean alpha diversity was positively associated with the red oak subgroup density ($r = 0.54$), due to black oak ($r = 0.65$) and scarlet oak ($r = 0.50$). None-the-less, no strong multiple factor predictive models could be developed. No associations were found between species richness and tree diameter for tree-base or midbole lichens.

At the microplot level, highly significant associations were observed among gamma diversity and ecological land type, geology, slope, aspect, and landform; however, these associations had no predictive ability (all R^2 values < 0.10) and were likely so highly significant due to the large sample size. At best, there is suggestive evidence that these features show some association with lichen diversity,

TABLE 3. Correlation coefficients for the association between oak species and species groups and the NMS ordination axes for ground, tree-base, midbole, and canopy lichens, corresponding to Figure 3. BA = basal area.

	Ground		Tree-bases		Midboles		Canopy	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Black oak BA	-0.18	0.04	-0.27	0.47	-0.31	-0.46	-0.02	-0.43
Black oak density	-0.09	-0.17	-0.20	0.60	-0.18	-0.37	-0.14	-0.15
Northern red oak BA	0.18	0.39	0.02	-0.30	-0.12	0.28	0.14	-0.08
Northern red oak density	0.04	0.65	-0.24	-0.35	-0.19	0.05	0.14	0.17
Post oak BA	-0.34	-0.25	0.09	-0.07	-0.39	0.29	-0.05	-0.18
Post oak density	-0.54	-0.17	-0.18	-0.16	-0.52	0.23	-0.47	0.01
Red oak BA	-0.78	0.13	-0.71	0.14	-0.70	-0.12	-0.86	0.22
Red oak group density	-0.57	0.11	-0.49	0.27	-0.42	-0.16	-0.77	0.17
Scarlet oak BA	-0.86	0.31	-0.81	-0.29	-0.63	-0.06	-0.94	0.44
Scarlet oak density	-0.52	0.14	-0.58	0.16	-0.23	-0.14	-0.78	0.61
Schumard oak BA	-0.56	0.61	-0.61	0.06	-0.75	-0.28	-0.07	0.78
Schumard oak density	-0.05	0.45	-0.39	0.14	-0.04	-0.40	0.01	0.68
White oak BA	0.68	0.02	0.55	0.01	0.73	0.11	0.83	-0.28
White oak density	0.25	0.20	0.04	0.41	0.40	-0.09	0.52	0.34
White oak group BA	0.45	-0.20	0.68	0.11	0.42	0.46	0.87	-0.35
White oak group density	-0.69	0.01	-0.39	0.53	-0.30	0.11	-0.22	0.05
Total BA	0.42	0.24	0.14	-0.42	0.52	-0.25	0.29	-0.02
Total density	0.57	0.14	0.20	0.10	0.48	-0.24	0.52	0.40

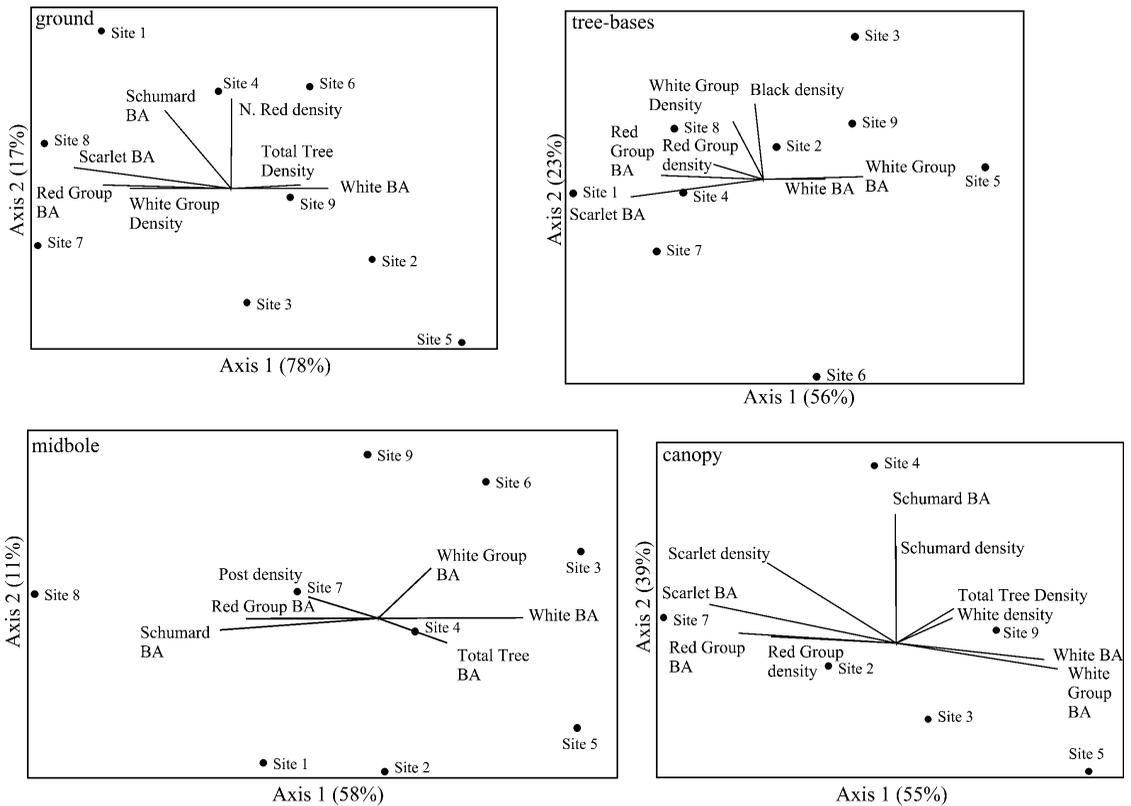


FIGURE 3. Site level NMS ordination diagrams showing the strong pattern of association of the density and basal area of the white and red oak groups and individual oak species with the measured lichen communities for the ground, tree-base, midbole, and canopy microhabitats. The length of the lines is proportional to the magnitude of the correlation of that variable with the ordination axes. All ordinations have been rotated such that white oak basal area (BA) corresponds to axis 1 to facilitate comparison.

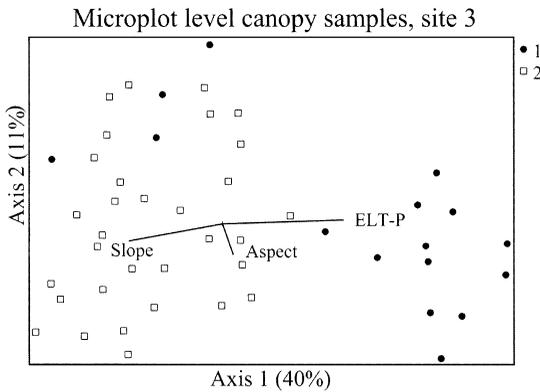


FIGURE 4. Microplot level NMS Ordination diagram of canopy samples in site three showing an example of the pattern of association of several site characteristics with the lichen communities at the subplot level. The length of the lines is proportional to the magnitude of the correlation of that variable with the ordination axes. An overlay of bedrock depth (1 = subsurface, 2 = surface) is shown.

but further study would be needed to elucidate these relationships.

Among canopy branch sizes, gamma diversity on the smallest size class (mean $\gamma = 17$, *s.d.* 5.5) was significantly lower than on the other size classes. The second smallest class (mean $\gamma = 27$, *s.d.* 3.4) and the third largest class (mean $\gamma = 33$, *s.d.* 4.7) were not significantly different from one another, but both were significantly lower than gamma diversity on the largest branches (mean $\gamma = 35$, *s.d.* 3.2).

DISCUSSION

The most important finding of this study has been the characterization of an Ozark lichen community at the end of the 20th century. Rather than a cataloguing of long-established taxa in a static ecosystem, our sampling represents more of a snapshot of communities that may still reflect radical changes in the Missouri landscape since settlement. Far from pristine, given the area's history of pre-settlement indigenous use of fire, extensive post-settlement deforestation and conversion to agriculture, and most recently fire suppression (Ladd 1991*b*), these sites are relatively un-impacted by the smog and pollution that have already seriously impacted lichen communities near urban areas throughout the country (e.g., McCune et al. 1997*a*) and that has been held responsible for such low species richness records as 15 species in Indianapolis (McCune 1988) and the barely dozen non-crustose species found in the Ohio River valley in the late 1980's (Showman 1990).

Although the species listed in Table 1 were previously known for Missouri, their microhabitat as-

TABLE 4. Diversity indices by microhabitat (G = ground, Tb = tree bases, M = midboles, C = canopy) across all sites and at the microplot level by site. *n* = sample size, γ = species richness, and α = average species per sample. Sample sizes at the microplot level ranged from 101–118 on the ground, 32–68 for tree bases and midboles, and 46–48 for canopy samples depending on the site. Sampling areas were 0.25 m² for all except canopy samples, which were of variable area. *Site-level alpha diversity was not significantly different among ground and tree-base samples, but alpha diversity on mid-boles was significantly higher than all other habitats while that on canopy branches was significantly lower than all other habitats. Standard deviations on the mean are shown in parentheses.

Site	G	Tb	M	C
All				
<i>n</i>	999	435	434	283
γ	107	122	118	82
α -site*	57.1 (6.3)	56.6 (7.6)	67.6 (5.3)	45.3 (4.5)
α -sp	4.6	6.8	9.2	8.9
1				
γ	54	40	54	—
α	5.3	7.3	8.6	—
2				
γ	62	39	59	30
α	4.4	6.4	11.1	9.6
3				
γ	64	34	51	40
α	4.4	5.5	7.4	8.3
4				
γ	63	40	62	31
α	4.7	6	8.4	9.5
5				
γ	57	28	57	30
α	4.2	6.2	11.7	7.8
6				
γ	49	28	49	—
α	3.7	4.1	7	—
7				
γ	52	33	46	33
α	5.3	7.1	10.5	8.3
8				
γ	54	33	42	—
α	5.1	5.9	6.3	—
9				
γ	60	37	47	32
α	4.6	8.9	10.2	8.5

sociations, relative frequencies, and relations to environmental conditions were previously unknown not only for the MOFEP sites but for Missouri, the Ozarks, and mid-continental North America in general. The species observed in this study are representative of Missouri lichens (Ladd 1991*a*, 1996, 2002). Despite a near-complete lack of comparable community studies in the Midwest and neighboring states, general comparisons can be made with li-

chen communities from other regions. Such comparisons reveal that Ozark woodlands include lichen associations that are among the most diverse lichen communities in the country. Studies of lichen communities in the hardwood dominated landscapes of New England have found highly variable, and notably lower, species richness, ranging from 40 to 136 species (Selva 1994). Community studies conducted in the Pacific Northwest have documented 97 species of epiphytic lichens in a coniferous stand in western Washington (McCune et al. 2000), 35 species of epiphytic macrolichens (i.e., not including crustose species) in comparably-aged stands in western Oregon (Neitlich 1993), and 45 species of macrolichens on old-growth canopy branches in the same region (Sillet 1995). In contrast, a mere 33 species of macrolichens were found in balsam fir stands in New Hampshire (Lang et al. 1980). Compared to the 140+ lichens (60+ of just macrolichens) found epiphytically in this study, we are quickly reminded of the tendency for lichen diversity to be higher in mixed hardwood forests than in conifer forests, especially those in the more northerly or colder climates. This contrast is particularly striking given that broad ocular surveys, such as those used in studies of other regions, are better suited to capturing total diversity than the stratified microplot sampling used in the current study (McCune & Lesica 1992).

Another important finding of this study has been quantitative support for the need to stratify sampling by microhabitat in lichen communities in this region. In order to effectively evaluate treatment effects resulting from the different harvest methods in the MOFEP study, the within-treatment variation in lichen communities must be as low as possible. Based on the diversity and variability in lichen species composition among the microhabitats in this study, it will be necessary to continue such stratification when re-measuring to evaluate treatment effects. While half as many lichen species were found on the ground (23) as opposed to tree trunks (50) or canopy branches (45) in Montana (Lesica et al. 1991), we found that ground diversity (107) was nearly 90% of tree bole diversity (122 bases, 118 midboles) and actually higher than canopy diversity (84), even after deducting the 16 ground taxa only found as suspected litterfall. We hypothesize that this high ground diversity and trend of lowering diversity with height above the ground is due to a) greater light penetration to the ground layer in these deciduous forests, b) more rapid desiccation in the windy Midwest at increased heights, a trend that has been documented in other regions (e.g., Szczawinski 1953), and c) the extreme microhabitat variability, and hence niche diversification, on the ground layer in these stands.

Patterns in lichen communities along canopy height, branch size, and host species gradients have been documented for other regions (e.g., McCune et al. 2000). Variation among branch sizes due to bark characteristics, water flow, age of the substrate, surface area for catching propagules, and successional patterns, have been previously observed (Esseen & Renhorn 1998; Sillet et al. 2000). That the ground microhabitat would be so diverse, and have such a diverse lichen flora, however, indicates that even greater stratification of this microhabitat among substrates will be necessary in future experimental studies in this region, in particular with respect to the treatment of litterfall. McCune and Lesica (1992) noted that variation in data on lichens from the ground microhabitat is often due to chance encounters of highly specific microsites. Indeed, in this case very unequal sampling of a large number of substrates has led us to believe that the ground flora of lichens in these stands is substantially larger than was observed.

The greater strength of host species over the other measured environmental gradients translates into a need for host species stratification in future sampling. Although we are unable to separate these influences, noting that the variation in species composition observed in these stands is normal, if not lower than, that seen throughout the Missouri Ozarks, the host species gradient is probably the most important determining factor for the presence/abundance of lichen species showing preferences for a given host tree species in this region.

Variation among downed woody debris decay conditions may be due to mortality of epiphytic material, bark condition, water retention, substrate stability, invertebrate/small vertebrate disturbance, and successional patterns (Söderström 1988). We strongly suspect that the highly desiccating conditions in these Ozark stands, plus the relatively small diameter of the coarse woody debris, translate into much drier coarse woody debris than in other regions, which may explain the low diversity of epixylic lichens on logs and branches of advanced decay classes. The lack of association of lichen species with the various white oak subgroup species suggests that sampling could be streamlined by aggregating this group, whereas stratification by tree species may be warranted for various red oak species, shortleaf pine, and hickory. Such stratification in future studies would likely enable a greater ability to distinguish patterns of lichen species composition and abundance across other environmental gradients.

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