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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

AN ANALYSIS OF SELECTED OKLAHOMA UPLAND FOREST STANDS INCLUDING BOTH OVERSTORY AND UNDERSTORY COMPONENTS

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

ROBERT KENNETH KENNEDY

Norman, Oklahoma

1973

AN ANALYSIS OF SELECTED OKLAHOMA UPLAND FOREST STANDS INCLUDING BOTH OVERSTORY AND UNDERSTORY COMPONENTS

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To my wife, Julaine, a loving thank you for her steadfast support through this entire endeavor.

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ABSTRACT

Twenty-five upland forest stands in Oklahoma were analyzed for percentage composition, diversity, vegetation-environment relationships and the correspondence of understory vegetation to overstory vegetation.

Stands were variously grouped for analysis by overstory leading dominant, section of state (precipitation gradient) and by characteristic overstory species into one of six community-types: oak-loblolly pine, oak-hickory-shortleaf pine, oak-hickory, oak-hickory savannah, oak savannah and oak shinnery.

Stands were analyzed individually by constructing polar (vegetational) and principal component (environmental) ordinations. Polynomial and linear regressions were calculated to show the interrelationships of vegetation parameters, vegetation-environment and the response of individual overstory species to a moisture gradient. Additionally, forty-four understory species and sixteen overstory species were classified into five groups according to distribution and importance over a geographic-precipitation gradient which corresponds to the prevailing east-west annual precipitation gradient in the state.

Diversity was calculated for the four vegetation strata in each stand, each community-type and for stands grouped according to leading dominant using relative basal area for overstory and importance percentage for understory strata in the Shannon-Wiener diversity function. Community diversity was expressed as the summation of the diversities of the four vegetation strata in each community-type.

AN ANALYSIS OF SELECTED OKLAHOMA UPLAND FOREST STANDS INCLUDING BOTH OVERSTORY AND UNDERSTORY COMPONENTS

PART I

THE OVERSTORY COMPONENT

INTRODUCTION

The state of Oklahoma is characterized by diversity in topography, climate, and vegetation. The topography is generally level to rolling, excepting the south central Wichita and Arbuckle Mountains and the Ozark, Boston, and Ouachita Mountains along the extreme eastern border. An elevational gradient runs northwesterly from southeastern McCurtain County (88m) to the northwestern border (610m) excluding the panhandle. Mean annual temperatures in the main body of the state vary from 17.3°C in the southeast to 15.0°C in the northwest, and average annual precipitation ranges from 125 cm in the southeast to 59 cm in the northwest, with localized southeastern accumulations of 140 cm (Oklahoma Water Resource Board, 1970). Average number of days without killing frost varies from 240 days in the southeast to 200 days in the northwest. The western portion of the state is therefore subject to greater temperature extremes and higher variability in the seasonality and intensity of precipitation.

Rice and Penfound (1959) classified the oak-hickory forest association in Oklahoma into five community types: oak-loblolly pine (Pinus taeda L.)[1] confined to the southern portion of McCurtain County, oak-hickory-shortleaf pine (Pinus echinata Mill.), oak-hickory forest, oak-hickory savannah, and oak savannah. Only the oak savannah is present in the western portions of the state, while all five community-types occur in the east. Five upland tree species contribute about 85% of the total basal area in the state and of these, post oak (Quercus stellata Wang.) and blackjack (Quercus marilandica Muenchh.) account for 68% (Rice and Penfound, 1959). Of the three remaining species, black oak (Quercus velutina Lam.) and black hickory (Carya texana Buckl.) are widely distributed over the eastern half of the state, while shortleaf pine is largely confined to the southeastern corner with a limited number of small disjunct populations in the Ozark highlands.

The objectives of the present study were to determine vegetational composition, population structure, and vegetation-environment relationships for the overstory component of 25 selected upland forest stands encompassing all five of the oak-hickory association community-types. The

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[1]Nomenclature follows Waterfall, 1966.

approximate locations for stands sampled in this study are presented in Figure 1.

Figure 1.--Map of the State of Oklahoma showing approximate locations for the 25 upland forest stands sampled.

METHODS

Stands selected for sampling were a minimum of 6.0 ha in size, representative of the community-type for that section of the state, upland in terms of topography and characteristic species, confined to a single aspect and relatively undisturbed by recent cutting or burning, although grazed areas were used if grazing was not severe. The sites are listed in Table 1.

Soil samples (0-20 cm) were taken at 10 randomly distributed points in each stand for soil texture and pH determinations. Bulk density (0-5 cm) was determined at these same 10 points using a sand displacement method (Rice, 1968). Soil samples were composited within a stand, the material air dried for 5-7 days, visible organic matter removed, and the remaining soil passed through a 2.0 mm sieve. Percentage of gravel (>2.0 mm) was determined and a textural analysis was done on the <2.0 mm separate using the hydrometer method of Bouyoucos (1936). The resulting percentages of sand, silt and clay were corrected for percent gravel and mean particle size was calculated for each stand (Table 1) using these percentages in a formula from Czarnowski (1964).

The tree strata were sampled using an augmented variable-radius technique (Rice and Penfound, 1955). Twenty-five to 35 points were taken in each stand and the basal area

TABLE 1.--Description of sampled stands showing stand number, county, legal description, elevation, slope percent, aspect, mean soil particle size, and soil pH.

Stand Number	County	Legal Description	Elevation (m.)	Slope Percent	Aspect	Mean Soil Particle Size (mm)	Soil pH 0-20 cm depth
1	McCurtain	Sec 5 T 9N R27E	121	-	-	.005	4.5
2	McCurtain	Sec 20 T 1S R24E	290	38	NE	.010	5.3
3	Choctaw	Sec 9 T 6S R19E	152	-	-	.006	4.6
4	Pushmataha	Sec 10 T 2S R21E	350	18	SE	.013	4.0
5	LeFlore	Sec 27 T 3N R27E	427	11	N	.017	5.7
6	Atoka	Sec 5 T 1S R13E	244	80	S	.034	5.1
7	Pittsburg	Sec 17 T 7N R16E	198	18	NW	.006	5.1
8	Johnson	Sec 32 T 4S R 7E	183	4	NW	.017	4.7
9	Cherokee	Sec 23 T 18N R20E	259	11	NW	.008	4.5
10	Pottowatomie	Sec 3 T 8N R 4E	305	-	-	.008	5.4
11	Wagoner	Sec 31 T 19N R16E	198	27	NE	.012	5.8
12	Lincoln	Sec 7 T 12N R 5E	274	4	N	.014	5.0
13	Cleveland	Sec 25 T 9N R 1E	305	22	NW	.005	4.7
14	Delaware	Sec 21 T 24N R25E	274	-	-	.007	4.8
15	Payne	Sec 1 T 17N R 2E	244	13	SE	.022	5.4
16	Grady	Sec 32 T 4N R 8W	427	26	NE	.023	5.4
17	Osage	Sec 13 T 26N R10E	259	18	E	.008	4.4
18	Canadian	Sec 13 T 11N R10W	442	11	NW	.015	6.1
19	Caddo	Sec 21 T 9N R12W	427	4	W	.025	5.7
20	Jackson	Sec 33 T 3N R18W	427	7	S	.032	6.2
21	Blaine	Sec 4 T 18N R12W	472	4	S	.012	5.6
22	Major	Sec 6 T 22N R10W	411	7	SE	.013	5.3
23	Kiowa	Sec 35 T 5N R20W	564	56	N	.009	6.3
24	Woodward	Sec 16 T 21N R17W	558	9	W	.030	6.0
25	Beckham	Sec 25 T 9N R25W	610	-	-	.033	6.0

calculated for each species. Density and dbh[2] size class were taken in 10-.006 Ha arms-length transects per stand. Size classes used were: (1) $<$ 1.4 m tall-seedlings, (2) 0-2.5 cm, (3) 2.5-5.0 cm, (4) 5.0-7.5 cm, (5) 7.5-10.0 cm, (6) $>$ 10.0 cm dbh. Only classes 2-6 were recorded for species in the arms-length transects. Seedling frequency was assessed from approximately 30, m^2 quadrats and cover was recorded by presence-absence in each decimeter increment of 10 line transects (10 m in length) resulting in 1000 dm increments per stand. Relative basal area was calculated for each size class of each species using class midpoints for saplings and relative cover for the seedling class. In addition, average potential solar insolation was calculated using aspect, slope and latitude from tables given by Frank and Lee (1966). Precipitation, evaporation and temperature data for each stand were taken from an Oklahoma Water Resources Board (1970) publication and the precipitation/evaporation ratio was calculated.

Two types of ordinations were used for data analysis purposes. A polar ordination (Bray and Curtis, 1957), using stands as species and species as attributes, placed stands on two dimensions based on stand similarity in species composition. Stands were positioned on the first axis by selecting the two most dissimilar stands (a and b) as end

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[2]Diameter at breast height (dbh).

stands. Stand a was the stand least like the others (lowest total similarity). Stand b was the stand least similar to stand a. The similarity values of all stands with stand b were each subtracted from 100, added to the similarity value for that stand with stand a, and the sum divided by 2. This quotient represents the average distance of each stand from the stand b end of the axis. End stands for the second axis were selected from the 15% increment along the first axis which contained the greatest number of stands, thereafter the procedure was the same. Relative basal areas of 40 tree species were used for this ordination.

A principal component ordination was constructed on 12 environmental variables, using the method of Jeffers (1967). In this analysis, the data used were all relative values, a correlation matrix was calculated, only eigenvectors > 1.0 were retained, and only variables having absolute scaled eigenvector values ≥ 0.7 were used to calculate the axis positions of stands.

RESULTS AND DISCUSSION

Forty tree species (>10.0 cm dbh) were encountered in the sample of 25 upland forest stands (Table 2) but only eight of these occurred as leading dominants (Table 3). Post oak was present in 88% of the stands, was a leading dominant in 12 stands, a codominant in one stand and occurred in a total of 18 stands with a relative basal area >10.0%.

Using the Rice and Penfound (1959) divisions of the state into sections as a basis for comparison, post oak was a leading dominant in all six sections and blackjack oak only in the northwest, southwest and codominant with post oak in one south central stand. The other six leading dominant species were much more restricted, not only because a small number of stands containing these dominants was sampled, but because the species themselves were more restricted in the state than either post oak or blackjack (Johnson and Risser, 1972; Rice and Penfound, 1959; Risser and Rice, 1971a).

Loblolly pine was sampled in only one plantation stand in the southeast section where 96% of the basal area was loblolly pine. This stand also exhibited the highest stand basal area of the 25 stands sampled (Table 3).

Shortleaf pine dominated two southeastern stands and was present in a third, while black hickory was dominant in one stand located in the coastal plain in the southeast section of the state.

TABLE 2.--Percentage presence, number of stands as leading dominant, mean basal area (%) in stands of occurrence, maximum basal area (%), and number of stands with basal area (%) greater than 10.0 for a species.

Species	Presence (%)	Number of stands as leading dominant	Mean basal area (%)	Maximum basal area (%)	Number of stands with basal area >10%
Acer saccharum	4	0	19	19	1
Amelancher arborea	4	0	2	2	0
Bumelia lanuginosa	32	0	2	6	0
Carya cordiformis	12	0	9	16	1
Carya illinoense	4	0	4	4	0
Carya ovata	8	0	10	14	0
Carya texana	52	1	11	29	6
Carya tomentosa	20	0	6	24	2
Celtis reticulata	16	0	1	2	0
Cercis canadensis	12	0	2	2	0
Cornus florida	8	0	8	12	1
Diospyros virginiana	4	0	1	1	0
Fraxinus pensylvanica	4	0	1	1	0
Juglans nigra	4	0	1	1	0
Juniperus virginiana	32	0	9	31	2
Liquidambar styraciflua	4	0	14	14	1
Maclura pomifera	4	0	1	1	0
Magnolia acuminata	4	0	12	12	1
Morus rubra	20	0	1	3	0
Ostrya virginiana	4	0	1	1	0
Pinus echinata	12	2	29	42	3
Pinus taeda	4	1	96	96	1
Prunus americana	4	0	1	1	0
Prunus mexicana	4	0	1	1	0
Ptelea trifoliata	4	0	1	1	0
Quercus alba	12	0	11	15	2
Quercus falcata	12	0	9	21	1
Quercus havardii	4	0	9	9	0

TABLE 2.--Continued

Species	Presence (%)	Number of stands as leading dominant	Mean basal area (%)	Maximum basal area (%)	Number of stands with basal area >10%
Quercus marilandica	80	5	27	86	15
Quercus muehlenbergii	8	0	2	2	0
Quercus phellos	4	0	1	1	0
Quercus shumardii	24	1	5	21	1
Quercus stellata	88	13	41	92	18
Quercus stellata x havardii	24	1	34	99	3
Quercus velutina	36	2	15	45	4
Robinia pseudoacacia	8	0	1	2	0
Sassafras albidum	4	0	3	3	0
Ulmus alata	20	0	8	18	1
Ulmus americana	20	0	3	7	0

TABLE 3.--Leading dominant in each stand, stand basal area (m^2/ha), basal area (%) of leading dominant and basal area (%) of highest subdominant species.

Lead Dominant	Stand Number	Stand Basal Area (m^2/ha)	Species Basal Area (%)	Highest Subdominant	Species Basal Area (%)
Pinus taeda	1	23.1	96.0	Quercus falcata	1.6
Pinus echinata	2	11.8	24.6	Carya tomentosa	24.0
	4	13.6	42.0	Quercus stellata	22.8
Carya texana	3	15.7	22.1	Quercus falcata	20.9
Quercus shumardii	5	13.9	20.7	Acer saccharum	19.0
Quercus velutina	9	12.8	45.2	Quercus marilandica	30.8
	14	14.2	34.8	Quercus stellata	17.4
Quercus stellata	6	8.8	35.4	Carya texana	29.2
	7	12.1	55.3	Carya texana	19.7
	8	16.2	56.5	Quercus velutina	15.3
	10	14.7	92.3	Quercus marilandica	4.8
	11	11.4	48.3	Quercus velutina	16.7
	12	13.3	60.7	Quercus marilandica	30.0
	13	13.9	40.5	Quercus marilandica	40.5
	15	14.7	75.8	Quercus velutina	6.2
	16	19.7	64.7	Quercus marilandica	34.2
	17	11.5	74.6	Quercus marilandica	24.6
	21	15.2	62.9	Quercus marilandica	34.2
	23	9.4	77.2	Quercus havardii	8.9
	24	4.6	60.0	Juniperus virginiana	20.0
Quercus marilandica	13	13.9	40.5	Quercus stellata	40.5
	18	4.1	60.1	Juniperus virginiana	31.0
	19	8.7	61.1	Quercus stellata x havardii	20.0
	20	8.9	49.6	Quercus stellata x havardii	40.1
	22	12.4	86.0	Ulmus americana	6.6
Quercus stellata x havardii	25	4.8	99.0	Celtis reticulata	1.0

Shumard's oak (Quercus shumardii Buckl.) was the leading dominant in one stand, located in the southeast on a deeply shaded, mesic north slope where sugar maple (Acer saccharum Marsh.) was subdominant. It was relatively unimportant in the other five stands of occurrence. Notably, five of the 17 single occurrence species in Table 2 were present in the Shumard's oak dominated stand, namely: sugar maple, sweet gum (Liquidambar styraciflua L.), magnolia (Magnolia acuminata L.), ironwood (Ostrya virginiana [Mill.] K. Koch) and sassafras (Sassafras albidum [Nutt.] Ness.).

Black oak was present in 9 stands, but was dominant only in 2 northeastern stands. It also occurs as the highest subdominant in 3 post oak dominated stands in the central section of the state.

The most western stand sampled was dominated by an oak hybrid or hybrid complex, hereafter referred to as shin oak (Quercus stellata x havardii). Trees in this stand resembled post oak except for their diminutive size, 0.6 to 4.6 m tall (Wiedeman and Penfound, 1960) and rather atypical leaves and acorns for post oak. Shin oak occurred in five stands and was a relatively minor component in the 4 stands where it was not dominant.

A vegetational polar ordination (Bray and Curtis, 1957) was done using stands as species and basal area percentage of 40 tree species as attributes (Figures 2 and 3). Circles represent one of the four basal area classes of post

Figure 2.--Vegetational polar ordination of 25 upland forest stands showing the basal area (m^2/ha) distribution for post oak. Closed circles represent stands where the species is a leading dominant, open circles where it is present, and a dot represents absence of the species. Basal area classes in order of increasing basal area and circle diameter are 0.02-3.4, 3.5-6.9, 7.0-10.2, 10.3-13.7 m^2/ha.

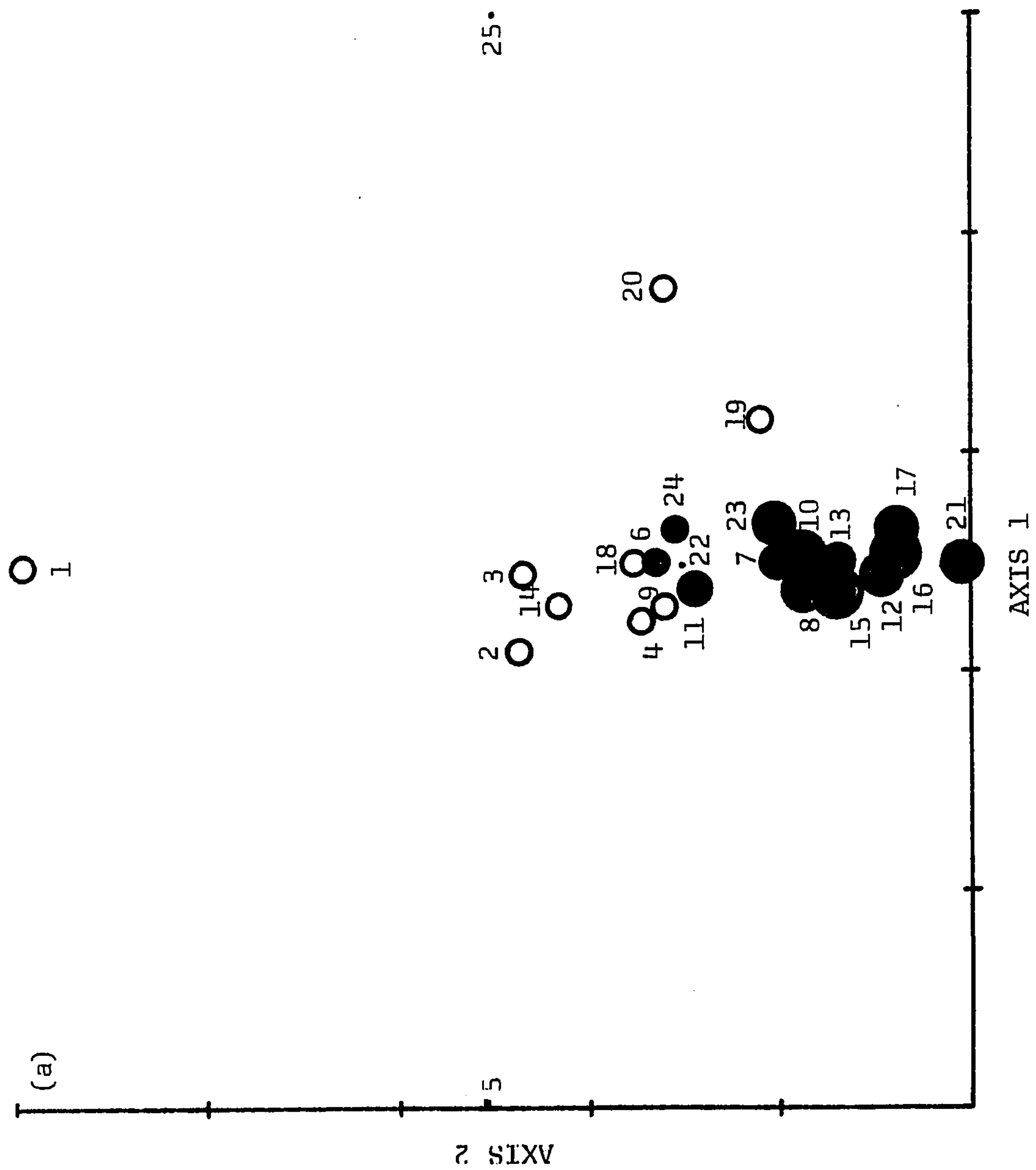
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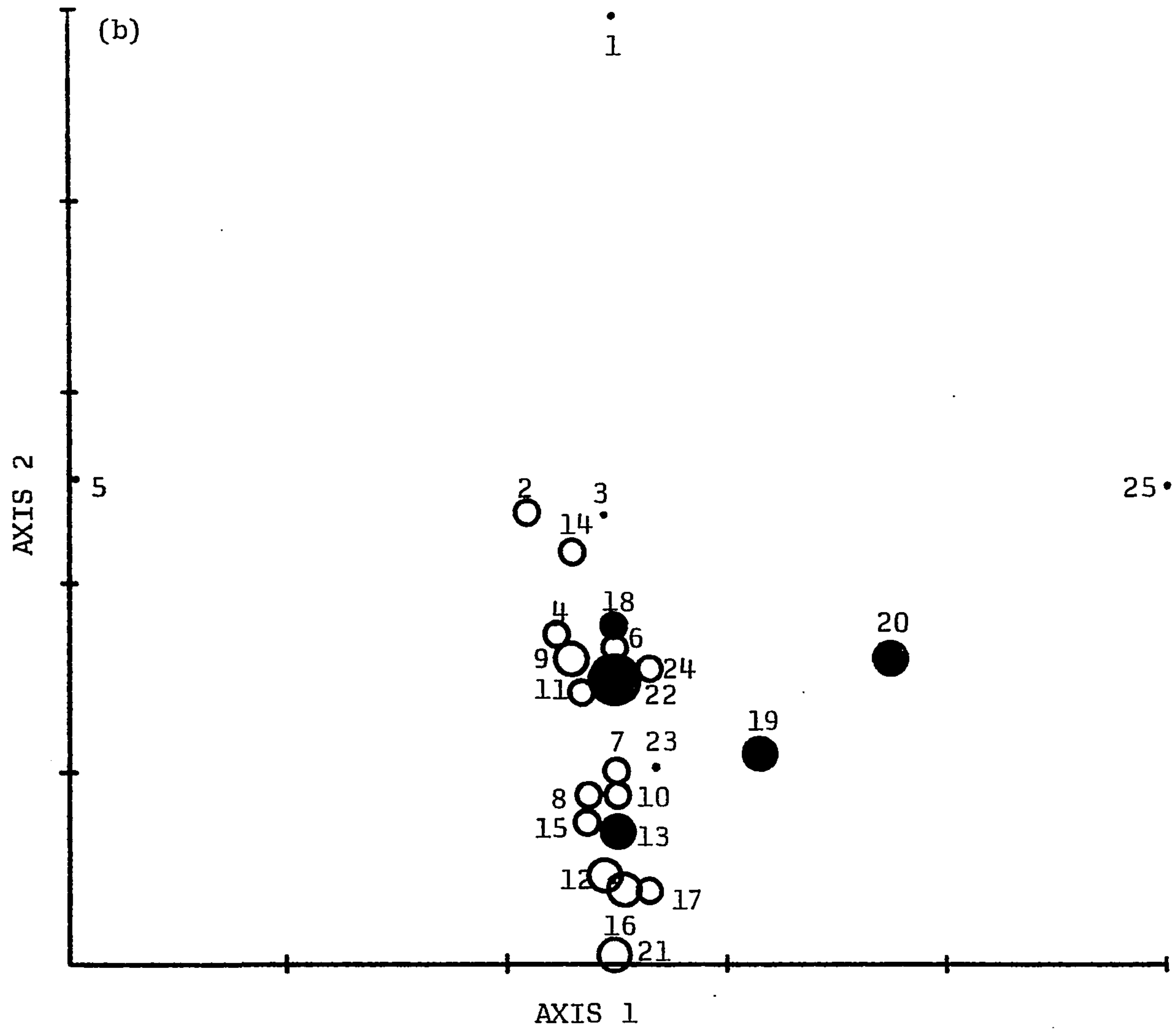
Figure 3.--Vegetational polar ordination of 25 upland forest stands showing the basal area (m^2/ha) distribution of blackjack.



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oak (Figure 2) and blackjack (Figure 3) in each stand. Only blackjack and post oak are plotted on the ordinations as these two species account for 57.0% of the total basal area in these 25 stands. The two most dissimilar stands (end stands on axis 1) were stand 5 (Shumard's oak) and stand 25 (shin oak) which had no species in common and contained neither post oak nor blackjack. Post oak stands fell into two groups, the larger group consisting generally of stands where basal area of blackjack is relatively high and the smaller group (stands 6, 11, 24) having some important third species with post oak basal areas at a somewhat reduced level. No single environmental factor or group of factors could be intuitively ascribed to either of the axes of this ordination without considering a number of exceptions.

In an attempt to relate the vegetation to the environment, a polar ordination was constructed using stands as species and 13 environmental parameters as attributes. Again, it was difficult to attribute any single factor to an axis and the use of iso-lines contributed little toward interpretation.

To check for correspondence between the vegetational ordination and the environmental ordination, a correlation was calculated between the same 50 measured interstand distances on each ordination. The correlation was significant ($r = 0.49$, $p = 0.01$) indicating a positive correspondence between the two ordinations.

In a further attempt to sort out environmental influence on the vegetation, a principal component ordination (Figures 4 and 5) was done on 12 environmental variables, using the method of Jeffers (1967). Figure 4 shows basal area of post oak, with circles representing the same basal area classes as in Figure 2, and Figure 5 represents blackjack. Axis 1 of the environmental ordination (Figures 4 and 5) accounted for 47.2% of the variance and was based on mean annual precipitation, pan evaporation, precipitation-evaporation ratio, percent sand, percent silt, and mean soil particle size. All of these variables were moisture related with precipitation, P/E ratio, and percent silt having positive values, placing the most mesic stands at the most positive (right hand) end of the axis.

The second axis accounted for 15.9% of the variance and was based on percent slope, percent gravel, percent clay and mean soil particle size. This axis constituted a soil texture gradient and placed stands with coarsest textured soils at the more negative (lower) end of the axis. The third axis accounted for 12.7% of the variation, but was based on only one significant scaled eigenvector, potential solar irradiation, and was not considered further.

The general distribution of stands on the ordination indicated that geographically eastern stands fell on the right hand side of the ordination (high positive values on axis 1). There were four notable exceptions to the general geographical

Figure 4.--Principal component ordination of 25 upland forest stands based on 12 environmental variables showing basal area (m^2/ha) distribution of post oak.

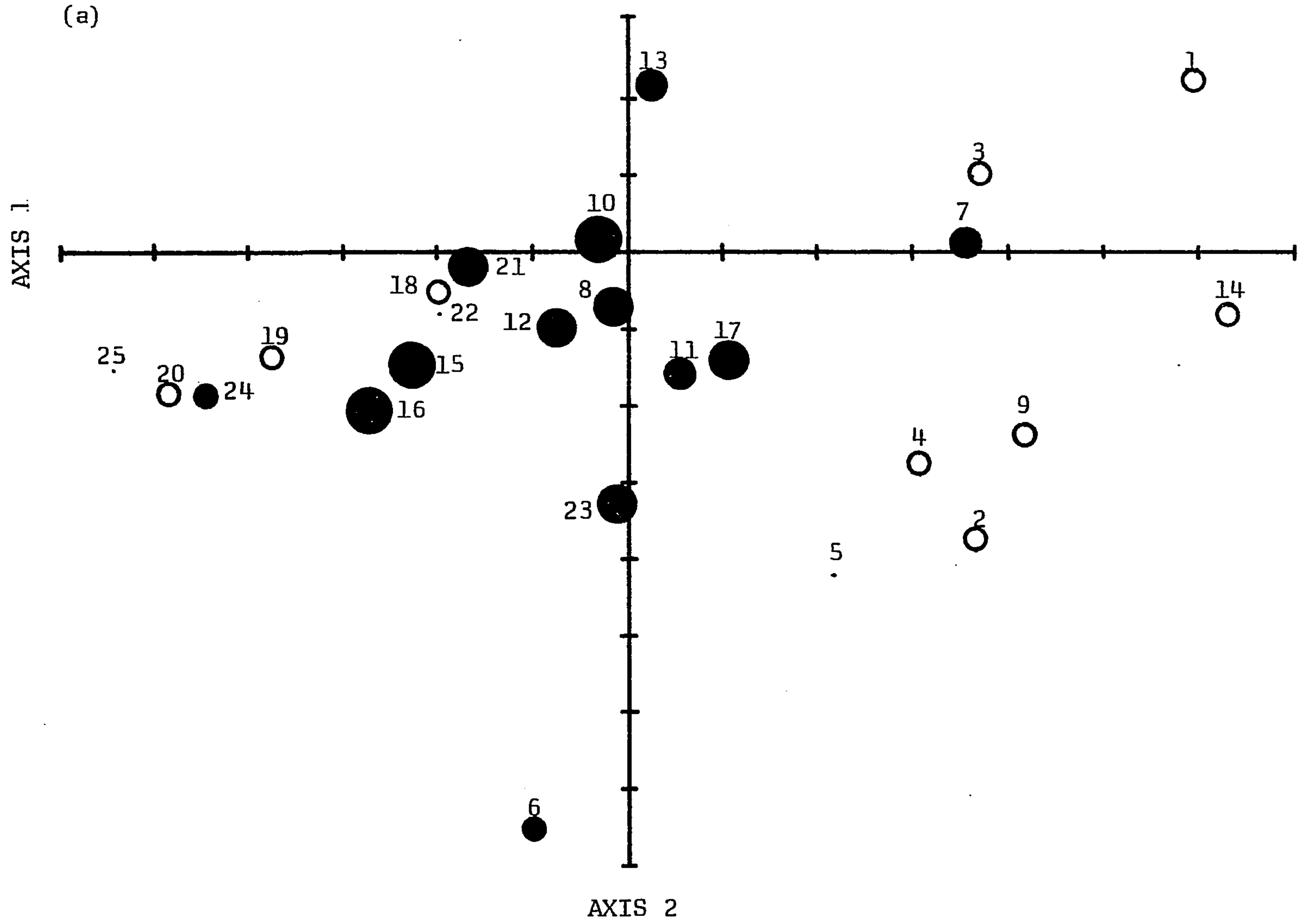
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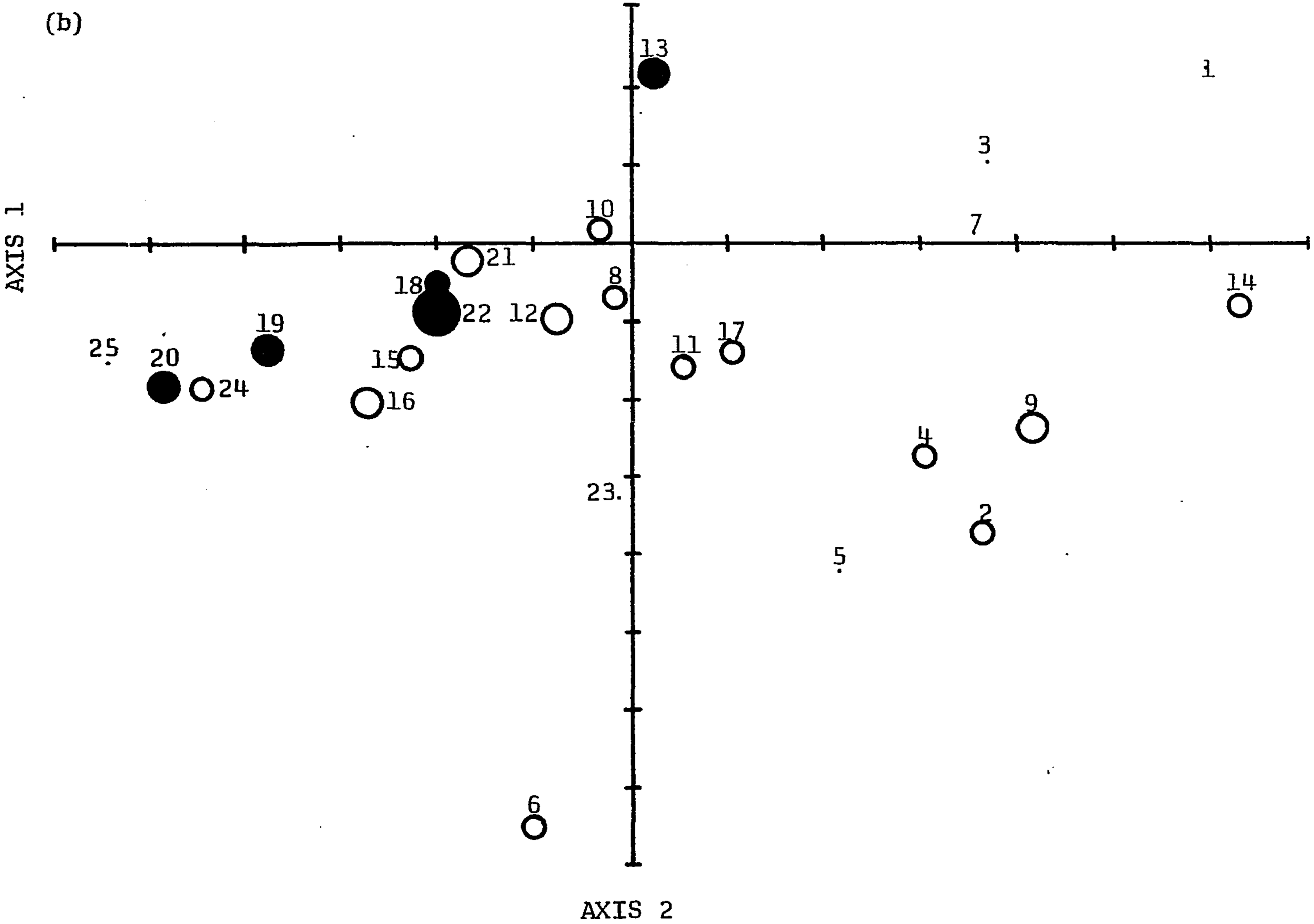
Figure 5.--Principal component ordination of 25 upland forest stands based on 12 environmental variables showing basal area (m^2/ha) distribution of blackjack.



(b)
AXIS 1
AXIS 2
13
1
3
10
7
21
18
22
12
8
14
19
25
20
24
15
16
11
17
9
4
23.
2
5
6

distribution. Stand 6, a southeast stand, occurred on a very steep south slope and had a very coarse textured soil; stand 23, a western stand, occurred on a steep north slope, had a relatively coarse textured soil, but proportionately less sand than any other western stand. Stands 15 and 16 were geographically central stands, but contained much higher percentages of sand than other central stands which corresponded to their placement within the geographically western group.

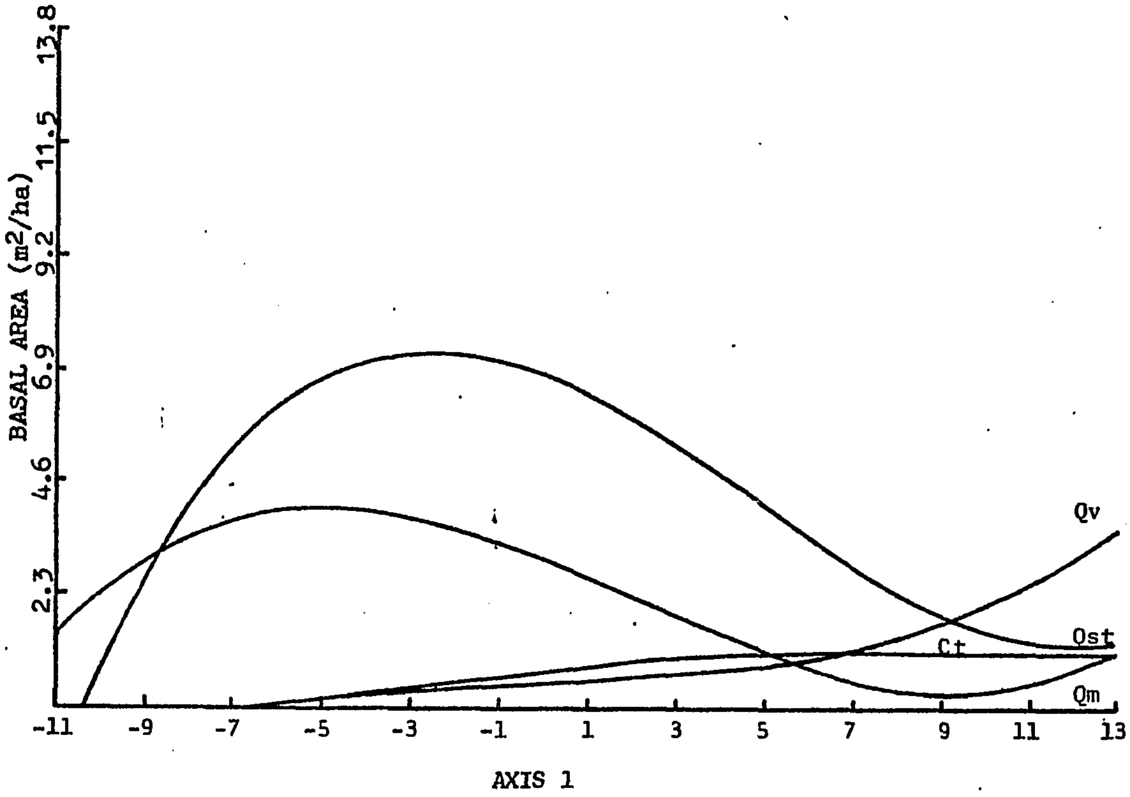
The two major tree species, post oak and blackjack, were quite well distributed over the ordination; however, blackjack dominated stands tend to be positioned closer to the xeric end of the ordination than do post oak dominated stands. Stands positioned toward the mesic end of the ordination were dominated by shortleaf pine, loblolly pine, black oak or Shumard's oak, all species which were important in the eastern portion of the state.

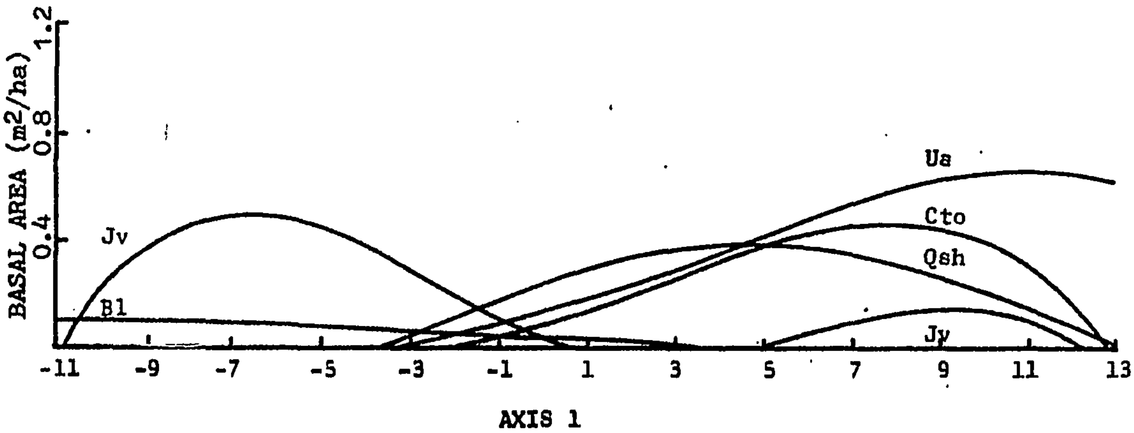
In order to interpret species distributions relative to the environment, polynomial regressions were calculated for species basal area in a stand relative to stand position on axis 1 (moisture gradient) of the environmental principal component ordination (Figure 6). Besides the four major species (Figure 6a), five minor species (Figure 6b) were selected for this analysis on the basis of state-wide basal area contribution. All species had a presence percentage $\geq$ 20%. Three of the minor species were generally important in the east, two in the west (Rice and Penfound, 1959).

Figure 6.--Distribution of basal area (m^2/ha) over a moisture gradient (axis 1 of the environmental ordination) for nine tree species. The degree of the polynomial regression was always at least 3 less than the number of data points.

(a) post oak (Qst), blackjack (Qm), black oak (Qv), and black hickory (Ct).

(b) winged elm (Ua), red cedar (Jv), Shumard's oak (Qsh), mockernut hickory (Cto), and chittamwood (Bl).


BASAL AREA (m2/ha)
13.8
11.5
9.2
6.9
4.6
2.3
Qv
Ost
Ct
Qm
-11
-9
-7
-5
-3
-1
1
3
5
7
9
11
13
AXIS 1


BASAL AREA (m2/ha)
1.2
0.8
0.4
Jv
Bl
Ua
Cto
Qsh
Jv
-11
-9
-7
-5
-3
-1
1
3
5
7
9
11
13
AXIS 1

Of the four major species, post oak peaked at a slightly xeric (-2) position, but was important over most of the gradient excluding the most xeric portion where it intergraded with shin oak. Blackjack peaked at an even more xeric position (-5) than post oak and had generally lower basal areas across the state with the lowest toward the mesic end of the gradient. Both black hickory and black oak peaked at the mesic end of the gradient with black oak at the most mesic (positive) position of any of the four species. Similar results were reported by Johnson and Risser (1972). The distributions of these four species overlapped on the moisture gradient excepting the most xeric portion where black oak and black hickory were absent.

Mockernut hickory (Carya tomentosa Nutt.), winged elm (Ulmus alata Michx.), and Shumard's oak all peaked in the mesic portion of the gradient which corresponded to their east and east central distributions (Phillips, Gibbs, and Matoon, 1959), chittamwood (Bumelia lanuginosa [Michx.] Persoon), was not of much importance in any stand, but had higher basal area in the west and appeared on the more xeric portion of the gradient.

Eastern red cedar (Juniperus virginiana L.) showed a bimodal distribution over the moisture gradient with highest basal area toward the xeric end. The geographical distribution of this species was statewide and the bimodality in Figure 6 was most certainly the result of stand selection which did not consider the presence of red cedar among the minimal criteria for selection.

To further document the general trends of species and stand distributions over the state, the Shannon-Wiener index of diversity was calculated for each stand. Species relative basal area percentages were used in calculating the index. The formula used for the Shannon-Wiener function,

$$H_{BA} = - \sum_{i=1}^{s} p_i \ln p_i$$

was symbolically slightly modified to accommodate relative values directly (Risser and Rice, 1971b). In the above equation, p_i is the relative basal area percentage of the ith species, ln is the natural log and s is the number of species in the stand. The associated equitability component e^H/s, which showed the distribution of basal area among the species, was also calculated with e being the base of the natural logarithms, H is the diversity function and s is the number of species. When the biomass is evenly distributed among the species, the equitability ratio equals 1.

Risser and Rice (1971b) found that Oklahoma stands with the highest Shannon-Wiener values, based on relative density, were dominated by species other than post oak or blackjack, had high basal area, and a greater number of species. Table 4 shows similar results using the 25 stands in this study. It should be noted that the loblolly pine

TABLE 4.--Leading dominant tree species, mean number of species per stand, number of stands in which species was dominant, mean basal area (m^2/ha), mean Shannon-Wiener index ($\overline{H}_{BA}$) and equitability for these stands.

Leading Dominant	Mean Number Species	Number of Stands	Mean Basal Area	$\overline{H}_{BA}$	e^H/S
Shumard's oak	13.0	1	13.8	2.11	0.63
Black hickory	10.0	1	15.7	1.81	0.61
Shortleaf pine	9.0	2	12.7	1.77	0.69
Black oak	10.0	2	13.5	1.66	0.58
Post oak	5.3	13	12.7	0.99	0.59
Blackjack	4.8	5	9.6	0.94	0.58
Loblolly pine	4.0	1	23.0	0.21	0.31
Shin oak	2.0	1	4.8	0.06	0.53

and shin oak stands both had a situation of extreme dominance by one species. Considering all stands, the higher Shannon-Wiener values were significantly correlated ($r = 0.80$, $p = 0.01$) with higher species numbers in stands (Figure 7), but no significant correlation was found between stand basal area and Shannon-Wiener values. The Shannon-Wiener values and numbers of species were each compared to stand position on the environmental (moisture) gradient (Figure 8). Both showed significant positive correlations over the gradient (species: $r = 0.53$, $p = 0.01$, H_{BA}: $r = 0.48$, $p = 0.05$) as both number of species and Shannon-Wiener values increased as mesophytism increased. This was related to the existence of the east-west moisture gradient as well as the response of the vegetation to it.

Analysis of the overstory by the method of leading dominants clearly masked not only compositional dissimilarities involving secondary species (McIntosh, 1972), but structural and age differences as well. To analyze both structure and reproduction of the species in these stands, the most important species (leading dominants) were examined for evidence of reproductive success (seedlings and saplings). Using the size class data, 12 species were evaluated (Table 5) on the basis of their relative basal area contribution to the canopy and sapling strata and the relative cover contribution of seedlings. Since both basal area and cover are correlated with biomass, comparisons can be made on the relative values between strata.

Figure 7.--Linear regression showing the relationship of overstory diversity to number of overstory species per stand.

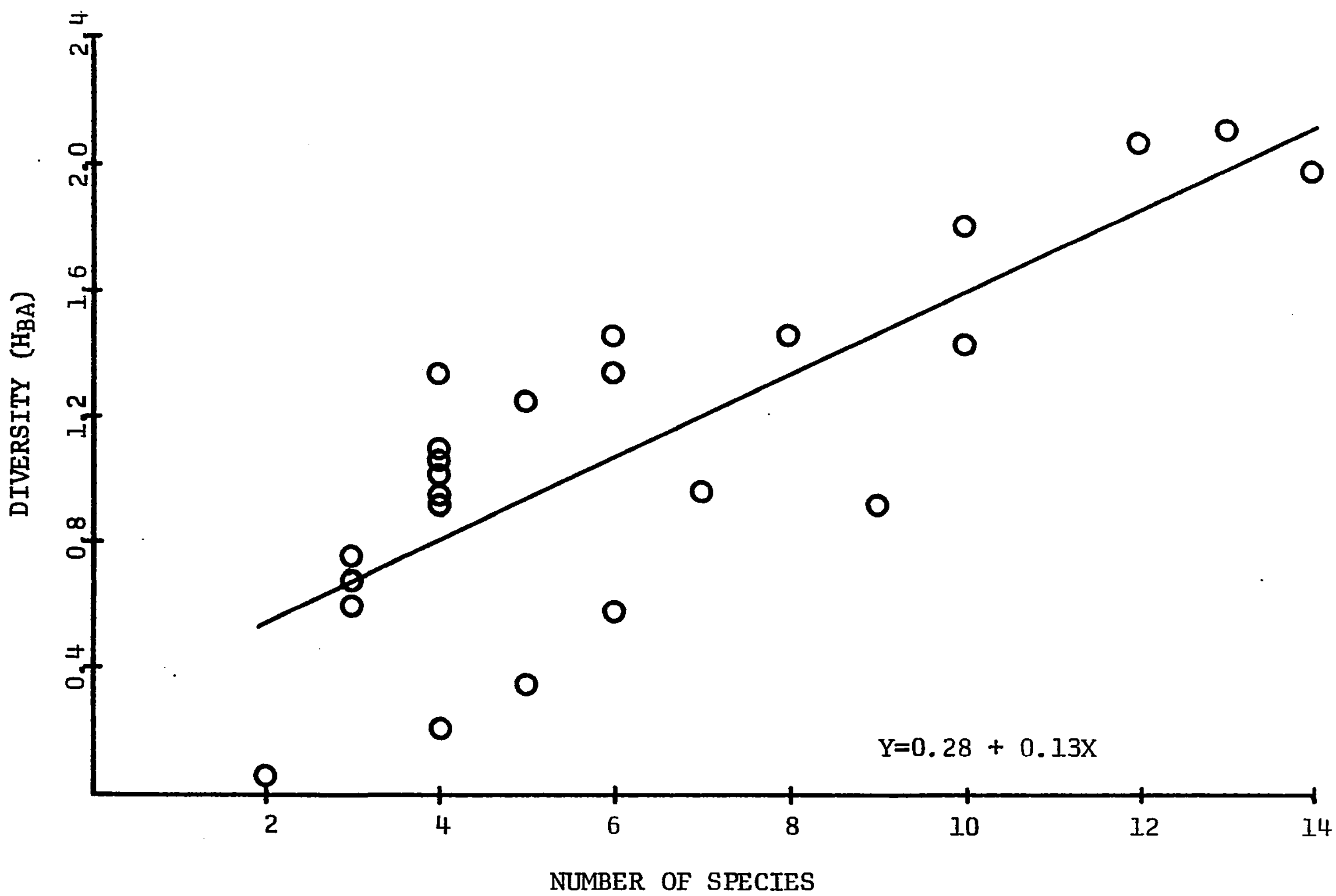
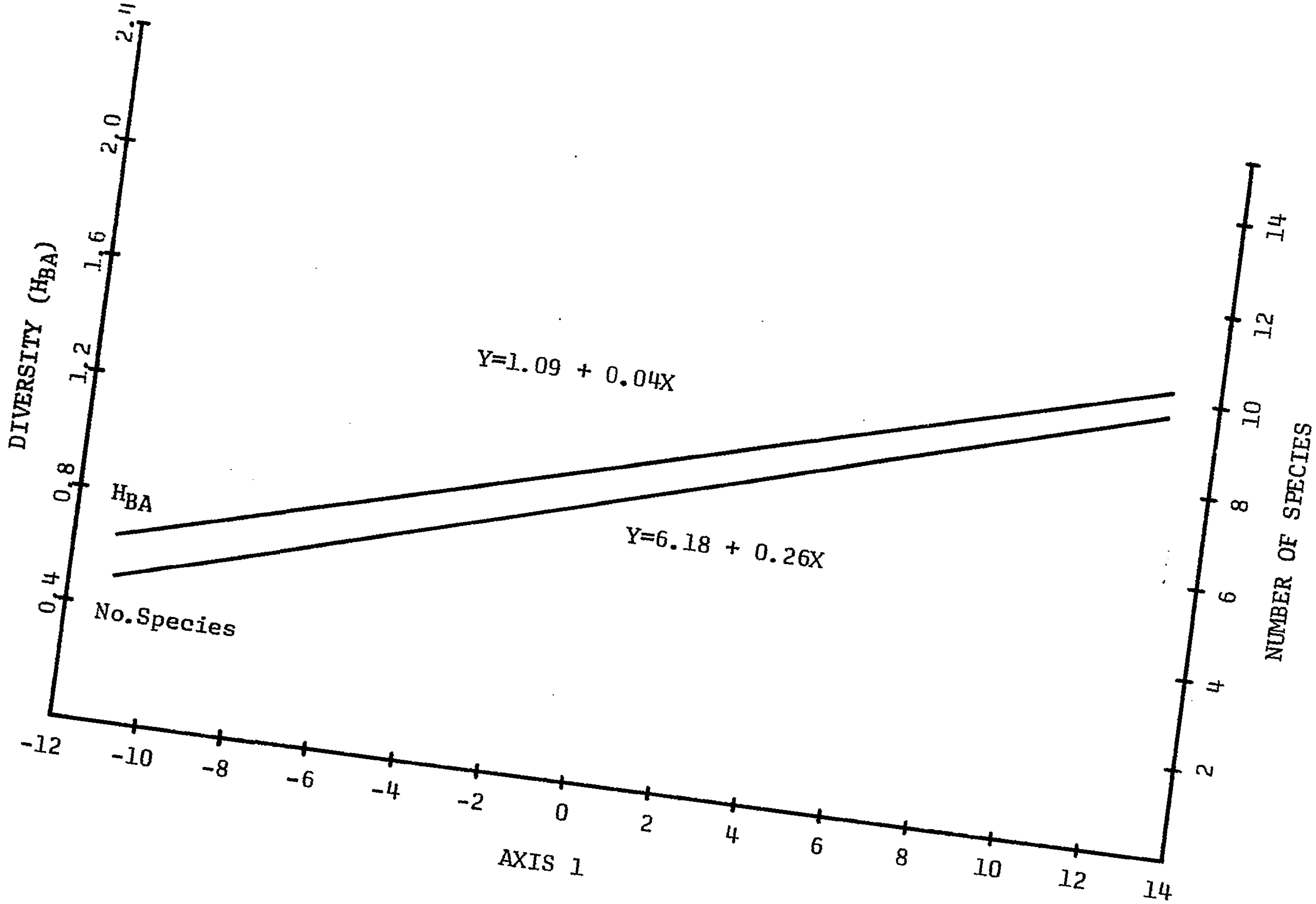

DIVERSITY (H_{BA})
2.4
2.0
1.6
1.2
0.8
0.4
Y=0.28 + 0.13X
2
4
6
8
10
12
14
NUMBER OF SPECIES

Figure 8.--Linear regression showing the relationship of both overstory diversity (H_{BA}) and number of species to the moisture gradient (Axis 1 of the environmental ordination).



DIVERSITY (H_{BA})
0.4
0.8
1.2
1.6
2.0
2.4
H_{BA}
No.Species
Y=1.09 + 0.04X
Y=6.18 + 0.26X
-12
-10
-8
-6
-4
-2
0
2
4
6
8
10
12
14
AXIS 1
NUMBER OF SPECIES
2
4
6
8
10
12
14

TABLE 5.--Mean basal area percentage of major trees, saplings (mean of 4 classes) and mean relative cover of seedlings in stands based on leading dominants (number of stands in parentheses).

Species	Leading Dominants							
	Shumard's oak (1)	Black oak (2)	Black hickory (1)	Shortleaf pine (2)	Post oak (13)	Blackjack (5)	Loblolly pine (1)	Shin oak (1)
Shumard's oak								
Canopy	21	4	0	0	1	0	0	0
Saplings	11	0	0	0	1	0	0	0
Seedlings	0	0	0	0	0	0	0	0
Black oak								
Canopy	2	40	0	5	4	0	0	0
Saplings	0	9	0	3	2	1	0	0
Seedlings	0	4	0	0	2	0	0	0
Black hickory								
Canopy	1	9	22	3	7	4	1	0
Saplings	0	4	4	8	9	6	6	0
Seedlings	4	2	13	0	5	3	8	0
Shortleaf pine								
Canopy	0	0	0	34	2	0	0	0
Saplings	0	0	0	17	2	0	0	0
Seedlings	0	0	0	47	1	0	0	0
Post Oak								
Canopy	0	15	11	16	62	13	1	0
Saplings	0	16	3	9	46	23	22	0
Seedlings	0	3	33	21	46	15	14	0
Blackjack								
Canopy	0	16	0	8	18	60	0	0
Saplings	0	11	0	7	17	36	0	0
Seedlings	0	5	0	7	14	26	0	0

TABLE 5.--Continued

Species	Leading Dominants: Shumard's oak (1)	Black oak (2)	Black hickory (1)	Shortleaf pine (2)	Post oak (13)	Blackjack (5)	Loblolly pine (1)	Shin oak (1)
Loblolly pine								
Canopy	0	0	0	0	0	0	96	0
Saplings	0	0	0	0	0	0	45	0
Seedlings	0	0	0	0	0	0	9	0
Shin oak								
Canopy	0	0	0	0	1	12	0	99
Saplings	0	0	0	0	1	7	0	88
Seedlings	0	0	0	0	1	15	0	73
Sugar maple								
Canopy	19	0	0	0	0	0	0	0
Saplings	7	0	0	0	0	0	0	0
Seedlings	14	0	0	0	0	0	0	0
White oak								
Canopy	8	0	0	12	0	0	0	0
Saplings	0	0	0	16	0	0	0	0
Seedlings	0	0	0	10	0	0	0	0
Southern red oak								
Canopy	0	0	21	3	0	0	2	0
Saplings	0	0	24	1	0	0	21	0
Seedlings	0	0	0	0	0	0	41	0
Winged elm								
Canopy	0	5	18	0	1	0	0	0
Saplings	0	5	4	1	6	0	0	0
Seedlings	0	15	13	0	3	0	0	0

The stand dominated by Shumard's oak showed sugar maple the only self sustaining canopy species. In terms of canopy basal area it was also the highest subdominant in a stand which had a rather equitable distribution of biomass between species (Table 4) and a large number of canopy species. The extremely low light (1.1% of incident) available for seedling growth would certainly favor establishment and eventual dominance of sugar maple which is particularly shade tolerant.

The black oak dominated stands of the northeast presented an entirely different situation. These stands were positioned at the mesic end of the moisture gradient and contained five species, including black oak which appeared to be reproducing at sustaining levels. Winged elm had as much seedling cover as the other four species together and the highest seedling/sapling ratio (Table 6) in the stands. The reproductive importance of winged elm was restricted to eastern and south central stands, although this species occurs in some relatively xeric habitats. Black oak appeared to reproduce well in either black oak dominated stands or in eastern post oak dominated stands (Tables 6 and 7).

Shortleaf pine was present in three stands; two where it was the leading dominant and one eastern post oak stand. Reproduction was evident on all three of these sites. Associated species, represented as saplings and seedlings, in the oak-pine community-type were post oak, blackjack and white oak (<u>Quercus alba</u> L.).

TABLE 6.--Mean ratio of relative seedling cover to relative sapling basal area for 11 important tree species with stands grouped by leading dominant and highest and lowest ratios for the species in any single stand given to indicate range within a dominant type.

Species Seedling/Sapling Ratio	Leading Dominant							
	Shumard's oak (1)	Black oak (2)	Black hickory (1)	Shortleaf pine (2)	Post oak (13)	Blackjack (5)	Loblolly pine (1)	Shin oak (1)
Winged elm								
Mean	0	3.0	3.2	0	0.5	0	0	0
Highest	0	3.2	3.2	0	1.0	0	0	0
Lowest	0	0	3.2	0	0	0	0	0
Black oak								
Mean	0	0.4	0	0	1.0	0	0	0
Highest	0	1.0	0	0	2.6	0	0	0
Lowest	0	0	0	0	0	0	0	0
Black hickory								
Mean	0	0.5	3.2	0	0.6	0.5	1.3	0
Highest	0	1.0	3.2	0	1.3	0.5	1.3	0
Lowest	0	0	3.2	0	0	0	1.3	0
Shortleaf pine								
Mean	0	0	0	2.7	0.5	0	0	0
Highest	0	0	0	28.0	0.8	0	0	0
Lowest	0	0	0	1.1	0	0	0	0
Post oak								
Mean	0	0.2	11.0	2.3	1.0	0.7	0.6	0
Highest	0	0.2	11.0	2.6	2.5	1.0	0.6	0
Lowest	0	0	11.0	1.9	0.3	0	0.6	0
Blackjack								
Mean	0	0.4	0	0.9	0.8	0.7	0	0
Highest	0	0.4	0	0.9	6.0	1.6	0	0
Lowest	0	0	0	0	0	0	0	0
Loblolly pine								
Mean	0	0	0	0	0	0	0.2	0
Highest	0	0	0	0	0	0	0.2	0
Lowest	0	0	0	0	0	0	0.2	0

TABLE 6.--Continued

Species Seedling/Sapling Ratio	Leading Dominant							
	Shumard's oak (1)	Black oak (2)	Black hickory (1)	Shortleaf pine (2)	Post oak (13)	Blackjack (5)	Loblolly pine (1)	Shin oak (1)
Shin oak								
Mean	0	0	0	0	1.5	2.1	0	0.8
Highest	0	0	0	0	1.6	4.1	0	0.8
Lowest	0	0	0	0	0	0	0	0.8
Sugar maple								
Mean	2.0	0	0	0	0	0	0	0
Highest	2.0	0	0	0	0	0	0	0
Lowest	2.0	0	0	0	0	0	0	0
White oak								
Mean	0	0	0	0.6	0	0	0	0
Highest	0	0	0	0.6	0	0	0	0
Lowest	0	0	0	0	0	0	0	0
Southern red oak								
Mean	0	0	0	0	0	0	2.0	0
Highest	0	0	0	0	0	0	2.0	0
Lowest	0	0	0	0	0	0	2.0	0

TABLE 7.--Mean basal area percentage of major trees, saplings (mean of 4 classes) and mean relative cover of seedlings in stands where post oak is the leading dominant (number of stands in parentheses).

Species	Section of State		
	Eastern (3)	Central (7)	Western (3)
Shumard's oak			
Canopy	1	1	0
Saplings	0	1	0
Seedlings	0	0	0
Black oak			
Canopy	6	4	0
Saplings	2	3	0
Seedlings	4	1	0
Black hickory			
Canopy	22	4	0
Saplings	21	7	0
Seedlings	12	4	0
Shortleaf pine			
Canopy	7	0	0
Saplings	8	0	0
Seedlings	6	0	0
Post oak			
Canopy	46	67	67
Saplings	31	52	46
Seedlings	25	53	51
Blackjack			
Canopy	11	22	16
Saplings	15	16	18
Seedlings	24	14	4
Loblolly pine			
Canopy	0	0	0
Saplings	0	0	0
Seedlings	0	0	0
Shin oak			
Canopy	0	0	3
Saplings	0	0	2
Seedlings	0	0	3

Loblolly pine exhibited reproduction only in the loblolly pine stand (extreme southeast corner of the state). Since this stand was a plantation, there were few other species in the canopy; however, southern red oak, post oak and black hickory constitute 49% of the sapling classes and 63% of the seedling cover. If distribution within the four sapling classes was considered, loblolly pine constituted 80% of the biomass of saplings >5.0 cm dbh, but only 8% for saplings <5.0 cm dbh.

In the black hickory stand approximately 60% of seedling cover was distributed among black hickory, post oak and winged elm, while these same 3 species only accounted for 11% of the four sapling classes. Chittamwood and osage orange (Maclura pomifera [Raf.] Schneider) accounted for 42% of the sapling class, but were not found as seedlings. Southern red oak (Quercus falcata Michx.) was not found in the seedling class, but constituted 24% of the sapling classes and was the highest subdominant canopy species. Seedling survival may have been affected by periodic light grazing in this stand resulting in the relatively low sapling representation by the major species. In general, black hickory appeared to be reproducing adequately in most stands where it was present (Table 5) and was particularly well represented in the post oak and black oak dominated stands of the oak-hickory community-type (Table 7).

Blackjack exhibited reproduction in stands where it occurred and had nearly equal percentages of saplings and seedlings in most stands (Tables 5, 6, 7), consequently, seedling/sapling ratios were near 1.0. Associated major species which showed reproduction in blackjack dominated stands are post oak, black hickory (except in western stands) and shin oak.

Shin oak was present only in the most western stands where reproduction appeared to be comparable to that of associated species; however, it had been suggested by Wiedeman and Penfound (1960) that most shin oak reproduction was vegetative which may account for the dense, nearly impenetrable nature of these stands as well as the formation of the taller mott vegetation scattered over the area.

Post oak showed relatively high percentages of saplings and seedlings in most stands and exhibited high variation in seedling/sapling ratios particularly when other species were leading dominants. It had the highest presence percentage (88%) in the state and was distributed over the entire length of the moisture gradient (Figure 6a).

In order to assess the importance and representation of each of the 62 species sampled to both the stand and the community-type, a method using the size class basal area was developed. This system weighted each size class according to its contribution of basal area or cover (seedlings), giving highest weight to the canopy. To assess the importance of each species in the stand the basal areas for each size class were summed for individual species and the total contribution of each species was divided by the grand total for all species (Table 8, footnote a). Stands were then classified on the basis of composition into one of six community-types and the community importance percentage (C.I.P.) was calculated by averaging the stand values for an individual species within a community-type. Mean similarity of stands within a community-type was also calculated and is presented in Table 8.

The six community-types and the number of species contained in each were: (1) oak-loblolly pine, 10; (2) oak-hickory-pine, 17; (3) oak-hickory, 42; (4) oak-hickory savannah, 23; (5) oak savannah, 18, and (6) oak-shinnery, 3 (Table 8).

The oak-hickory savannah had the highest mean similarity of the four community-types containing more than one stand. This was not unexpected as the four most important species in the state were consistently present and showed sustaining levels of reproduction. The gently rolling topography over which these stands were scattered also produced fewer extreme habitats relative to the broad species tolerances which were distributed over them. All of the oak-hickory savannah stands were dominated by post oak with a C.I.P. ratio (post oak:blackjack) of approximately 3:1.

Figure 9 visually documents the relationship of the six community-types to selected environmental variables in a

TABLE 8.--Mean community importance percentage[a] for 62 species in stands classified by community-type (number of stands in parentheses).

Species	Community-Type: Oak-loblolly pine (1) 100.0[b]	Oak-hickory-pine (3) 44.6	Oak-hickory (6) 28.7	Oak-hickory savannah (6) 63.9	Oak savannah (8) 37.9	Oak-shinnery (1) 100.0
Acer rubrum	+[c]	-	-	-	-	-
Acer saccharum	-	-	2.7	-	-	-
Amelanchier arboreum	-	0.5	+	-	-	-
Asimina triloba	-	-	1.4	-	-	-
Bumelia lanuginosa	-	0.1	0.2	0.7	2.9	-
Carya cordiformis	-	-	4.5	-	-	-
Carya illinoense	-	-	0.6	-	-	-
Carya ovata	-	1.3	1.9	-	-	-
Carya texana	2.1	10.6	9.8	6.5	-	-
Carya tomentosa	-	10.8	0.2	2.5	-	-
Celtis laevigata	-	-	-	+	-	-
Celtis reticulata	-	-	-	-	4.2	0.4
Cercis canadensis	-	-	1.1	0.6	0.3	-
Cornus drumondii	-	-	+	0.4	0.2	-
Cornus florida	2.0	-	3.1	-	-	-
Crataegus sp.	-	-	+	-	-	-
Crataegus crus-galli	-	-	-	-	+	-
Crataegus mollis	-	-	-	0.2	-	-
Crataegus spathulata	0.3	-	0.1	-	-	-
Diospyros virginiana	-	0.1	1.1	-	-	-
Fraxinus americana	-	-	-	-	-	-
Fraxinus pensylvanica	-	-	0.2	-	-	-
Ilex decidua	-	-	+	+	-	-
Juglans nigra	-	-	+	-	-	-
Juniperus virginiana	-	0.1	1.0	1.1	5.1	-
Liquidambar styraciflua	-	-	1.9	-	-	-
Lonicera albiflora	-	-	-	-	+	-
Maclura pomifera	-	-	0.4	-	-	-
Magnolia acuminata	-	-	1.5	-	-	-
Morus rubra	-	-	0.5	0.8	+	-
Nyssa sylvatica	-	-	+	-	-	-
Ostrya virginiana	-	-	0.7	-	-	-
Pinus echinata	-	28.0	-	-	-	-
Pinus taeda	84.4	-	-	-	-	-

TABLE 8.--Continued

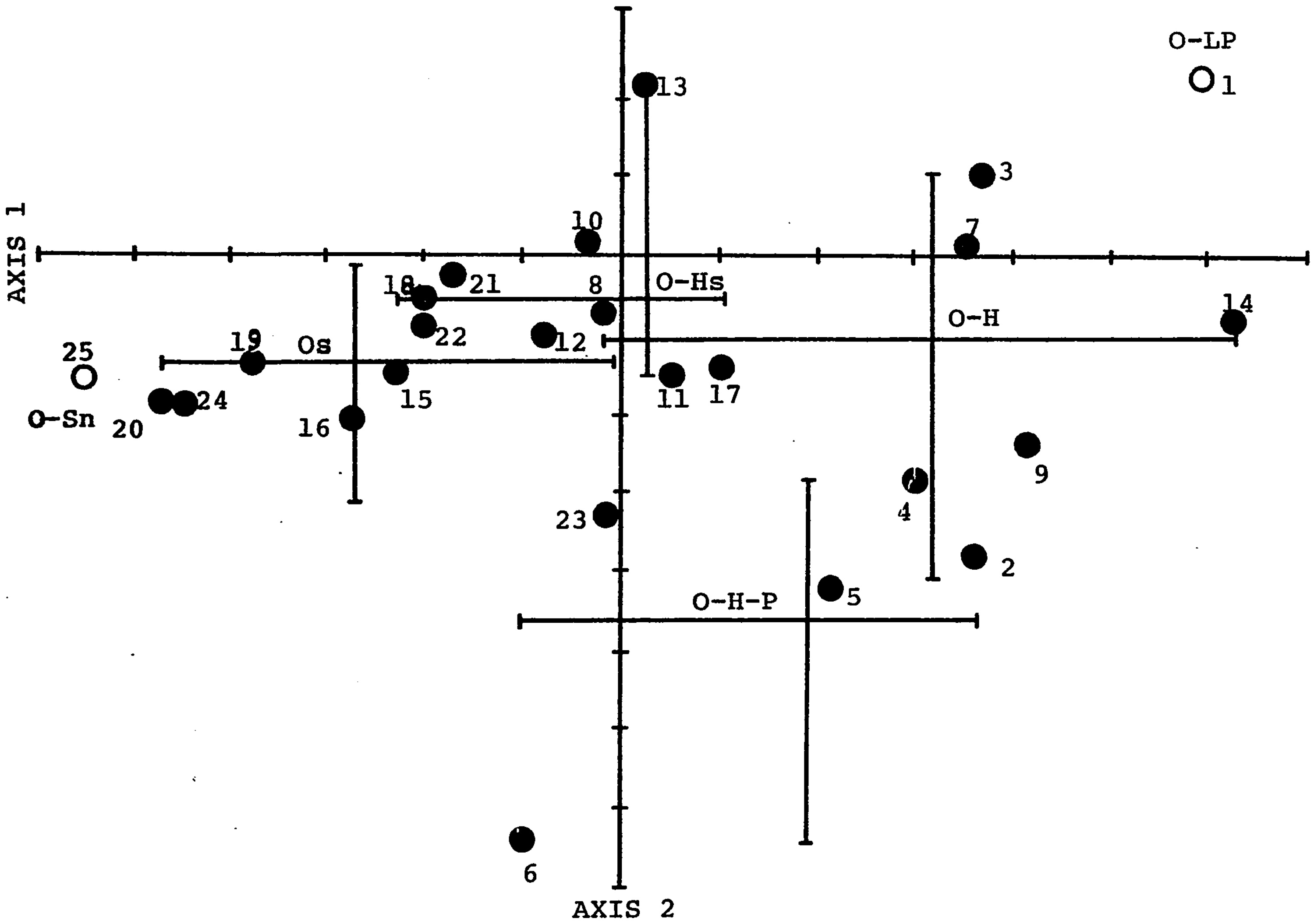
Species	Oak-loblolly pine (1) 100.0[b]	Oak-hickory-pine (3) 44.6	Oak-hickory (6) 28.7	Oak-hickory savannah (6) 63.9	Oak savannah (8) 37.9	Oak-shinnery (1) 100.0
Prunus americana	-	-	-	0.3	-	-
Prunus gracilis	-	-	+	-	-	-
Prunus mexicana	-	0.2	-	+	-	-
Prunus serotina	-	-	+	-	-	-
Ptelea trifoliata	-	-	-	-	+	-
Quercus alba	-	8.9	1.0	-	-	-
Quercus falcata	6.9	1.2	3.6	-	-	-
Quercus havardii	-	-	-	-	2.0	9.3
Quercus marilandica	-	10.8	8.0	18.3	33.9	-
Quercus muehlenbergii	-	-	0.3	0.1	0.2	-
Quercus phellos	+	-	0.2	-	-	-
Quercus shumardii	-	-	3.7	0.3	-	-
Quercus stellata	4.2	20.4	23.8	62.9	38.8	-
Quercus stellata x havardii	-	-	-	-	8.9	90.4
Quercus velutina	-	2.5	11.7	4.8	-	-
Rhus copallina	0.1	-	-	+	-	-
Rhus glabra	-	-	-	0.1	1.1	-
Rhus radicans	-	-	+	-	-	-
Robinia pseudoacacia	-	0.5	3.9	-	-	-
Sapindus drumondii	-	-	-	-	0.3	-
Tilia americana	-	-	-	+	-	-
Tilia caroliniana	-	-	3.9	-	-	-
Ulmus alata	-	0.2	8.3	0.2	-	-
Ulmus americana	-	-	1.1	0.1	1.2	-
Ulmus rubra	+	-	-	+	-	-
Vaccinium arboreum	-	1.9	0.2	-	-	-
Viburnum prunifolium	-	-	-	-	0.2	-

[a]Community importance percentage (C.I.P.) $= \left(\sum_{j=1}^{6} B_j\right)_i 100 / \sum_{i=1}^{s} \left(\sum_{j=1}^{6} B_j\right)_i$ where B_j is the biomass contribution in terms of basal area or cover percentage of the jth diameter class for the ith species, and s is the total number of species in the stands.

[b]Mean similarity (2w/(a+b) for stands within a community-type based on basal area percentage of 40 species.

[c]Community importance percentage is <.1.

Figure 9.--Principal component ordination based on 12 environmental variables showing the environmental range of six upland forest community-types (see text for explanation).


AXIS 1
AXIS 2
O-LP
O-Hs
O-H
Os
O-Sn
O-H-P
1
2
3
4
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6
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25

principal component ordination. The base axis is identical to that in Figure 4; axis 1 being principally a moisture relationship and axis 2 being principally soil texture. The four small axes superimposed on the ordination represent the moisture-texture range within a community-type based on individual component stand values. Several areas of environmental overlap were evident, particularly between the oak-hickory, oak-hickory savannah and oak savannah. The vegetational similarities (community overlap) are apparent from Table 8. Had more than one stand been sampled in the two extreme community-types, the entire spectrum of vegetation-environment relations would be much clearer.

Community-types common to the eastern part of the state were generally mesic and had a wide textural range, partially due to the variable nature of the topography. The central-western community-types were more xeric and had overall less variability in topography, texture and moisture relations.

The community-type (oak-hickory) with the greatest variability in terms of environment also included the most species (42), had 17 species not found in other community-types, had higher Shannon-Weiner index values, and had 4 of the 6 stands dominated by species other than post oak or blackjack.

SUMMARY

Twenty-five upland forest stands were analyzed for vegetational composition, vegetation-environment relationships and population structure of the overstory.

A total of 62 overstory species were encountered during the course of this study; however, only post oak and blackjack were important statewide.

A polar ordination using species basal area showed the vegetational similarity between stands. End stands on the ordination were dominated by Shumard's oak and shin oak on the first axis and loblolly pine and post oak on the second axis. Distribution of stands on the ordination was greatly influenced by the presence of post oak which occurred in 88% of the stands and was a leading dominant in 13 stands.

Eight species were found as leading dominants in at least one stand. In order of decreasing presence percentage they were: post oak, blackjack, black hickory, black oak, Shumard's oak, shin oak, shortleaf pine, and loblolly pine.

A principal component ordination using 12 environmental variables ordinated stands relative to moisture and soil texture. Geographically eastern stands were positioned on the mesic end of the moisture axis and western stands occurred on the more xeric end. Post oak dominated stands were found in intermediate positions on the gradient while blackjack dominated stands showed more xeric positions. A black oak stand was the most mesic.

Polynomial regressions were calculated for nine species using species basal area versus position on the moisture gradient. The four major species, in order of increasing mesophytism, were blackjack, post oak, black hickory and black oak. The five minor species were chittamwood, eastern red cedar, Shumard's oak, winged elm and mockernut hickory.

The Shannon-Wiener index of diversity was calculated for each stand using species relative basal area. Stands with the highest diversity were dominated by species other than post oak or blackjack, had relatively high basal areas, and had high species numbers. Both number of species and diversity increased as mesophytism increased.

Twelve species were evaluated for reproductive success: Shumard's oak, black oak, black hickory, shortleaf pine, post oak, blackjack, loblolly pine, shin oak, sugar maple, white oak, southern red oak and winged elm. Of these, only Shumard's oak was not reproducing at a sustaining level in any stand including the stand which it dominated.

Of the eight leading dominant species, all except Shumard's oak, loblolly pine and shin oak were reproducing in eastern post oak dominated stands. In central post oak stands, only post oak, blackjack, black hickory and black oak showed reproduction. In western post oak stands only post oak, blackjack and shin oak were reproducing.

Stands were classified into one of six community-types on the basis of characteristic overstory species. Using the sum of the size class basal areas of each species, a community importance percentage (C.I.P.) was calculated by averaging stand values within a community-type for a specific species. The most important species in each community-type, listed for each in order of decreasing C.I.P., were: (1) oak-loblolly pine, loblolly pine, southern red oak; (2) oak-hickory-pine, shortleaf pine, post oak; (3) oak-hickory, post oak, black oak, black hickory; (4) oak-hickory savannah, post oak, blackjack, black hickory; (5) oak savannah, post oak, blackjack, and (6) oak-shinnery, shin oak.

The oak-hickory community-type had the greatest environmental variability (based on the environmental ordination), included the most species, had the highest diversity index and contained 17 species not found in other community-types.

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AN ANALYSIS OF SELECTED OKLAHOMA UPLAND FOREST STANDS INCLUDING BOTH OVERSTORY AND UNDERSTORY COMPONENTS

PART II

THE UNDERSTORY COMPONENT AND UNDERSTORY-OVERSTORY RELATIONSHIP

INTRODUCTION

The main objectives of this study were to characterize the understory vegetation of six upland forest community-types in terms of composition, vegetation-environment relationships, species diversity, and correspondence of understory to overstory.

Twenty-five upland forest stands were sampled (Figure 1) including six community-types: oak-loblolly pine (*Pinus taeda* L.),[1] oak-hickory-shortleaf pine (*Pinus echinata* Mill.), oak-hickory, oak-hickory savannah, oak savannah, and oak-shinnery (Rice and Penfound, 1959; Wiedeman and Penfound, 1960). Only the oak savannah and oak-shinnery types are found in the western portion of the state, while all except the oak-shinnery are found in the eastern sections.

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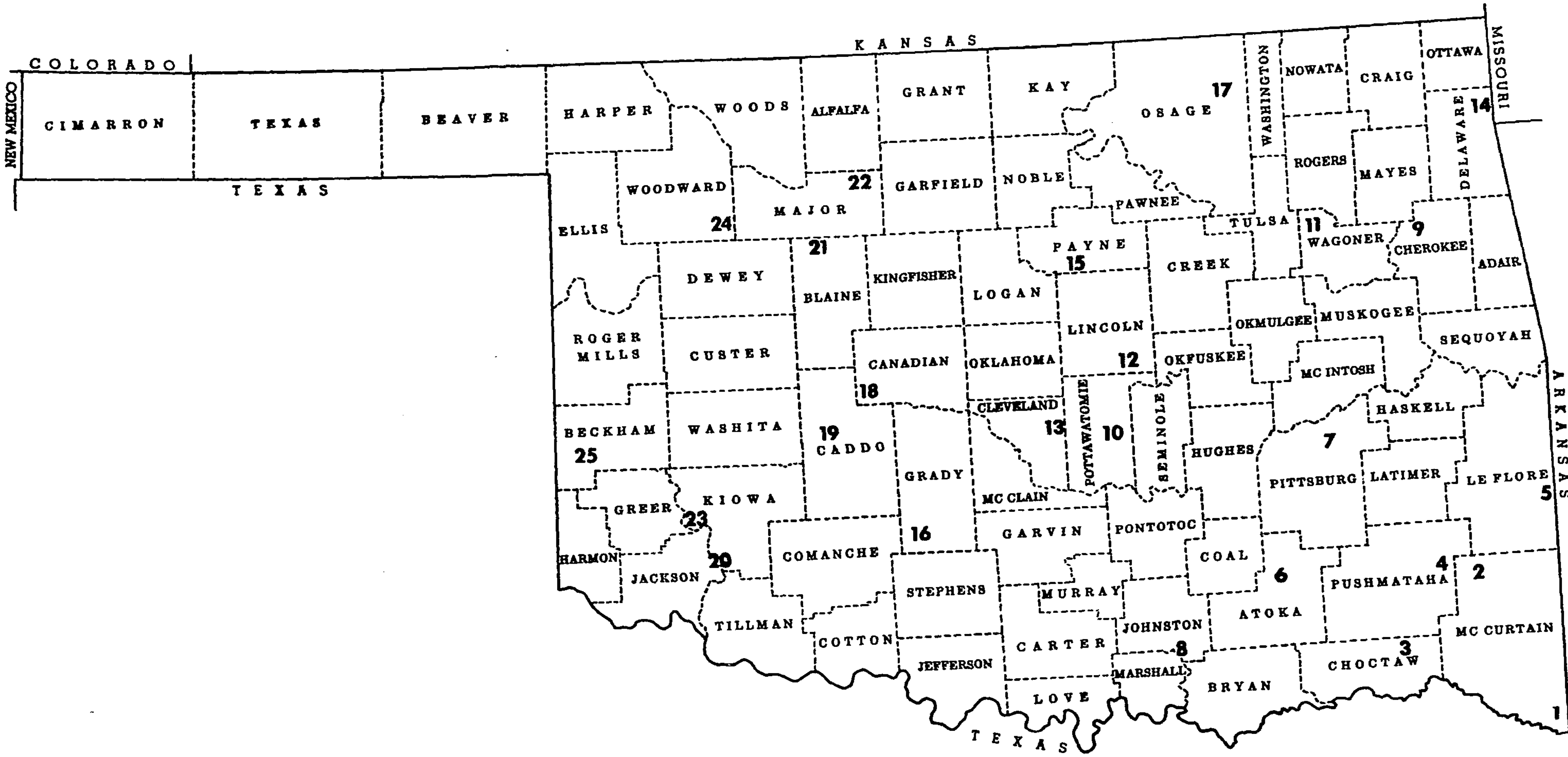
[1]Nomenclature follows Waterfall, 1966.

Figure 1.--Map of the State of Oklahoma showing approximate locations for the 25 upland forest stands sampled.


KANSAS
COLORADO
NEW MEXICO
TEXAS
MISSOURI
ARKANSAS
CIMARRON
TEXAS
BEAVER
HARPER
WOODS
ALFALFA
GRANT
KAY
OSAGE
17
WASHINGTON
NOWATA
CRAIG
OTTAWA
14
DELAWARE
MAYES
ROGERS
WOODWARD
22
GARFIELD
NOBLE
PAWNEE
MAJOR
24
ELLIS
TULSA
11
WAGONER
9
CHEROKEE
ADAIR
21
PAYNE
15
CREEK
DEWEY
KINGFISHER
LOGAN
BLAINE
LINCOLN
OKMULGEE
MUSKOGEE
SEQUOYAH
ROGER MILLS
CUSTER
CANADIAN
OKLAHOMA
12
OKFUSKEE
MC INTOSH
18
CLEVELAND
POTTAWATOMIE
SEMINOLE
13
10
HASKELL
BECKHAM
25
WASHITA
19
CADDO
GRADY
HUGHES
7
PITTSBURG
LATIMER
LE FLORE
5
MC CLAIN
KIOWA
GREER
23
16
GARVIN
PONTOTOC
COAL
HARMON
20
JACKSON
COMANCHE
STEPHENS
MURRAY
6
PUSHMATAHA
4
2
TILLMAN
COTTON
JOHNSTON
ATOKA
CARTER
8
3
MC CURTAIN
JEFFERSON
MARSHALL
CHOCTAW
BRYAN
LOVE
1

Two tree species, post oak (Quercus stellata Wang.) and blackjack (Quercus marilandica Muenchh.) account for about 68% of the total basal area in the state with post oak probably the greatest contributor statewide (Rice and Penfound, 1959) due to wide moisture and nutrient tolerances (Johnson and Risser, 1972).

The Oklahoma upland forest overstory has been well documented in terms of species composition (Bruner, 1931; Luckhardt and Barclay, 1938; Barclay, 1947; Rice and Penfound, 1955, 1959; Risser and Rice, 1971a; Johnson and Risser, 1973). Related studies have dealt with overstory diversity (Risser and Rice, 1971b), vegetation environment relationships (Luckhardt and Barclay, 1938; Rice, 1960, 1962; Johnson and Risser, 1972), relation of woody vegetation to geology and soil type (Buck, 1964), and host specificity and frequency of bark lichens (Adams and Risser, 1971a, 1971b).

The understory vegetation of Oklahoma upland forests is not well represented in the literature. The majority of these studies have been floras with minimal emphasis on species importance in specific communities (Ortenburger, 1928a, 1928b; Barclay, 1933; Little, 1938; Luckhardt and Barclay, 1938; Eskew, 1938; Dale, 1956).

The woody understory has received some emphasis in terms of species presence (Rice and Penfound, 1959; Johnson and Risser, 1973) and percentage composition (Penfound, Shed and Jennison, 1965; Carnes and Penfound, 1968).

Galloway (1965) studied an actively eroding canyon in west-central Oklahoma, providing not only overstory composition, but importance values for herbs, shrubs and woody vines of the area. Other studies which include compositional percentages for understory plants are Penfound, Shed and Jennison (1965), Parks and Barclay (1966), Carnes and Penfound (1968), and Rice and Pancholy (1972). Rice and Pancholy (1972) reported percentage composition of important herbs from two climax community-types; tall-grass prairie and post oak-blackjack forest. The herb stratum of an oak-hickory-pine climax community included in other aspects of this study was not sampled due to the sparseness of herbaceous cover.

Both topography and climate exhibit some diversity in the State of Oklahoma. Topography is generally rolling with the exception of the Wichita and Arbuckle Mountains in the south-central portion of the state and the Ozark, Boston and Ouachita Mountains in the east. An elevational gradient runs northwesterly from southeastern McCurtain County (88 m) to the northwestern border (610 m) excluding the panhandle. Average annual precipitation ranges from 125 cm in the southeast to 59 cm in the northwest, with local southeastern accumulations of 140 cm (Oklahoma Water Resources Board, 1970). Mean annual temperatures in the main body of the state range from 17.3°C in the southeast to 15.0°C in the northwest, while the average number of days without killing frost varies from 240 days in the southeast to 200 days in the northwest.

Generally, the western portion of the state is subject to greater temperature extremes and higher variability in the seasonability and intensity of precipitation than is the east.

METHODS

Criteria for stand selection were: a minimum stand size of 6.0 ha, representative of the community-type for that section of the state, upland in terms of topography and characteristic overstory species, confined to a single aspect and relatively undisturbed by recent cutting or burning, although grazed areas were used if grazing was not severe. The sites are listed in Table 1.

Precipitation, evaporation and temperature data for each stand were taken from an Oklahoma Water Resources Board (1970) publication and the precipitation/evaporation (P/E) ratio was calculated. Each site was additionally characterized for the percent of incident solar radiation available at 90 cm above the soil surface by averaging 100 light readings taken with a Model 756, Weston Illumination Meter. Readings were always taken as close to 12:00 noon as possible on a clear day at approximately 10 m intervals in a random walk. The average of five readings taken in the open was used as the maximum value. In addition, average potential solar insolation was calculated using aspect, slope and latitude from tables given by Frank and Lee (1966).

Soil samples (0-20 cm) were taken at 10 randomly distributed points in each stand for soil texture and pH determinations (Table 1). Bulk density (0-5 cm) was determined

TABLE 1.--Description of sampled stands showing stand number, county, legal description, elevation, slope percent, aspect, mean soil particle size, and soil pH.

Stand Number	County	Legal Description	Elevation (m.)	Slope Percent	Aspect	Mean Soil Particle Size (mm)	Soil pH 0-20 cm depth
1	McCurtain	Sec 5 T 9N R27E	121	-	-	.005	4.5
2	McCurtain	Sec 20 T 1S R24E	290	38	NE	.010	5.3
3	Choctaw	Sec 9 T 6S R19E	152	-	-	.006	4.6
4	Pushmataha	Sec 10 T 2S R21E	350	18	SE	.013	4.0
5	LeFlore	Sec 27 T 3N R27E	427	11	N	.017	5.7
6	Atoka	Sec 5 T 1S R13E	244	80	S	.034	5.1
7	Pittsburg	Sec 17 T 7N R16E	198	18	NW	.006	5.1
8	Johnson	Sec 32 T 4S R 7E	183	4	NW	.017	4.7
9	Cherokee	Sec 23 T 18N R20E	259	11	NW	.008	4.5
10	Pottowatomie	Sec 3 T 8N R 4E	305	-	-	.008	5.4
11	Wagoner	Sec 31 T 19N R16E	198	27	NE	.012	5.8
12	Lincoln	Sec 7 T 12N R 5E	274	4	N	.014	5.0
13	Cleveland	Sec 25 T 9N R 1E	305	22	NW	.005	4.7
14	Delaware	Sec 21 T 24N R25E	274	-	-	.007	4.8
15	Payne	Sec 1 T 17N R 2E	244	13	SE	.022	5.4
16	Grady	Sec 32 T 4N R 8W	427	26	NE	.023	5.4
17	Osage	Sec 13 T 26N R10E	259	18	E	.008	4.4
18	Canadian	Sec 13 T 11N R10W	442	11	NW	.015	6.1
19	Caddo	Sec 21 T 9N R12W	427	4	W	.025	5.7
20	Jackson	Sec 33 T 3N R18W	427	7	S	.032	6.2
21	Blaine	Sec 4 T 18N R12W	472	4	S	.012	5.6
22	Major	Sec 6 T 22N R10W	411	7	SE	.013	5.3
23	Kiowa	Sec 35 T 5N R20W	564	56	N	.009	6.3
24	Woodward	Sec 16 T 21N R17W	558	9	W	.030	6.0
25	Beckham	Sec 25 T 9N R25W	610	-	-	.033	6.0

at these same 10 points using a sand displacement method (Rice, 1968). Soil samples were composited within a stand, the material air dried for 5-7 days, visible organic material removed, and the remaining soil passed through a 2.0 mm sieve. The percentage of gravel (>2.0 mm) was determined and a textural analysis done on the <2.0 mm separate using the hydrometer method of Bouyoucos (1936). The resulting percentages of sand, silt and clay were corrected for percent gravel and mean particle size was calculated for each stand using these percentages in a formula from Czarnowski (1964).

The overstory vegetation strata were sampled using an augmented variable-radius technique (Rice and Penfound, 1955). Twenty-five to 35 points were taken in each stand and the basal area calculated for each species. Species density was calculated from 10 arms-length transects (0.006 ha each) per stand. Tree seedling densities were not recorded in these transects.

Understory vegetation (including tree seedlings) frequency was assessed from approximately 30, m^2 quadrats per stand and cover was recorded by presence-absence in each decimeter increment of 10 line transects (10 m in length), resulting in 1000 dm increments per stand. Species importance percentages were calculated using (relative frequency + relative cover)/2.

A principal component ordination was constructed on 12 environmental variables with the method of Jeffers (1967).

In this analysis, the data used were all relative values, a correlation matrix was calculated, only eigenvectors >1.0 were retained, and only variables having absolute scaled eigenvector values ≥ 0.7 were used to calculate the axis positions of stands.

RESULTS AND DISCUSSION

In order to document and compare the distribution, importance, and relation to environment of selected understory species across the state, stands were classified into community-types on the basis of characteristic overstory species (Rice and Penfound, 1959). Table 2 gives the mean importance percentages for 94 of the 280 understory species encountered in this study in each of the six community-types. Species included were present in at least 3 stands or 12% of the 25 stands. Of the remaining 186 understory species, 59 species had a presence percentage of 8.0% and 127 species were present in only one stand (4.0%). Table 3 shows the distribution of species numbers within community-types. The oak-hickory savannah has the largest understory species total and exhibits the greatest number of herbaceous species. The oak-shinnery community-type shows the smallest number of species in each category.

Exclusive species were those which occurred only within stands of a specific community-type and although a large portion of these species were found in only one stand, exclusiveness does include species with presence percentages higher than 4.0%. The oak savannah community-type contained the greatest number of exclusive species, partially due to the higher level of disturbance (particularly grazing) found

TABLE 2.--Mean importance percentages of 94 understory species for six upland forest community-types. Species included were present in at least 3 of the 25 stands sampled (number of stands in parentheses).

Species	Community-Type					
	Oak loblolly pine (1)	Oak hickory pine (3)	Oak hickory (6)	Oak hickory savannah (6)	Oak savannah (8)	Oak shinnery (1)
Acacia angustissima		1		+	+	
Acalypha gracilens			+[a]		+	
Achillea millefolium				+		
Ambrosia artemisiifolia				+		
Ambrosia psilostachya				+	2	
Andropogon gerardii			1	3	+	
Andropogon scoparius	4	5	3	10	12	6
Andropogon ternarius				+	+	
Antennaria plantaginifolia		6	1	3		
Aphanostephus skirrhobasis					1	+
Artemisia ludoviciana				+	+	
Asclepias verticillata	+	+		+		
Ascyrum hypericoides	+	5	+	1		
Aster patens		2	+	+		
Baptisia leucophaea	+		+	+		
Bouteloua curtipendula				+	1	+
Bouteloua gracilis				+	3	
Bouteloua hirsuta				+	+	
Bromus japonicus				+	+	
Carex sp.	+	+	4	3	4	
Cassia nictitans	+			+	+	
Chenopodium album	+				+	
Chloris verticillata					+	

TABLE 2.--Continued

Species	Community-Type					
	Oak loblolly pine (1)	Oak hickory pine (3)	Oak hickory (6)	Oak hickory savannah (6)	Oak savannah (8)	Oak shinnery (1)
Clitoria mariana	4	2	1	5		
Cocculus carolinus			+	+	3	
Commelina erecta				1	3	3
Conyza canadensis					1	
Cornus drumondii			+	1	+	
Crataegus spathulata	+		+			
Croton capitatus		+		+	+	
Cyperus sp.	3			+	+	
Cyperus ovularis		+	+	+	+	
Danthonia spicata		11	4	2		
Desmodium sp.		+	+	+		
Desmodium paniculatum		+	+	+		
Elymus virginicus			+	+	+	
Eragrostis spectabilis				+	+	
Erigeron strigosus	+	+	+	1	+	
Euphorbia corollata				+		
Festuca octoflora			+	+	+	
Galium pilosum	+		+	+		
Ilex decidua		+	+			
Lechea tenuifolia				1	+	
Lepidium sp.				+	+	
Lespedeza sp.		+		+	+	
Lespedeza procumbens				2		
Lespedeza repens	2	3				
Lespedeza striata	2	+				
Linum sulcatum	+	+	+			
Monarda fistulosa	2	+	+			

TABLE 2.--Continued

Species	Community-Type					
	Oak loblolly pine (1)	Oak hickory pine (3)	Oak hickory (6)	Oak hickory savannah (6)	Oak savannah (8)	Oak shinnery (1)
Muehlenbergia sobolifera		+	+			
Opuntia sp.		+	+	+		
Oxalis sp.	+	+	+	+		
Panicum boscii	+	+	+			
Panicum dichotomum	4	5	+	+		
Panicum linearifolium		2		1		
Panicum oligosanthes			+	2	+	
Panicum sphaerocarpon		1	2	2		
Parthenocissus quinquefolia	3	3	7	9	5	
Paspalum ciliatifolia					2	1
Phlox pilosa		+	+		+	
Polygonatum canaliculatum			+			
Psoralea tenuiflora				+	+	
Quercus prinoides				+		
Rhus aromatica		+	4	3	3	+
Rhus copallina	1	+	+	+		
Rhus radicans	12	+	8	2	3	
Rhynchosia latifolia	3	3	+	+		
Rosa foliolosa				1		
Rosa setigera		+	+	+		
Rudbeckia hirta		1	2	2	+	
Ruellia humilis		+	+	+		
Sanicula canadensis	+		2	+		
Scutellaria parvula				+		
Setaria viridis				+	+	
Smilax bona-nox	+	2	2	+		

TABLE 2.--Continued

Species	Community-Type					
	Oak loblolly pine (1)	Oak hickory pine (3)	Oak hickory (6)	Oak hickory savannah (6)	Oak savannah (8)	Oak shinnery (1)
Similax rotundifolia			+	+		
Solidago sp.	2	+	+	2	+	
Sorghastrum nutans			+	+	+	
Spermolepis echinata		+		+	+	
Sphenopholis obtusata		1	+	+		
Sporobolus cryptandrus				+	3	20
Stylosanthes biflora	4	2	+	+		
Symphoricarpos orbiculatus			2	4	1	
Tephrosia virginiana		3	+	+		
Tridens flavus			+	+	1	
Ulmus rubra			+	+		
Uniola sessiliflora	9	+	1			
Vaccinium arboreum		1	+			
Vernonia baldwinii			+	1	2	
Viola pedata		3	+			
Vitis sp.	1	1	+	+	+	
Vitis riparia			1	+	+	
Vitis rotundifolia			+			

[a]Mean importance percentage (I.P.) <1.0.

TABLE 3.--Average number of species present in each community-type by understory stratum and the number of species which are present only in a single community-type (exclusive species).

Understory Category	Community-Type: Oak loblolly pine	Oak hickory pine	Oak hickory	Oak hickory savannah	Oak savannah	Oak shinnery
Total species	44	42	39	48	33	16
Shrub species	7	5	6	7	4	2
Tree seedling species	4	7	6	5	5	2
Herb species	33	30	27	37	25	12
Exclusive species	10	11	38	28	56	1

in these western sites which allows the invasion of a number of weedy adventive species.

Only little bluestem (Andropogon scoparius Michx) was found in all six community-types; however, grape (Vitis sp. L.), sedge (Carex sp. L.), goldenrod (Solidago sp. L.), poison ivy, Rhus radicans L.), and Virginia creeper (Parthenocissus quinquefolia [L.] Planch.) were present in all but the oak shinnery type and skunkbrush (Rhus aromatica Ait.) was present in all except the oak-loblolly pine community-type. Since only a single stand was sampled in both the oak shinnery and oak-loblolly pine community-types, the apparent lack of absolute ubiquity in these six species may be somewhat misleading.

Table 4 presents mean importance percentages of shrubs and understory trees for the six community-types. The oak-hickory community-type contained the most understory tree species (10) while the oak-hickory savannah and oak savannah had the most shrubs, 10 and 11 species respectively. Mean importance percentages were relatively low for all species; however, some species reached relatively high values in specific stands as evidenced by Rhus radicans with an I.P. of 11.8 under oak-loblolly pine (Stand 1) and 42.5 in one oak-hickory stand (Stand 5).

The Shannon-Wiener index was calculated for each understory stratum of each stand to assess understory diversity. Species importance percentages were used in the

TABLE 4.--Mean importance percentage of shrubs and understory trees in six upland forest community-types (number of stands in parentheses).

Species	Community-Type					
	Oak loblolly pine (1)	Oak hickory pine (3)	Oak hickory (6)	Oak hickory savannah (6)	Oak savannah (8)	Oak shinnery (1)
Understory trees						
Amelanchier arborea	-	0.1	-	-	-	-
Asimina triloba	-	-	1.1	-	-	-
Cercis canadensis	-	-	0.9	1.2	0.3	-
Cornus florida	5.0	0.1	0.7	-	-	-
Crataegus sp.	0.6	-	0.2	0.4	-	-
Diospyros virginiana	-	0.2	0.8	-	-	-
Ilex decidua	-	0.1	+	-	-	-
Prunus mexicana	-	0.3	+	0.1	-	-
Quercus havardii	-	-	-	-	+	8.5
Quercus phellos	1.3	-	-	-	-	-
Sapindus drumondii	-	-	-	-	0.4	-
Sassafras albidum	-	-	0.7	-	-	-
Shrubs						
Amorpha fruticosa	-	-	-	+	0.2	-
Ascyrum hypericoides	0.6	5.0	0.4	1.1	-	-
Ceanothus americanus	-	-	+	-	0.1	-
Cornus drumondii	-	-	0.1	1.3	0.9	-
Hamamelis vernalis	-	-	0.8	-	-	-
Lonicera albiflora	-	-	-	-	+	-

TABLE 4.--Continued

Species	Community-Type					
	Oak loblolly pine (1)	Oak hickory pine (3)	Oak hickory (6)	Oak hickory savannah (6)	Oak savannah (8)	Oak shinnery (1)
Shrubs (continued)						
Prunus angustifolia	-	-	-	0.2	-	-
Prunus gracilis	-	-	+	-	0.3	-
Ptelea trifoliata	-	-	-	-	+	-
Quercus prinoides	-	-	-	0.4	-	-
Rhus aromatica	-	0.3	3.6	3.0	2.8	0.6
Rhus copallina	1.1	0.2	+	0.1	-	-
Rhus glabra	-	-	+	0.4	1.0	-
Rhus radicans	11.8	1.0	8.2	2.4	2.7	-
Ribes ordoratum	-	-	-	-	+	-
Symphoricarpos orbiculatus	-	-	1.9	3.3	1.4	-
Vaccinium arboreum	-	1.5	0.1	-	-	-
Vaccinium stamineum	0.9	1.4	-	-	-	-
Viburnum prunifolium	-	-	-	-	0.1	-

[a]Mean importance percentage <0.1.

function,

$$H_{IP} = - \sum_{i=1}^{s} p_i \ln p_i,$$

where p_i was the importance percentage of the ith species, ln is the natural log and s is the number of species in the stand.

Table 5 shows mean, maximum and minimum diversity for the six community-types by stratum and diversity for the total community. Community diversity is the sum of the Shannon-Wiener values for all four strata. The relationship of understory diversity (sum of the three understory strata diversities) to the number of understory species is shown in Figure 2a. This high positive correlation ($r = 0.88$, $p = 0.01$) showed a trend similar to that of overstory diversity versus number of overstory species ($r = 0.80$, $p = 0.01$); however, there was no significant correlation between overstory diversity and any one of the following: total understory diversity, herbaceous diversity, shrub diversity, tree seedling diversity, total number of understory species or number of species within a specific understory stratum. A significant inverse relationship was found ($r = -0.57$, $p = 0.01$) between herbaceous diversity and shrub diversity (Figure 2b).

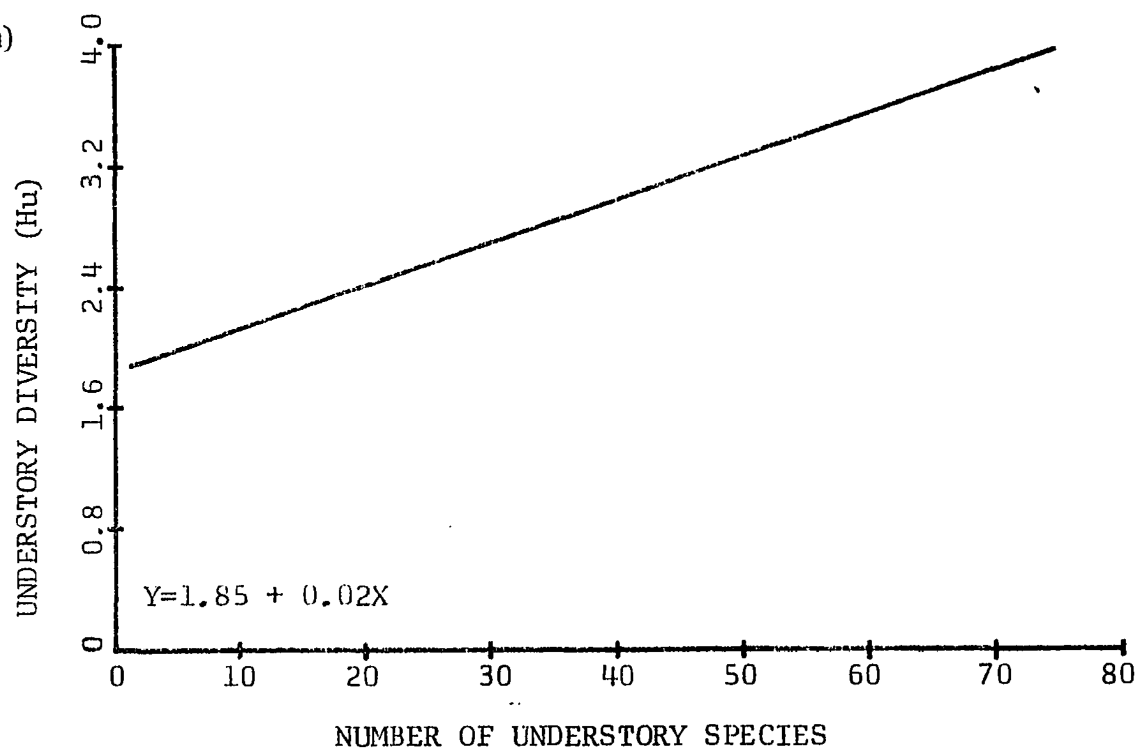
TABLE 5.--Mean, maximum and minimum species diversity (Shannon-Wiener values) by stratum and community diversity for six upland forest community-types based on importance percentages for understory species and relative basal area for overstory species.

Stratum	Community-Type					
	Oak loblolly pine	Oak hickory pine	Oak hickory	Oak hickory savannah	Oak savannah	Oak shinnery
Overstory						
Mean	0.21	1.62	1.65	0.90	0.88	0.06
Maximum	0.21	2.07	2.11	1.46	1.07	0.06
Minimum	0.21	1.34	1.25	0.35	0.58	0.06
Shrub						
Mean	0.61	0.33	0.45	0.47	0.34	0.24
Maximum	0.61	0.49	0.82	0.63	0.64	0.24
Minimum	0.61	0.24	0.15	0.07	0.01	0.24
Tree Seedling						
Mean	0.63	0.54	0.43	0.42	0.45	0.47
Maximum	0.63	0.61	0.57	0.71	0.95	0.47
Minimum	0.63	0.49	0.20	0.25	0.09	0.47
Herbaceous						
Mean	2.04	2.40	2.05	2.28	2.01	1.40
Maximum	2.04	2.67	2.58	2.88	3.13	1.40
Minimum	2.04	2.01	1.08	1.65	0.59	1.40
Community	3.49	4.89	4.58	4.07	3.68	2.17

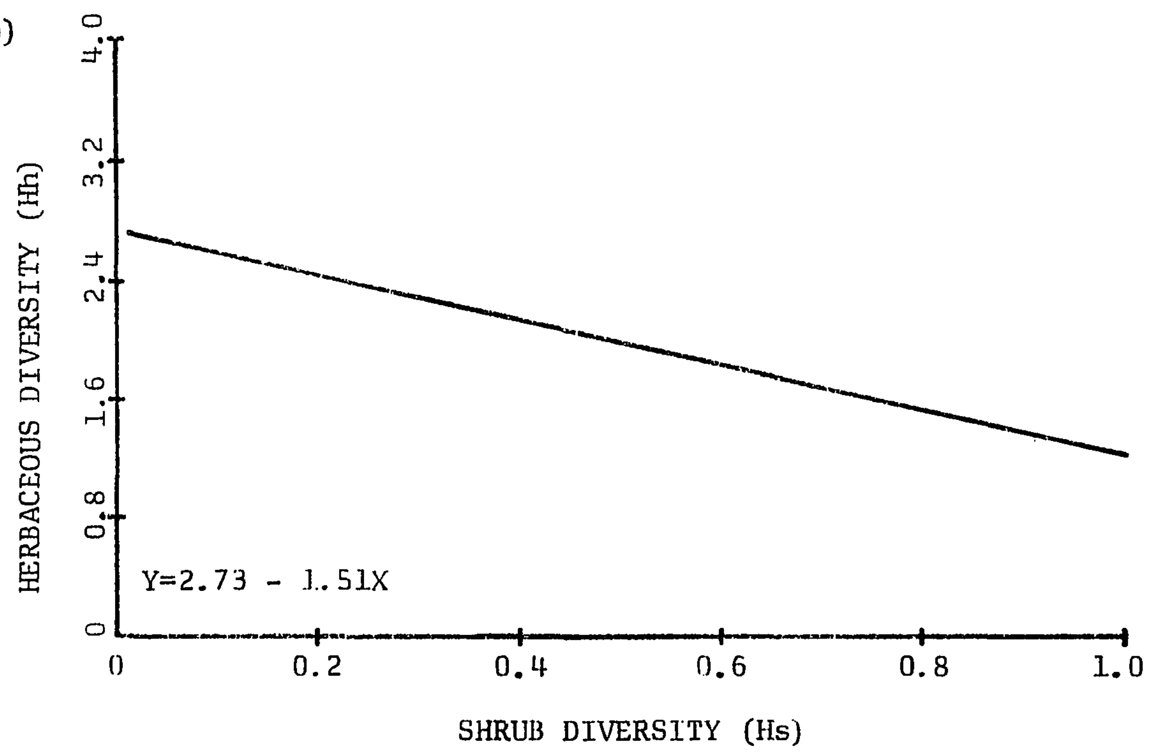
Figure 2a.--Linear regression showing the relationship of understory diversity (Hu) to the number of understory species for 25 upland stands in Oklahoma.

Figure 2b.--Linear regression showing the relationship of herbaceous diversity (Hh) to shrub diversity (Hs) for 25 upland forest stands in Oklahoma.

(a)


UNDERSTORY DIVERSITY (Hu)
0
0.8
1.6
2.4
3.2
4.0
Y=1.85 + 0.02X
0
10
20
30
40
50
60
70
80
NUMBER OF UNDERSTORY SPECIES

(b)

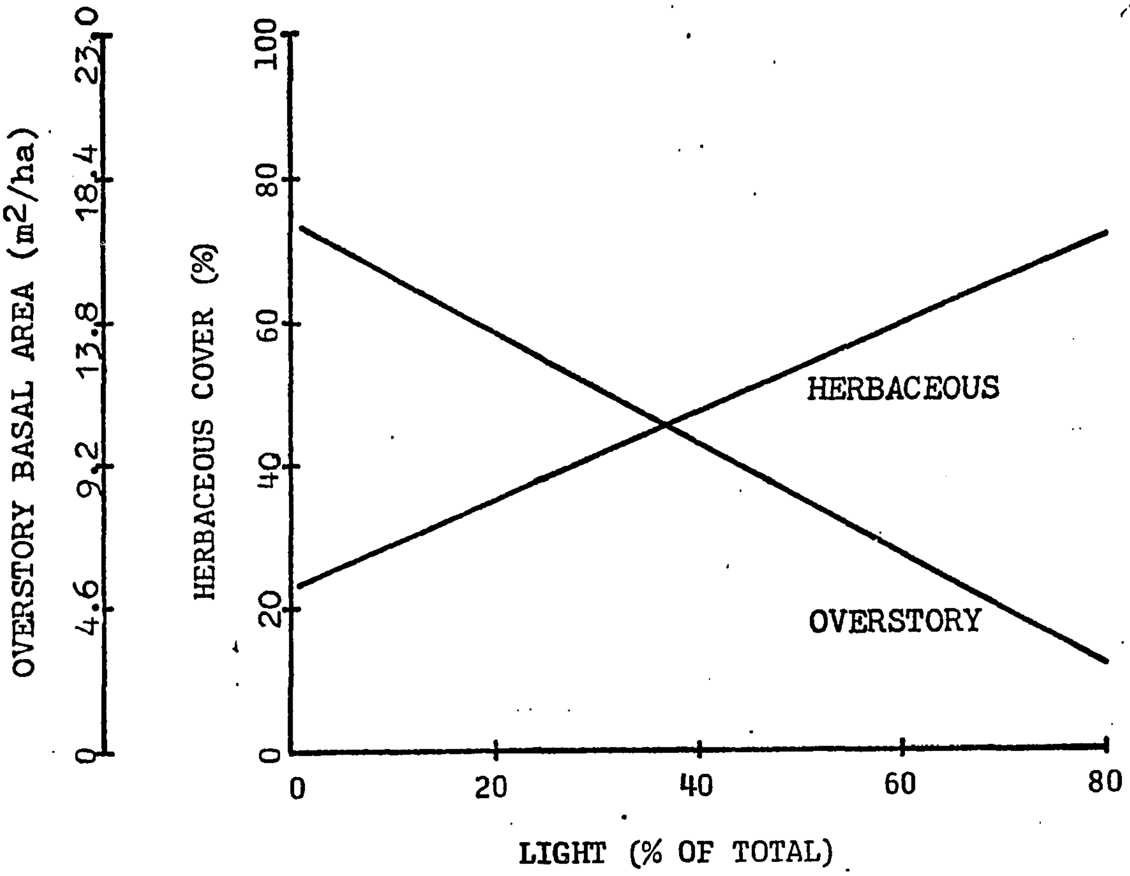

HERBACEOUS DIVERSITY (Hh)
0
0.8
1.6
2.4
3.2
4.0
Y=2.73 - 1.51X
0
0.2
0.4
0.6
0.8
1.0
SHRUB DIVERSITY (Hs)

While comparisons of diversity between strata gave some indication of relationship, they did not elucidate the factors which were responsible for understory species distribution or importance.

A number of vegetation characteristics were compared to several environmental factors which, either singly or in combination, may have influenced species distribution and importance. Percentage of light available at 90 cm above the soil surface was measured in each stand and these values were compared to overstory stand basal area (Figure 3). These two parameters showed a significant inverse linear relationship ($R = -0.70$, $p = 0.01$) indicating that as stand basal area decreased, the percent of total light available at 90 cm increased. Even more interesting was the direct linear relationship ($r = 0.49$, $p = 0.05$) between percent herbaceous cover and percent available light (Figure 3) coupled with the fact that percent herbaceous cover and overstory basal area were not significantly correlated. Neither total understory cover nor percent shrub cover were correlated significantly with percent light; however, the correlation of overstory basal area to number of shrub species was significant ($r = 0.56$, $p = 0.01$). It appears that if overstory basal area influenced herbaceous cover, the influence was indirect and not mediated by a single factor.

In order to examine the influence of several environmental variables on the vegetation, a principal component

Figure 3.--Linear regression of overstory stand basal area and herbaceous cover percentage correspondence to light availability (percent of total) at 90 cm above the soil surface for 25 upland forest stands in Oklahoma.


OVERSTORY BASAL AREA (m^2/ha)
0
4.6
9.2
13.8
18.4
23.0
HERBACEOUS COVER (%)
0
20
40
60
80
100
HERBACEOUS
OVERSTORY
0
20
40
60
80
LIGHT (% OF TOTAL)

ordination was constructed using 12 environmental variables by the method of Jeffers (1967). Figure 4(a-d) shows the distribution of total understory cover, herbaceous cover, shrub cover and tree seedling cover over the environmental ordination. Size of circle represents the cover class into which each stand falls. Cover classes for total understory (Figure 4a) and herbaceous stratum (Figure 4b) are from smallest circle size to largest: (1) 0.1-24.9%, (2) 25.0-49.9%, (3) 50.0-74.9%, and (4) 75.0-99.9%. Cover classes and size of circle (smallest to largest) for shrub stratum (Figure 4c) and tree seedlings (Figure 4d) are: (1) dot representing no cover, (2) 0.1-9.9%, (3) 10.0-24.9%, and (4) >25.0%.

Mesophytism increased from left to right on the ordination and there was a gradual decrease in total understory cover with increased mesophytism (Figure 4a). Stands intermediate to xeric on the ordination showed higher herbaceous cover than the more mesic stands (Figure 4b) and generally had lower numbers of species. Shrub cover was relatively constant over the gradient (Figure 4c) with only stand 5 having >25% cover; however, the number of shrub species increased slightly from xeric to mesic. The number of tree seedling species was quite constant over the gradient, but cover in this stratum was higher toward the xeric end, relatively depressed in intermediate stands and slightly higher toward the mesic end of the ordination (Figure 4d).

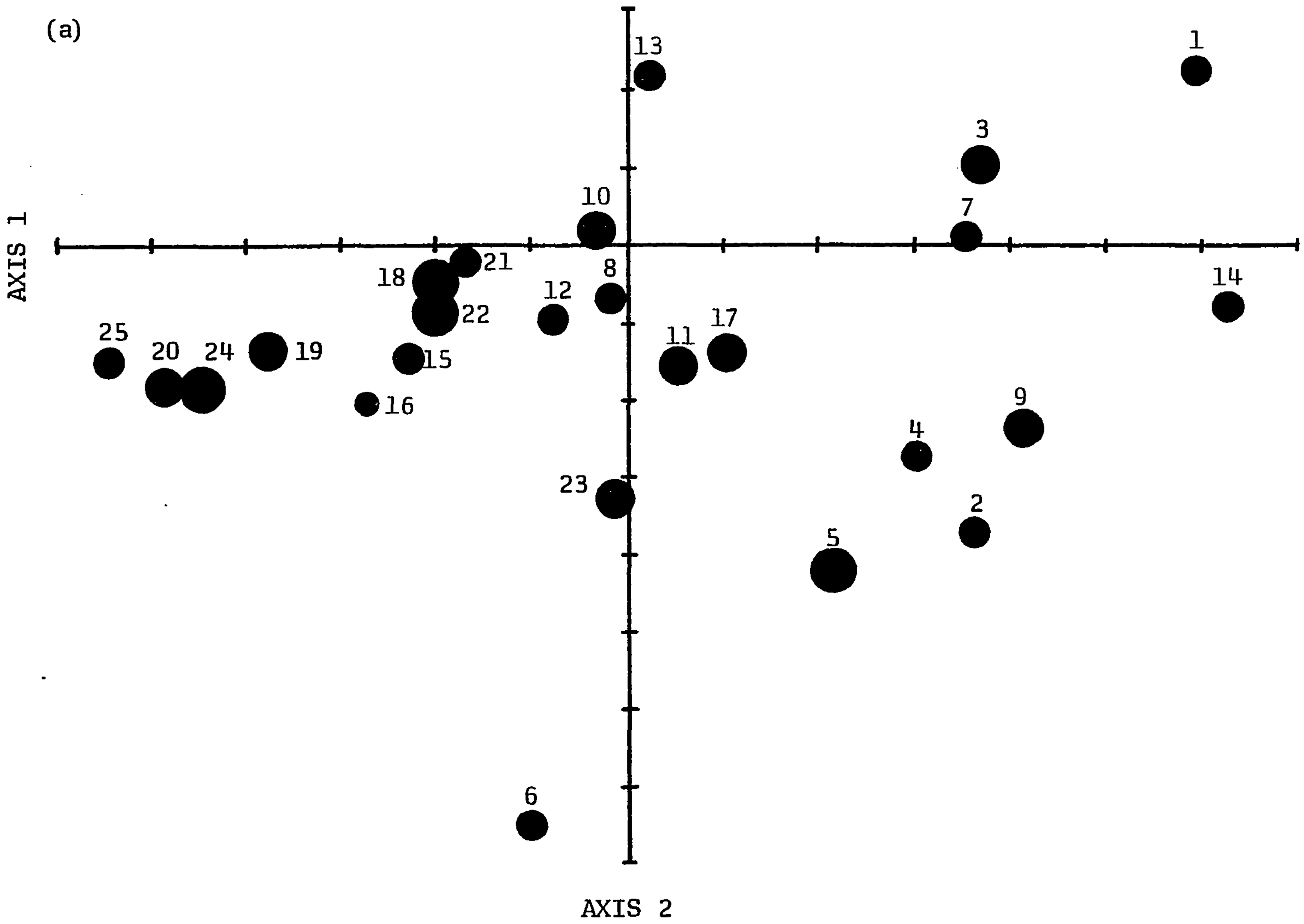
Figure 4.--Principal components ordination of stands based on 12 moisture related environmental variables.

(a) total understory cover

(b) herbaceous cover

(c) shrub cover

(d) tree seedling cover (see text for explanation).


(a)
AXIS 1
AXIS 2
1
2
3
4
5
6
7
8
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11
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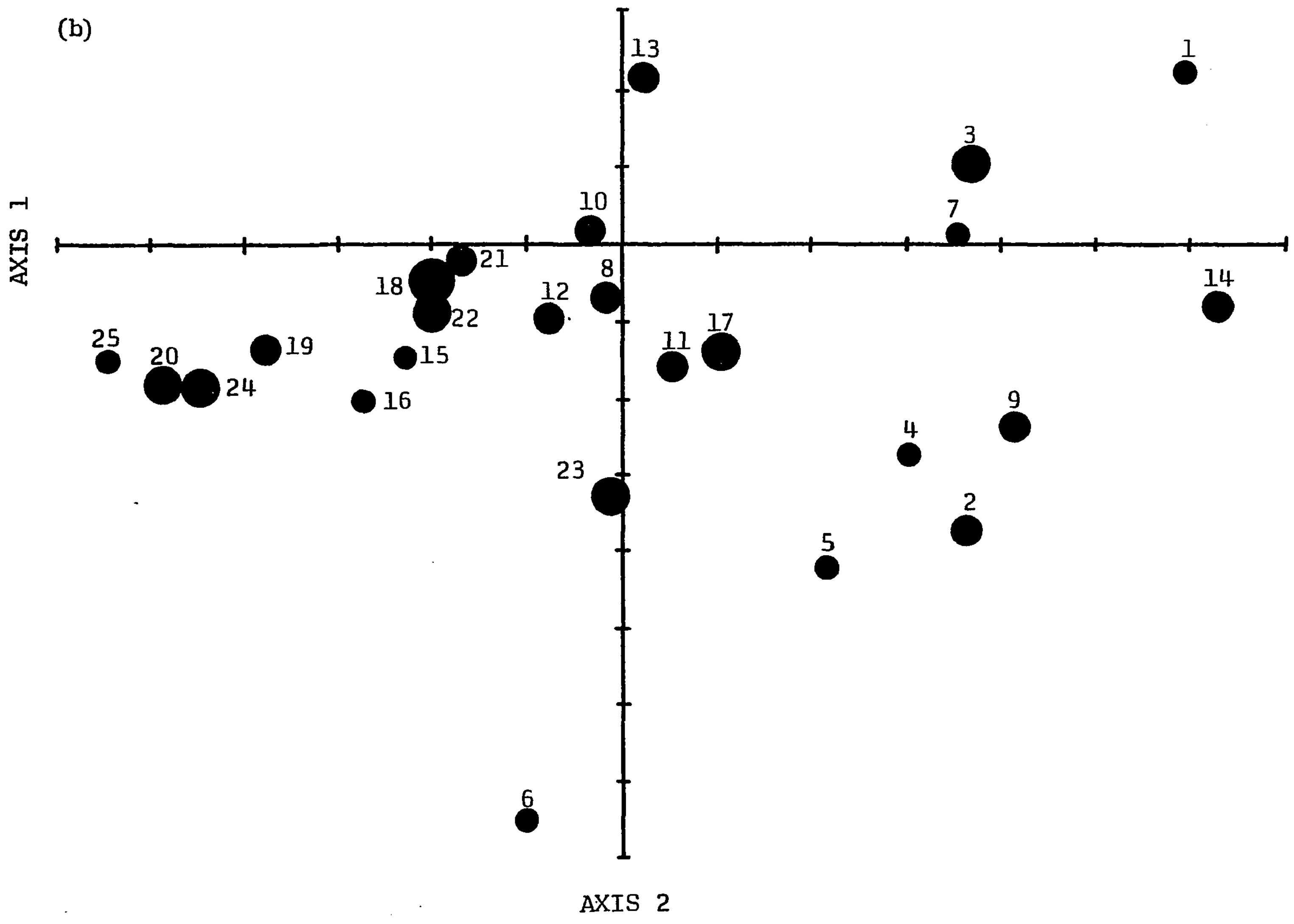
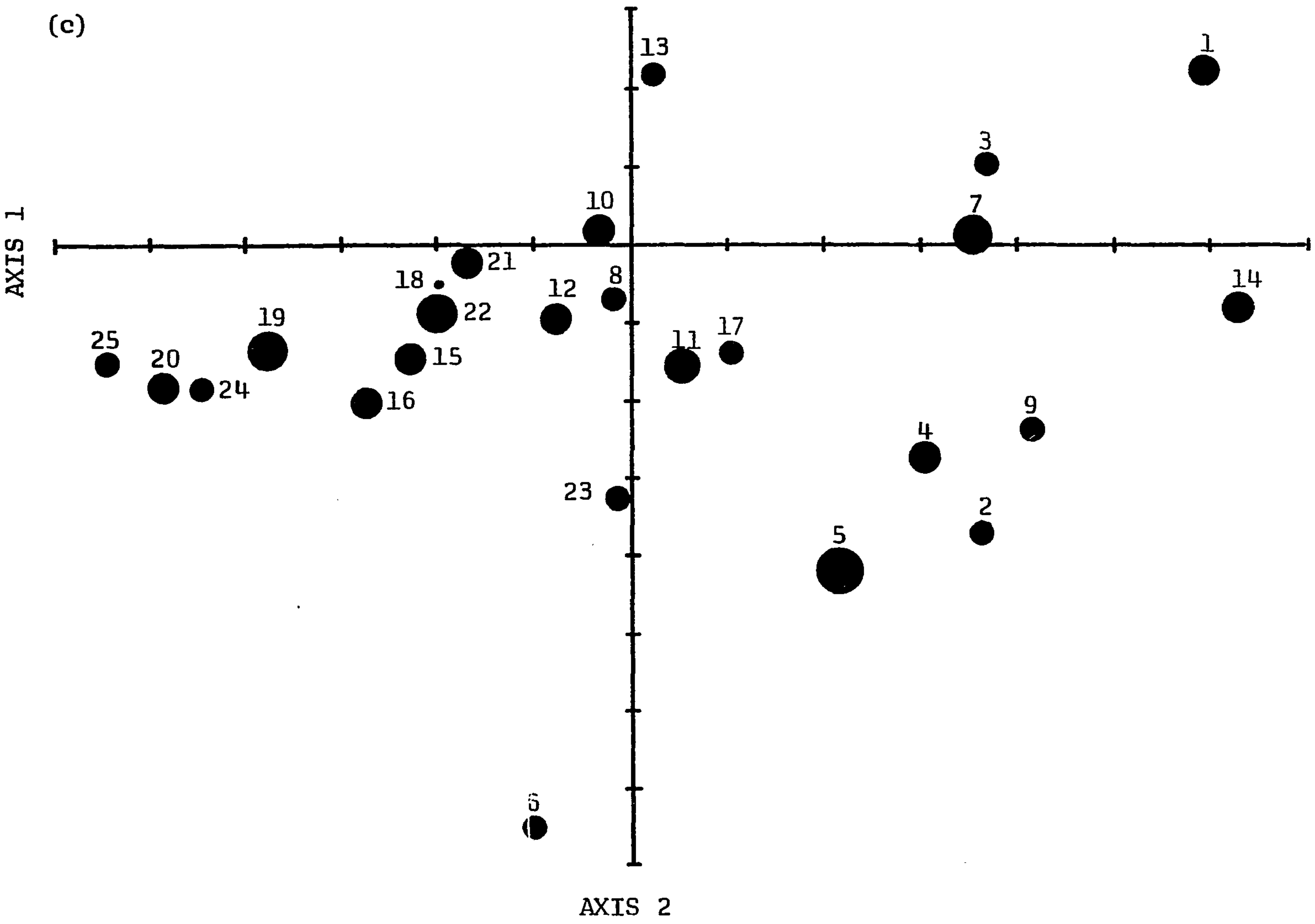
13
14
15
16
17
18
19
20
21
22
23
24
25


(b)
AXIS 1
AXIS 2
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

(c)


AXIS 1
AXIS 2
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2
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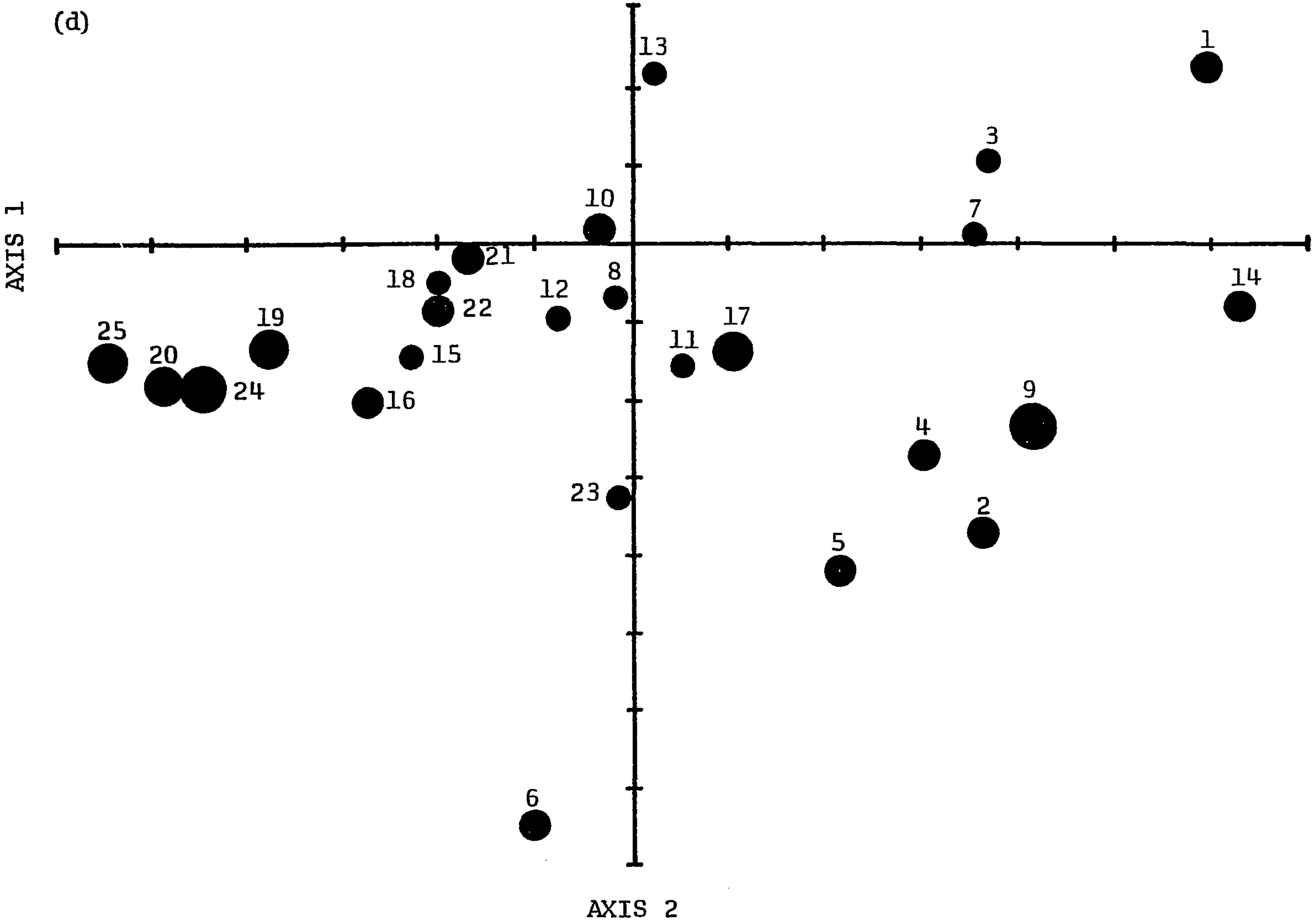
24
25

(d)


AXIS 1
AXIS 2
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25

Since the environmental ordination represents a complex of primarily moisture-texture related variables, comparison of the response of vegetation to mean annual precipitation seemed warranted, as this parameter showed a reasonably well-defined east-west gradient. Stands were ordered on the basis of mean annual precipitation which resulted in a natural separation into three geographic precipitation groups, namely: eastern, central and western. Forty-four selected understory species were arranged in five groups on the basis of their importance percentage and distribution over the geographic-precipitation gradient (Table 6) and the same procedure was done with 16 tree species (Table 7).

The species in Group I (Table 6) were all shrubs and understory trees with restricted eastern distributions. The overstory species in Group I (Table 7) had even more restricted eastern distributions, but were important overstory components in these mesic stands. All of the stands classified as eastern on the geographic-precipitation gradient occur on the mesic (right hand) side of the environmental ordination except stand 6, which occurred on a steep south slope and had the coarsest textured soil of any stand. Group I consisted in total of overstory and understory species with restricted eastern distributions with the exception of sugar maple (Acer saccharum Marsh.), which occurred as disjunct stands in the west-central canyons of the state (Rice, 1960, 1962).

Table 6-- Importance percentage (relative frequency+relative cover)/2 of selected understory species classified by section of state. Stands are arranged from left to right in order of decreasing annual precipitation (55 inches in stand 2 to 23 inches in stand 25).

	SECTION OF STATE																								
	EASTERN										CENTRAL							WESTERN							
Species	2	4	1	5	3	14	9	7	6	11	8	10	12	17	13	15	16	19	18	22	21	20	23	24	25
Group I																									
Cornus florida	+[a]		5	3		1	+																		
Asimina triloba				7			+																		
Hamamelis vernalis				5																					
Vaccinium arboreum		+					+		4																
Ilex decidua		+			+	+																			
Amelanchier arborea		+			+																				
Quercus phellos			1		+																				
Vaccinium stamineum		4	+																						
Sassafras albidum						4																			
Group II																									
Carex sp.	2	1	+	+	7	9		3		6	5	+	+	5	1	3	1			17	12			+	
Ascyrum hypericoides	2	12	+		+		+	+	1		1	+	4		2										
Parthenocissus quinquefolia	8		3	8	6	15	+	+	+	18	12	1	3	4	4	25	25	+		7	5				
Rhus radicans	2	+	12	43	6	+				+	+	+	5	+	7	1	10			7	4				
Smilax bona-nox	4	2	+	+	6	2			+	1	5	3	+			1									
Clitoria mariana	2	2	4		4	+	3		3	1	1	1	25		3										
Danthonia spicata	8	11					13	10	15					4											
Antennaria plantaginifolia	7	4					3	4	7	8	+	5		4	+										
Rhynchosia latifolia	6	1	3			+	1					3	+		+	2									
Stylosanthes biflora	+	4	4		4		1			+		1	1	+	+										
Erigeron strigosus	1	+	+				+	+	+	1	2	+	3	+	+	+			+						
Rudbeckia hirta	1	+					2	+	1	2	7	2		6	+				2						
Group III																									
Andropogon gerardii							2	3		+	3	1	2	11	3					+					
Festuca octoflora							+	+			+		4		+	1			3	+					
Panicum sphaerocarpon		+					+	4	3	+	6	3	2	+	5										
Aster patens							4	+	6	+				3											
Lespedeza repens							9	12	5																
Lespedeza procumbens										4		2		9											
Cornus drumondii					+						+	2	+		1	4	7								
Quercus prinoides												+	+		1										

Table 6-- (Continued)

Species	SECTION OF STATE																								
	EASTERN										CENTRAL							WESTERN							
	2	4	1	5	3	14	9	7	6	11	8	10	12	17	13	15	16	19	18	22	21	20	23	24	25
Group IV																									
Andropogon scoparius	1	5	4				2	7	9		7	4	7	11	37			13	3	12	15		26	25	6
Cercis canadensis				+	2	+				+	2	2	+			5				+	1		+		
Vernonia baldwinii					2					2		4	+	+	+		+			5	6		1	4	
Symphoricarpos orbiculatus					+	8				3	3	6	2		2	9	4		+		7				
Rhus aromatica								21	+	14			4				3	12			2	5	+	+	+
Cocculus carolinus						2				+		+				2					17	4			
Panicum oligosanthes										+	+		3	4	+				+	+	+		6	1	
Tridens flavus								+		1	3	+	+	+						+			6	3	
Group V																									
Aphanostephus skirrhobasis																		+	7			2			+
Bouteloua curtipendula													2					2		+	4		5	1	+
Bouteloua gracilis															+			+	11	1	3			5	
Bouteloua hirsuta															+			+	1				+	+	
Commelina erecta															7			6				18		2	3
Paspalum sp.																		3	7	2		15		2	1
Sporobolus cryptandrus															3				11	+	+	4		6	20

[a] Species importance percentage <1.0.

Table 7-- Relative basal area of selected overstory tree species classified by section of state. Stands are arranged from left to right in order of decreasing annual precipitation (55 inches in stand 2 to 23 inches in stand 25).

	SECTION OF STATE																								
	EASTERN										CENTRAL							WESTERN							
Species	2	4	1	5	3	14	9	7	6	11	8	10	12	17	13	15	16	19	18	22	21	20	23	24	25
Group I																									
Acer saccharum				19																					
Carya ovata	5			14																					
Liquidambar styraciflua				14																					
Pinus echinata	26	42							20																
Pinus taeda			96																						
Quercus alba	10	15		8																					
Quercus falcata		5	2		21																				
Group II																									
Carya texana	5		1	1	22	12	5	20	29	16	6	2			18		3								
Carya tomentosa	24					1				12	1				1										
Quercus shumardii				21		2	5			1	2			1											
Quercus stellata	9	23	1		11	17	13	55	35	48	57	92	61	75	41	76	65	16	6		63	1	77	60	
Quercus velutina	8	1		2		35	45			17	15		8			6									
Ulmus alata					18	10		8		1	6														
Group IV																									
Juniperus virginiana								5	3						3		3	20	2	6	31				
Quercus marilandica	2	14				1	31	12	16	5	11	5	30	25	41	5	35	61	60	86	34	50		15	
Group V																									
Quercus stellata x havardii																		20				40	5	5	99

The species in Group II (Table 6) were classified as eastern cosmopolitan, as they occurred in many stands throughout the east and central sections of the state. The overstory analogues of this group (Table 7) were quite important in the eastern and central sections and, with the exception of post oak (*Quercus stellata* Wang.), were slightly more restricted than the understory species.

The understory species of Group III had no overstory counterpart, except perhaps post oak which has a high basal area over the same portion of the gradient. These understory species were important only in the intermediate range of the gradient.

The classification of western cosmopolitan was applied to the species in Group IV. These species were wide ranging in terms of distribution, but were generally more important in the central-western portion of the gradient (Tables 6 and 7). Little bluestem falls in this group and exhibits this property remarkably. The Group IV overstory species fit the same patterns of distribution and importance.

Group V understory species were predominantly grasses of xeric habitats and exemplified the western oak savannah contact with the mixed-grass prairie. The overstory was characterized by the occurrence of the oak hybrid (*Quercus stellata* x *havardii*) as well as both post oak and blackjack in varying amounts.

It appeared that the distribution and importance of understory species were independent of overstory type and both understory and overstory species appeared to assort independently on the basis of the individual species ability to maintain itself in a specific habitat or set of environmental conditions.

SUMMARY

Twenty-five upland forest stands were sampled to characterize the understory vegetation in terms of composition, vegetation-environment relationships, diversity, and the correspondence of understory to overstory.

Each of the 25 stands was classified as a member of one of six upland forest community-types: oak-loblolly pine, oak-hickory pine, oak-hickory, oak-hickory savannah, oak savannah, and oak-shinnery. All except the oak-shinnery type were found in the eastern part of the state.

Understory vegetation was divided into three strata: shrubs, tree seedlings and herbaceous plants. The oak-hickory savannah contained the largest number of total understory species and the largest number of herbaceous species. The oak savannah had the greatest number of shrubs and exclusive (single occurrence) species with the oak-shinnery having the smallest number of species in every stratum including the overstory.

Ninety-four of the 280 understory species encountered were present in at least three of the 25 stands. Only little bluestem was present in all six community-types; however, grape, sedge, goldenrod, poison ivy and Virginia creeper were present in all but the oak-shinnery type and skunkbrush was present in all except the oak-loblolly pine community-type.

The Shannon-Wiener index of diversity was calculated for each stratum using species importance percentages for understory strata and relative basal area for overstory strata. Community diversity was calculated by summation of the values for all four strata within a specific community-type. The oak-hickory-pine community-type showed the highest community diversity and the highest diversity in the herbaceous stratum.

A linear regression analysis showed that as the number of understory species increased so did understory diversity; however, as shrub diversity increased, herbaceous diversity decreased.

When a number of vegetation characteristics were compared to percentage of light available at 90 cm above the soil surface using regression analysis, the following relationships were found: (1) overstory stand basal area was inversely related to percentage light, (2) percent herbaceous cover was directly related to percentage light, and (3) neither percent shrub cover nor total understory cover were significantly correlated to percentage light; however, overstory stand basal area was significantly correlated with number of shrub species.

The environmental principal component ordination showed a gradual decrease in total understory cover with increasing stand mesophytism. The increased herbaceous cover seen in xeric and intermediate stands was closely followed by correspondingly low numbers of species. Percent shrub cover showed a marked constancy over the gradient with localized eastern peaks while the number of shrub species increased slightly from xeric to mesic. Tree seedling cover was relatively constant with slightly higher values toward the xeric and mesic ends of the moisture gradient and slightly depressed in intermediate stands.

Forty-four understory species and 16 overstory species were arranged into five geographic-precipitation groups. Group I consisted of nine understory tree and shrub species and seven overstory tree species which had restricted eastern distributions. Group II contained ten herbaceous, two shrub and six overstory tree species which were classified as eastern cosmopolitan since they occurred in a number of eastern and central stands with relatively high importance. Group III contained six herbaceous and two shrub species which were largely restricted to the central portion of the state. There were no overstory species included in this group as none of the overstory species showed this type of restriction in importance or distribution unless the high basal area of post oak over this portion of the gradient was considered. Group IV was represented by five herbaceous, two shrub, one understory tree, and two overstory tree species. This group was termed western cosmopolitan. Group V consists of seven herbaceous and one overstory tree species with distribution more or less restricted to xeric habitats characteristic of the western oak savannah contact with the mixed-grass prairie.

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