VEGETATION ANALYSIS, ENVIRONMENTAL RELATIONSHIPS, AND POTENTIAL SUCCESSIONAL TRENDS IN THE MISSOURI FOREST ECOSYSTEM PROJECT

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Abstract: The vegetation data set of the Missouri Forest Ecosystem Project (MOFEP, initiated by the Missouri Department of Conservation) in the Ozark Mountains of southeastern Missouri was ordinated by Detrended Correspondence Analysis (DCA) to identify vegetation gradients and potential environmental influences. The first DCA axis represented a strong gradient in black oak importance and segregation of this species from white ash, black walnut, eastern redcedar, sugar maple and bitternut hickory. Some Spearman rank correlation coefficients between Axis 1 and measured environmental variables were significant but not high, suggesting that unmeasured factors (e.g., disturbance history, soil pH) were associated with species distribution along the first axis. The second axis clearly separated mesic species (bitternut hickory, black walnut, white ash and sugar maple) from xeric species (shortleaf pine, eastern redcedar, post oak and blackjack oak). Aspect and aspect x slope variables correlated strongly with Axis 2 scores and species importance, suggesting that this axis represented a habitat moisture gradient. Potential canopy replacement in MOFEP forests was examined by analysis of overstory-understory relationships and density vs. size class distributions. White oak likely will become more important in MOFEP forests with time, as this species is relatively abundant in the understory, while relative abundance of red oak group species and shortleaf pine is substantially reduced compared to that in the overstory.

INTRODUCTION

The Missouri Forest Ecosystem Project (MOFEP) in the Ozark Mountains of southeastern Missouri represents one of the most extensive and comprehensive long-term ecological studies undertaken in the eastern United States (Brookshire and Hauser 1993). There have been few quantitative studies of the vegetation in the region and none of this extent (Nigh and others 1985, Read 1952, Ware and others 1992, Zimmerman and Wagner 1979). The baseline vegetation data set collected for this project offered an opportunity to provide an initial, coherent view of the nature and condition of this ecosystem and its plant population dynamics. Specifically, this study was undertaken to provide an ecological analysis of MOFEP forests with regard to tree species composition and dominance, vegetation-environment relationships, and potential successional trends.

METHODS

Data Analysis

The nine MOFEP study sites are located in Carter, Ripley and Shannon counties in the southeastern Missouri Ozarks and range in size from 260 and 527 ha. Study areas, vegetation plot design and data collection were described in detail by Brookshire and Hauser (1993). For the purposes of the present study, data consisted of 644 0.2 ha circular "tree" plots on which species and diameter of all individuals ≥11.4 cm (4.5 in) dbh were recorded. Additionally, within the boundary of each tree plot, species and diameter were recorded on four nested 0.02 ha plots for woody

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plants ("saplings") that were between 3.8 and 11.3 cm (1.5-4.5 in) dbh. Within each 0.02 ha plot, "seedling" data were recorded by species on a concentric 0.004 ha plot for plants > 1 m tall and < 3.8 cm (1.5 in) dbh.

Indirect gradient analysis of overstory species was conducted using tree plot data and Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980). Tree Importance Value (IV = relative density + relative basal area) by species for each plot was used as an indicator of abundance. As employed in this study, output of the DCA procedure provides gradients in overstory species composition in two or more dimensions. Composition of major forest types on MOFEP study sites was assessed by averaging IV data across plots of the same Ecological Land Type (ELT) (Miller 1981). TWINSPAN analysis (Hill 1979) of the MOFEP data set also was conducted, but provided no detectable advantage in forest classification over that offered by the ELT system (data not shown).

The relationships among DCA axis scores, species importance value and environmental factors were explored by Spearman rank correlation analysis using the CORR procedure of SAS (SAS Institute 1988). Correlation analysis allowed identification of: (1) species that contribute to vegetation gradients extracted in the ordination process and (2) environmental factors that may influence species distribution and dominance across ordination gradients. Spearman rank correlation was used instead of Pearson linear correlation to free the analysis of assumptions of linearity in relationships between species importance and environmental factors and of normality in distribution of vegetation across the ordination gradients (Dollar and others, 1992). Environmental data were obtained from data sets supplied by the Missouri Department of Conservation that contained information for each 0.2 ha plot indicating slope %, aspect (° azimuth) and slope position (1= floodplain, 5=ridgetop). For correlation analysis, aspect was transformed trigonometrically using a function that provided a maximum value (+1) for NE aspects (45°) and minimum value (-1) for SW aspects (225°) (Beers and others 1966):

$$\text{Transformed aspect} = \text{COS (Aspect} - 45°)$$

This transformation provides a representation of the "mesicness" continuum of topographic orientation, with NE aspects providing the most "mesic," SW aspects the most "xeric" environments, and other aspects being assigned intermediate values along this microenvironmental continuum. Another variable was derived from transformed aspect by multiplying it by slope % based on the tendency of microclimatic influences to be accentuated by the slope of the land (Frank and Lee 1966).

Potential successional trends in these forests were investigated through overstory-understory and size class analysis on groups of plots segregated by ELT classification. Data from the overstory plots mentioned previously and those of the four 0.02 ha sapling plots were merged, and differences between understory (≤19.05 cm dbh) and overstory (>19.05 cm dbh) relative densities of important species of each ELT were assessed by t-tests after arcsin square root transformation (Dollar and others 1992, Sokal and Rohlf 1981).

Plot density (#/ha) of seedlings (from 0.004 ha plots), saplings and trees (as mentioned above) was assembled and segregated by ELT, and data for each species were plotted by diameter class [< 1.5 in (3.8 cm), 1.5-4.5 in(3.8-11.4 cm), 4.5-7.5 in (11.4 cm-19.1 cm), 7.5-10.5 in (19.1-26.7 cm), 10.5-13.5 in (26.7-34.3 cm), 13.5-16.5 in (34.3-41.9 cm), 16.5-19.5 in (41.9-49.5 cm), 19.5-22.5 in (49.5-57.2 cm), 22.5-25.5 in (57.2-64.8 cm), > 25.5 in (64.8 cm) dbh] for further analysis of population structure and potential replacement of canopy trees (Harcombe and Marks 1978, Harcombe 1987, Johnson 1992, McCarthy and Wistendahl 1988). Density vs. size class relationships for different species were compared visually and statistically (using χ^2-based comparison of frequency distributions across size classes) (Sokal and Rohlf, 1981).

RESULTS AND DISCUSSION

Ordination and Classification

Seventy percent of the variation in vegetation composition was displayed in the first two (of four total) DCA ordination axes. The sample ordination graph, using the first two axes, displayed a dense cloud of plots toward the lower left-hand corner, with a far more scattered and sparse distribution of plots to the right and upper portions of the graph (Fig. 1). The DCA species ordination graph (Fig. 2) and correlation analysis of DCA plot scores with species IV (Table 1) indicated that the first DCA axis represented a strong gradient in black oak (*Quercus velutina* Lam.) importance and segregation of this species from species such as white ash (*Fraxinus americana* L.), black walnut (*Juglans nigra* L.), eastern redcedar (*Juniperus virginiana* L.), sugar maple (*Acer saccharum* Marsh.) and bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch). Black oak was more abundant in plots with low Axis 1 scores while the latter group of species was important in plots with high Axis 1 scores. In a similar fashion, the second DCA axis clearly separated mesic species such as bitternut hickory, black walnut, white ash, and sugar maple (high Axis 2 scores) from xeric species such as shortleaf pine (*Pinus echinata* Mill.), eastern redcedar, post oak (*Quercus stellata* Wangenh.) and blackjack oak (*Quercus marilandica* Muenchh.) (low Axis 2 scores).

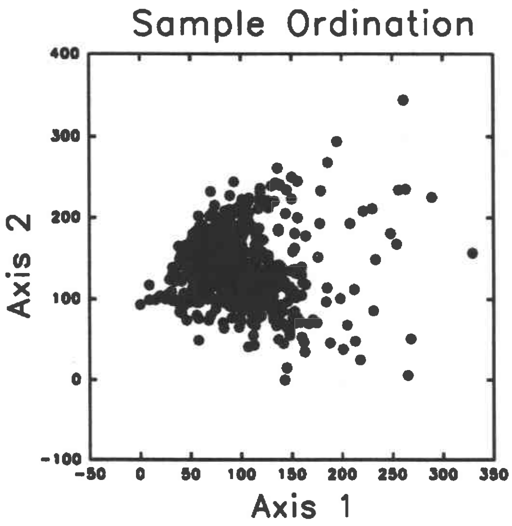

Figure 1. Distribution of plots across two-dimensional ordination space derived from DCA ordination of tree importance values of 644, 0.2 ha plots.

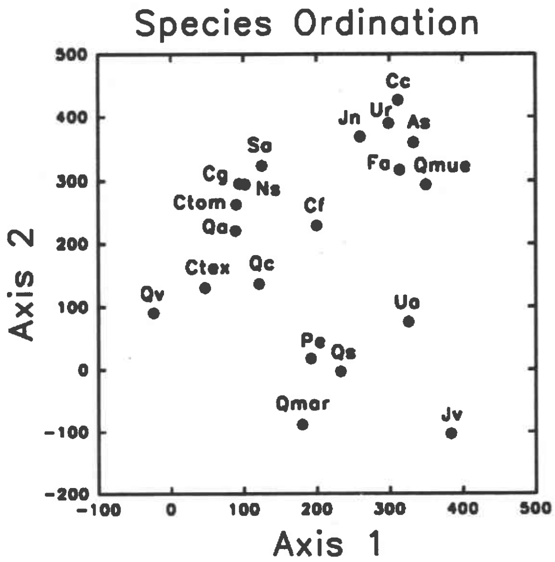

Figure 2. Scatter plot of species across two-dimensional ordination space derived from DCA ordination of tree importance values. Species key: Pe= shortleaf pine; Qc= scarlet oak; Qv= black oak; Qs= post oak; Qa= white oak; Qmue= chinkapin oak; Qmar= blackjack oak; Ns= black gum; Cg= pignut hickory; Cc= bitternut hickory; Ctex= black hickory; Ctom=mockernut hickory; Sa= sassafras; Cf= flowering dogwood; Jv= eastern redcedar; Ur= slippery elm; Ua= winged elm; Fa= white ash; As= sugar maple; Jn= black walnut.

When Axis 1 scores were correlated with environmental factors, some relationships were apparent, with the strongest correlations shown between axis scores and slope position (Table 2A). In practical terms, this correlation indicated that black oak was more important on ridgetop positions. However, in general, environmental correlations with Axis 1

Table 1. Spearman correlation coefficients between DCA axis scores and species importance values. ** p≤0.01; * p≤0.05

Species	Ordination Axis Axis 1	Axis 2
ACERSAC*	0.24**	0.25**
CARYCOR	0.18**	0.25**
CARYGLA	-0.11**	0.46**
CARYTEX	-0.24**	0.06
CARYTOM	-0.08*	0.42**
CORNFLO	0.02	0.25**
FRAXAME	0.29**	0.25**
JUGLNIG	0.16**	0.39**
JUNIVIR	0.32**	-0.04
NYSSSYL	-0.02	0.42**
PINUECH	0.44**	-0.53*
QUERALB	-0.03	0.57**
QUERCOC	0.12**	0.02
QUERMAR	0.12**	-0.48*
QUERMUE	0.47**	0.19**
QUERSTE	0.31**	-0.57*
QUERVEL	-0.89**	-0.25*
SASSALB	-0.03	0.27**
ULMUALA	0.39**	0.08
ULMURUB	0.28**	0.35**

*Species codes for Tables 1, 2 and 3. ACERSAC = sugar maple; CARYCOR = bitternut hickory; CARYGLA = pignut hickory; CARYTEX = black hickory; CARYTOM = mockernut hickory; CORNFLO = flowering dogwood; FRAXAME = white ash; JUGLNIG = black walnut; JUNIVIR = eastern redcedar; NYSSSYL = black gum; PINUECH = shortleaf pine; QUERALB = white oak; QUERCOC =scarlet oak; QUERMAR = blackjack oak; QUERMUE = chinkapin oak; QUERSTE = post oak; QUERVEL = black oak; SASSALB = sassafras; ULMUALA = winged elm; ULMURUB = slippery elm.

were not strong (i.e., less than 0.3), suggesting that some unmeasured factor likely was important in determining species composition across this axis. Plausible candidates are disturbance history and soil factors (especially pH, Nigh and others 1985, Ware and others 1992). In contrast to these relatively weak Axis 1-environment correlations, the transformed aspect and aspect x slope variables correlated more strongly ($r = 0.43$ to 0.46) with Axis 2 DCA sample scores. This result is consistent with the distribution of species shown in the species ordination graph (Fig. 2). Hence Axis 2 of the DCA ordination appeared to represent a habitat moisture gradient.

MOFEP Forest Composition

Forests of the two most common ELT classifications (17 and 18) (Table 3) consisted of nearly equal abundances of black and scarlet oak. White oak (*Quercus alba* L.) was somewhat greater in importance on ELT 18 plots (side slopes N/E aspects; deep soils; Miller, 1981) than on 17 plots (side slopes S/W aspects; deep soils). In contrast, shortleaf

Table 2. Spearman correlation coefficients (with probability level below) between DCA ordination axis scores and environmental variables (A) and between environmental variables and species Importance Values (B). For species codes see Table 1.

(A)

	Axis 1	Axis 2
Slope (%)	0.001	0.08
	0.98	0.04
Slope position	-0.29	-0.25
	<0.01	<0.01
Aspect*	-0.22	0.43
	<0.01	<0.01
Aspect x slope*	-0.19	0.46
	<0.01	<0.01

(B)

	ACERSAC	CARYCOR	CARYGLA	CARYTEX	CARYTOM	CORNFLO	FRAXAME	JUGLNIG	JUNIVIR	NYSSSYL
Slope (%)	-0.02	-0.08	-0.10	-0.07	0.02	0.15	0.001	-0.07	0.09	0.12
	0.59	0.04	0.01	0.10	0.69	<0.01	0.98	0.07	0.03	<0.01
Slope position	-0.13	-0.14	0.01	0.07	-0.12	-0.16	-0.13	-0.05	-0.05	-0.22
	<0.01	<0.01	0.76	0.10	<0.01	<0.01	<0.01	0.25	0.23	<0.01
Aspect*	0.01	0.03	0.29	0.15	0.19	0.26	0.03	0.10	-0.07	0.22
	0.94	0.46	<0.01	<0.01	<0.01	<0.01	0.43	<0.01	0.06	<0.01
Aspect x Slope*	0.01	0.05	0.33	0.15	0.21	0.28	0.07	0.12	-0.10	0.23
	0.90	0.24	<0.01	<0.01	<0.01	<0.01	0.07	<0.01	0.01	<0.01

	PINUECH	QUERALB	QUERCOC	QUERMAR	QUERMUE	QUERSTE	QUERVEL	SASSALB	ULMUALA	ULMURUB
Slope (%)	0.10	0.12	0.15	-0.04	0.01	-0.26	-0.07	0.01	0.04	-0.04
	<0.01	<0.01	<0.01	0.32	0.81	<0.01	0.06	0.99	0.34	0.36
Slope position	-0.01	-0.20	-0.14	0.17	-0.25	0.13	0.37	-0.07	-0.22	-0.16
	0.97	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.07	<0.01	<0.01
Aspect*	-0.40	0.19	0.04	-0.32	-0.09	-0.30	0.04	0.18	-0.04	0.04
	<0.01	<0.01	0.37	<0.01	0.03	<0.01	0.32	<0.01	0.35	0.37
Aspect x Slope*	-0.45	0.17	0.02	-0.32	-0.06	-0.27	0.01	0.19	-0.04	0.04
	<0.01	<0.01	0.66	<0.01	0.12	<0.01	0.87	<0.01	0.33	0.26

* Aspect transformed trigonometrically (see text).

Table 3. Mean Tree Importance Values of MOFEP plots classified by Ecological Land Type (ELT). (n= number of plots in ELT)

	ELT*												
	1	5	6	7	11	15	17	18	19	20	21	22	23
n=	1	28	2	6	89	5	257	213	19	8	4	3	9
SPECIES													
ACERSAC*		1.46	4.10		0.02		0.15	0.10	3.00	1.13			0.42
CARYCOR		3.81	7.70		0.03	0.38	0.05	0.14	0.76				
CARYGLA	19.40	11.77	32.15	6.15	10.87	5.60	3.80	10.98	3.14	5.85	0.55	0.70	1.55
CARYTEX	10.70	9.59	14.10	11.75	12.35	8.14	7.06	8.87	6.28	14.65	8.92	4.13	4.47
CARYTOM	10.80	9.96	15.05	35.15	7.52	5.86	6.22	10.01	4.76	5.77		2.73	0.98
CORNFLO	11.50	1.45		1.56	0.43	0.32	0.97	2.55	2.13	0.48		4.30	0.94
FRAXAME		2.27	2.65		0.22		0.34	0.37	3.89	2.21		1.70	1.36
JUGLNIG		2.92	12.80	1.31	1.71		0.39	0.97	2.59	0.75			
JUNIVIR							0.37	0.03	1.78		10.10	0.60	9.58
NYSSSYL	26.10	6.21	16.40	12.31	1.42	1.04	2.42	4.45	1.35	7.32	0.80	1.03	
PINUECH		11.04		9.41	12.75	9.32	25.25	7.45	31.35	15.36	22.17	13.03	25.35
QUERALB	63.70	43.03	45.95	28.23	30.03	16.58	38.98	47.40	32.63	66.61	20.62	21.16	10.72
QUERCOC	26.10	28.53	24.30	36.00	28.79	14.68	46.88	47.96	35.05	40.26	40.52	15.30	35.76
QUERMAR		0.33		0.36	2.88	9.08	3.05	0.24	0.87	0.47	33.55	17.46	15.52
QUERMUE		5.71	2.40	3.16			0.89	0.49	25.23	3.13	4.15	15.13	20.77
QUERSTE	6.40	25.58		15.56	18.15	16.38	12.48	7.09	29.20	9.97	11.42	46.30	40.67
QUERVEL	20.70	20.80	10.95	30.01	71.80	112.44	49.13	48.28	8.93	18.65	34.00	29.56	26.76
SASSALB		0.49		2.85	0.16		0.15	0.53	0.11	0.85			
ULMUALA		1.52	1.15	0.55	0.01		0.35	0.21	2.56	0.80	13.22	0.73	1.53
ULMURUB		5.82	3.40	0.68	0.25		0.27	0.40	1.77	0.22		0.56	0.23

*Species code: see Tab. 1. ELT Codes (Miller, 1981): 1-Low flood plains/loamy and mixed alluvial soils; 5,6-Upland waterways/deep cherty soils; 7-Toe slopes/deep loamy soils; 11-Narrow ridges/deep cherty soils; 15-Broad ridges/deep loamy and clayey soils; 17-Side slopes/South and West aspects/deep soils; 18-Side slopes/North and East aspects/deep soils; 19-Side slopes/South and West aspects/shallow soils; 20-Side slopes/North and East aspects/shallow soils; 21-23-Side slopes/very shallow limestone soils

pine was more important on ELT 17 plots. Other tree species on these plots generally had importance values greater than 1 and less than 15 and included pignut, black and mockernut hickories (*Carya glabra* (Mill.) Sweet, *C. texana* Buckl., *C. tomentosa* (Poir.) Nutt.), black gum (*Nyssa sylvatica* Marsh.) and post and blackjack oak. These hickory species and black gum tended to be more important on ELT 18 plots, while blackjack and post oaks were more important on ELT 17 plots. Plots of ELT 11 (narrow ridges/deep cherty soils) were dominated by black oak with smaller contributions by scarlet (*Quercus coccinea* Muenchh.), white and post oaks. Lower importance values were associated with shortleaf pine, the three above-mentioned species of hickory, and black gum. Plots of ELT 19 (side slopes S/W aspects; shallow soils) were characterized by the highest shortleaf pine and chinkapin oak (*Quercus muehlenbergii* Engelm.) importance values among all ELT classes, with similar contributions by scarlet, white, and post oaks. Most important on plots characterized as "Upland Waterways" (ELT 5, 6) was white oak, followed by scarlet, post and black oak, and shortleaf pine and previously-mentioned species of hickory. Moreover, there was a small, but notable, contribution on ELT 5 plots of mesic species such as black walnut, black gum, sugar maple bitternut hickory, and slippery elm (*Ulmus rubra* Mühl). Although the sample sizes of remaining ELT classes were quite small, it is worth noting that white oak importance was quite high on ELT 20 (side slopes N/E aspects; shallow soils) and those species that prefer soil high in calcium, such as eastern redcedar and chinkapin oak (Fowells 1965), were important on ELT 21-23 plots.

Correlation of species importance values with environmental parameters (Table 2B) reinforced the qualitative relationships noted above between ELT-based environmental characterizations and species distribution and abundance. Species associated with ELTs categorized as having South and West-facing slopes (shortleaf pine and blackjack and post oaks) tended to be negatively correlated with the transformed aspect and aspect x slope % variables. In contrast, species that were more important on ELTs associated with North- and East-facing slopes (white oak, species of hickory, black gum, and black walnut) tended to be positively and significantly correlated with these two parameters. Black oak correlated most highly with slope position, being most important on ridgetop positions and showing little correlation with aspect. In contrast, more mesic-site species (for this region) such as sugar maple, bitternut hickory, white ash, black gum, white oak, and winged (*Ulmus alata* Michx.) and slippery elm were associated with lower slope positions.

MOFEP plots show species composition and abundance typical of the generally xeric forests of the region (Braun 1972, Nelson 1985, Read 1952, Ware and others 1992). On ridgetop and upper slope forests a combination of black, scarlet, post and white oaks and shortleaf pine dominate, with relative importance shifting among black oak (ridgetops), scarlet, black and post oaks and shortleaf pine (S- and W-facing slopes), and white oak and hickories (N- and E-facing slopes). On lower slopes white oak tends to attain an importance similar to that associated with mesic (North and East) aspects on upper slopes. On the relatively infrequent mesic sites associated with upland draws and ephemeral streams, mesic species of the region such as sugar maple, bitternut hickory, black gum and black walnut, along with more abundant white oak may be found.

According to Nelson's (1985) scheme, MOFEP forests would appear to variously fit the classifications of xeric to dry-mesic forests on limestone/dolomite, chert and sandstone substrates. This conclusion is consistent with that of Brookshire and Hauser (1993). MOFEP forests similarly fit into Braun's (1972) categorization of Oak-Pine and southern division Oak-Hickory forests. There were some exceptions to Nelson's and Braun's descriptions, however. Particularly noteworthy was the scarcity of northern red oak (*Quercus rubra* L.) in MOFEP forests despite its inclusion in forests of the region by both Nelson and Braun. Similarly, Ware and others (1992) identified northern red oak as a common constituent of upland forests near the Current River in the same general area. Secondly, is the abundance of scarlet oak in the MOFEP study sites and its restriction to the Oak-Chestnut Region by Braun (1972) (she nowhere mentions it as occurring in Oak-Hickory forests). Scarlet oak also fails to appear in the species lists of Ware and others (1992). It might be speculated that, given the morphological similarity of scarlet oak to northern red and black oaks, variation in species identification might be responsible for these discrepancies.

Overstory-Understory Relationships

Figures 3-7 illustrate differences between overstory (>19.05 cm dbh) and understory (≤19.05 cm dbh) relative densities of major species of common ELTs . Some trends were apparent: (1) In every ELT examined, there was evidence of substantial depletion of understory populations of shortleaf pine and major red oak group species (scarlet and black oak); (2) In three of five major ELT classes (11, 17, 18, representing 92% of plots) white oak relative density in the understory was significantly greater than that in the overstory; (3) A number of other species that currently are not very important in the overstory show greater relative abundances in the understory [i.e., black gum, mockernut hickory, black hickory and sassafras (*Sassafras albidum* (Nutt.) Nees)].

Overstory-understory relationships varied somewhat with ELT classification. The understory relative densities of red oak group species and shortleaf pine tended to be greater in plots of ELTs that were more xeric in character (especially ELT 11 and 17, Figs. 4 and 5) compared with more mesic ELTs (5 and 18 Figs. 3 and 6). However, understory relative densities of these species were substantially reduced on ELT 19 plots, which also presumably was quite xeric. As mentioned above, relative density of understory white oak was greater than that in the overstory in three ELTs (11, 17 and 18, Fig. 4, 5 and 6). In the other two abundant ELTs (5 and 19) relative density of understory white oak was less than that in the overstory, but because there were few black or scarlet oak and shortleaf pine plants in the understory of forests of these ELTs, white oak was still the most common understory tree species. Other species that tended to show increased relative density in the understory (black gum, black and mockernut hickory, sassafras) showed little apparent relationship between relative abundance and ELT (and hence microenvironment). Post oak was relatively less abundant in the understory than in the overstory in all ELTs, but the differences were substantially less than those shown by red oak group species and shortleaf pine.

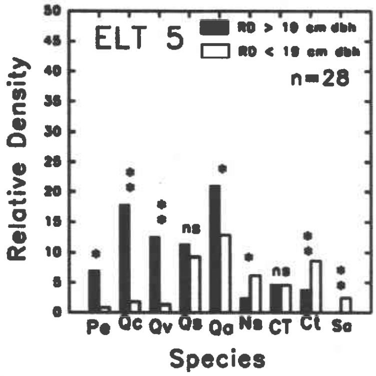

Figure 3. Overstory and understory relative density for major species on ELT 5 plots. Asterisks above each pair of histogram bars indicate highly significant (**$p \leq 0.01$) and significant (*$p \leq 0.05$) differences between overstory and understory pairs. Bar pairs with "ns" are not significantly different ($p > 0.05$). Species codes: Pe-shortleaf pine, Qc-scarlet oak; Qv-black oak; Qs-post oak; Qa-white oak; Ns-black gum; CT-black hickory; Ct-mockernut hickory; Sa-sassafras..

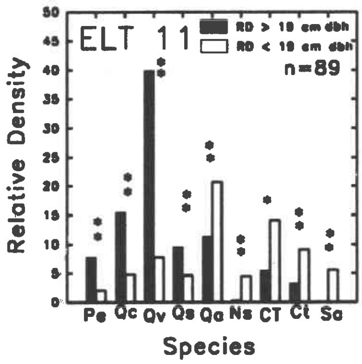

Figure 4. Overstory and understory relative density for major species on ELT 11 plots. Asterisks above each pair of histogram bars indicate highly significant (**$p \leq 0.01$) and significant (*$p \leq 0.05$) differences between overstory and understory pairs. Bar pairs with "ns" are not significantly different ($p > 0.05$). Species codes: see legend for Fig. 3.

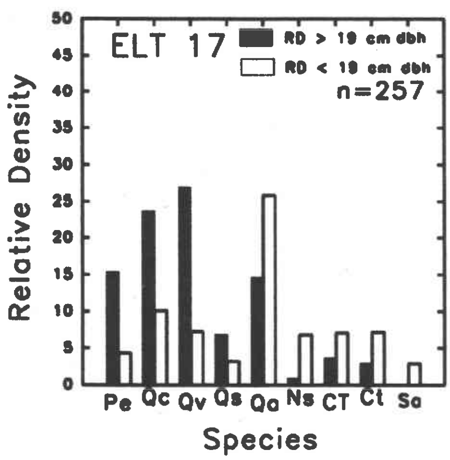

Figure 5. Overstory and understory relative density for major species on ELT 17 plots. All bar pairs are significantly different ($p \leq 0.01$). Species codes: see legend for Fig. 3.

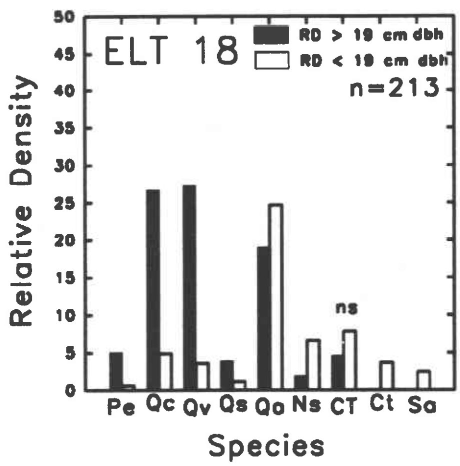

Figure 6. Overstory and understory relative density for major species on ELT 18 plots. All bar pairs except that marked with "ns" are significantly different ($p \leq 0.01$). Species codes: see legend for Fig. 3.

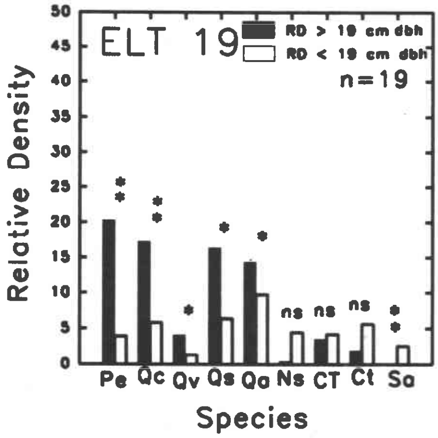

Figure 7. Overstory and understory relative density for major species on ELT 19 plots. Asterisks above each pair of histogram bars indicate highly significant (**p≤0.01) and significant (*p≤0.05) differences between overstory and understory pairs. Bar pairs with "ns" are not significantly different (p>0.05). Species codes: see legend for Fig. 3.

Density-Size Class Distribution Relationships

χ^2-tests of distribution differences across size classes indicated that there were highly significant (p≤0.01) differences among species in every ELT (data not shown). Density vs. size class plots were constructed for major species and ELTs [see Fig. 8 for an example (ELT 17)]. In general, the results offered further confirmation of previously-noted patterns of species dominance and potential replacement across ELTs.

However, several new distribution patterns were shown in these plots and not elsewhere: (1) In all ELTs white oak abundance was greatest in the 1.5-4.5 in (3.8-11.4 cm) dbh size class, decreasing in all larger and the one smaller size class; (2) Most other abundant species in the understory (black gum, sassafras, black hickory, mockernut hickory) had greatest density in the smallest size class; (3) Some species that currently are abundant in the overstory (black, scarlet, and post oak and shortleaf pine) showed shallow negative slopes; (4) Density of red oak group species and shortleaf pine were much reduced in smaller size classes compared with those of white oak and other understory species, supporting the general trends and conclusions shown by overstory-understory analysis (see above). However, red oak group species are present in densities > 50/ha even in smaller size classes in certain ELTs, particularly those that are more xeric (e.g., 17, Fig. 8). Density of shortleaf pine is everywhere less than 25/ha; (5) The differences between ELT 17 and 18 in relative density of red oak group species and shortleaf pine vs. white oak were attributable to differences in absolute abundance in the former group. Absolute density of white oak in the understory was quite similar on both ELTs (data not shown; see also Brookshire and Hauser 1993).

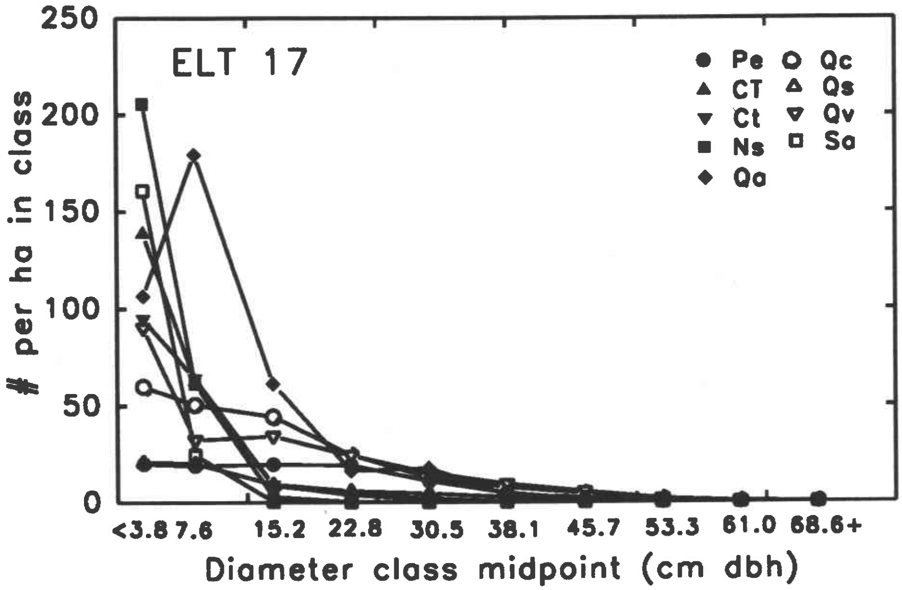

Figure 8. Mean density vs. size class relationships for important species on ELT 17 plots. Species codes: see legend for Fig. 3.

These data are consistent with trends we have seen elsewhere in the Ozarks (Jenkins and Pallardy, 1993). There is strong evidence in the MOFEP data set and from other research in the Missouri Ozarks that white oak has the potential to increase in importance throughout the region. The ecological basis of this potential change *may* be ascribable to white oak's greater longevity and shade tolerance (Dougherty and others 1980, Fowells 1965). The size class distributions further indicate that white oak apparently has experienced a "pulse" of recruitment, with the greatest abundance of this species found in the next-to-smallest size class. Other species, particularly black gum, some of the hickories, and sassafras show great abundance in the smallest size class. One might speculate that observers of long-term forest succession in the Ozark region might see these species becoming more important, but it is debatable whether they (except perhaps for the hickories) have canopy potential given the xeric environment of the Ozarks and the greater microclimatic stress associated with ascent to an unprotected canopy position (Nigh and others 1985, Pallardy and others 1988). On the other hand, the current position of white oak as a canopy dominant throughout much of the MOFEP study area indicates that its short-term increase in abundance is nearly certain.

Future trends in abundance of scarlet and black oak in MOFEP site forests may differ somewhat from those of shortleaf pine. In the former pair there is still sufficient regeneration to anticipate a continuing, if less prominent, contribution of both red oak species to future forest overstories. This is especially true on xeric ELT 11, 17, and 19 sites. In contrast, seedlings and saplings of shortleaf pine are nowhere abundant and one might predict a uniform decline in the abundance of this species through time in canopies of undisturbed forests of the MOFEP project.

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