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Ordination and classification of mature bottomland forests in North Central Oklahoma

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Collins, S. L., P. G. Risser, and E. L. Rice (Dept. Bot. Microbiol., Univ. Oklahoma, Norman, OK 73019). Ordination and classification of mature bottomland forests in north central Oklahoma. *Bull. Torrey Bot. Club* 108: 152-165. 1981.—Ordination and classification techniques were used to determine the pattern of species, stands, and community-types in the north central bottomland forests of Oklahoma. A polar-reciprocal averaging ordination (PO-RA) indicated an east to west stand compositional gradient existed in this region. Also along this gradient, species diversity and evenness decreased from east to west. Cluster analysis and discriminant functions analysis were used to classify the stands into 5 community-types. A plot of these community-types on the PO-RA ordination indicated that the community-types also showed an east to west gradient. It was hypothesized that this compositional gradient results from the elimination of floodplain species from western counties due to a decrease in available soil moisture from precipitation.

Key Words: bottomland forests; PO-RA ordination; classification; cluster analysis; discriminant functions analysis; Oklahoma.

Although all vegetation is affected by a complex of environmental variables, bottomland forests are particularly interesting because of the influence of topography and accompanying stochastic processes such as flooding frequency, depth, and duration. Often a vegetational gradient exists between the streamside and adjacent upland habitats, ostensibly due to flood frequency and soil moisture continua (Bell 1974). This vegetation gradient results from establishment and growth of species on favorable microsites based upon specific physiological, structural, and life history adaptations (Franz and Bazzaz 1977). Studies of streamside to upland forest vegetation gradients are numerous (Gemborys and Hodgkins 1971; Day and Monk 1974; Fonda 1974; Johnson *et al.* 1976; Bell and del Moral 1977; Robertson *et al.* 1978) and it appears that this gradient phenomenon is primarily a successional gradient resulting from the changes in river terrace levels

due to silt deposition, erosion, and stabilization of the top soil by vegetation.

However, no studies have examined the compositional gradients of mature floodplain forests across a geographic region, although both Braun (1950) and Curtis (1959) speculated about species compositional patterns in these forests. Braun thought that species composition of the southern floodplain forests was similar throughout large areas of the southern states, a hypothesis partially substantiated by Robertson *et al.* (1978). However, a variety of dominance types within a region was suggested by Curtis (1959) who stated that the changes in proportion and numbers of dominant species with geographic distance are great in the floodplain community. In fact, small changes of environmental factors at a site or between sites often are accompanied by marked compositional differences (Bell and del Moral 1977; Franz and Bazzaz 1977; Robertson *et al.*, 1978). It has been uncertain whether or not these changes are orderly or random along a geographic gradient, thus the purpose of this paper.

Continuum analyses of riparian forests are made difficult, but interesting, by the variation in floodplain topography, depth

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to the water table, flooding frequency, and changes in river flow, all of which may confound both spatial and temporal environmental gradients. Fortunately, however, data from Rice (1965) are appropriate to determine if a pattern exists in floodplain forest communities across a geographic gradient. Rice analyzed the mature bottomland forests in ten north central Oklahoma counties and found that *Ulmus americana*³ was a major component of the climax vegetation, being dominant in 38 of 47 stands. He also classified the 47 stands on the basis of leading dominants into ten community-types six of which were dominated by *U. americana*.

The objectives of this study were twofold: (1) to determine if vegetation and species trends exist across a geographic range in the bottomland forests of north central Oklahoma, using data from Rice (1965) and gradient analysis techniques, and (2) to reclassify the stands by cluster analysis in an effort to reduce the number of community-types to fewer homogeneous groupings than Rice originally designated. By using both ordination and classification, one may provide a more pragmatic data base concerning the distribution of species and the typification of communities (Kessell 1979). Finally, these new community-types have been analysed to determine if a continuum of community-types occurs in bottomland forests along a geographic gradient.

DESCRIPTION OF THE STUDY AREA. The forest vegetation of central Oklahoma forms a transition from the mesic, eastern deciduous forest to the drier grasslands and shrublands in the western United States (Risser and Rice 1971b). Upland forests in this region are dominated by *Quercus stellata*, *Q. marilandica*, and *Carya texana*. The associated bottomland forests are compositionally quite different, consisting of a variety of species including *Ulmus americana*, *Fraxinus pennsylvanica*, *Populus* spp., *Celtis laevigata*, *C. occidentalis*, *Salix nigra*, *Acer negundo*, and *Sapindus drummondii*. A general description of the physical features and climate of Oklahoma can be found in Rice and Penfound (1959).

Materials and methods. Rice (1965) collected data from mature floodplain forests in 10 north central Oklahoma counties (Fig. 1). Only stands free from cutting were sampled; however, some stands were being grazed or had been grazed in the past. A total of 38 tree species was recorded from the 50 stands. Originally, Rice discarded three stands deemed successional from his analysis but all stands are used in this report.

Data were collected by the augmented variable radius method (Rice and Penfound 1959). With this technique basal area was measured in each stand with an angle gauge at 40 evenly spaced points; frequency and density were obtained between points in forty 0.004-ha (0.01-acre) arms-length rectangles (Penfound and Rice 1957). Importance values (IV) were calculated for each species in each stand by summing the relative values of frequency, density, and basal area.

DATA ANALYSES. Community and species gradients were analysed by reciprocal averaging (RA, Hill 1973) and polar ordination (PO, Bray and Curtis 1957). These methods were chosen because they have been shown to reproduce simulated environmental gradients more accurately than other techniques such as principal components analysis (Gauch *et al.* 1977; Robertson 1978; Whittaker and Gauch 1978). Both RA and PO were performed after the deletion of rare species (those with < 10% constancy), and with log₁₀ transformation of the importance value data (del Moral and Watson 1978). Percentage similarity was used as the distance measure for PO. End stand selection for axis 1 of the PO was based upon the RA ordination. That is, the stands at the extremes of axis 1 of the RA were used as end stands for the first PO axis. The second PO axis end stands were selected by a method similar to that of Bray and Curtis (1957) and which most nearly approximated axis orthogonality (Gauch 1977:55). The PO-RA ordination was chosen over the simple RA so that polar ordination could be employed with an objective selection of end stands. Experience with the data indicated that a better separation of stands in two dimensions occurred with PO rather than RA. Not sur-

³ Nomenclature follows Waterfall (1972).

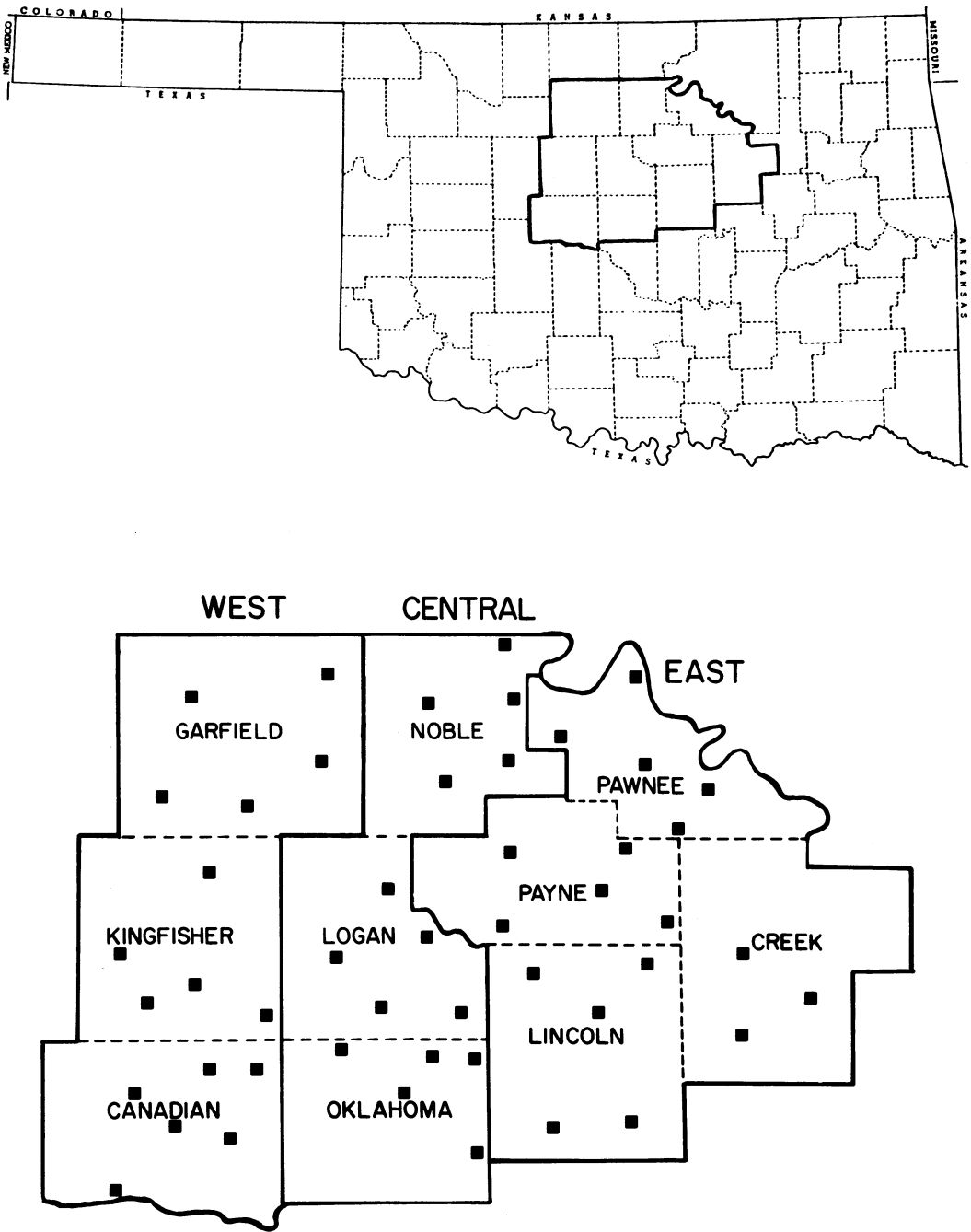


Fig. 1. A map of the state of Oklahoma showing the location of the study area and the geographic division of counties within the study area. Squares denote locations of sampled stands.

prisingly, the RA ordination yielded a pattern of stand distribution along the first axis similar to that of the PO-RA; however, little separation of stands by RA occurred in subsequent axes. This problem with RA has previously been noted by Peet (1978). All ordinations were produced by Cornell Ecology Program CEP-25 (Gauch 1977).

Classification of stands was accomplished by using an unweighted pair group cluster analysis with Euclidean distance (UPGMA, Sneath and Sokal 1973), a polythetic, agglomerative, hierarchical technique. This analysis was performed on unstandardized importance value data after the removal of rare species as in the PO-RA ordination. Robertson (1978) found that classifications using Euclidean distance (ED) did not perform well for grouping bottomland forest types from Illinois; however, del Moral (1975) has successfully used ISODATA, a non-hierarchical clustering method, to group upland vegetation. Our clusters were generally interpretable in conjunction with our PO-RA ordination, thus we feel that ED can be of value when analyzing stand relationships. Clustering was performed using NT-SYS (Rohlf, Kishpaugh, and Kirk 1974).

del Moral (1975) has suggested using discriminant function analysis (DFA) as a means of improving numerical classifications. We used DFA in this manner to assess the accuracy of our pair group cluster analysis. DFA attempts to minimize within-group variance (based upon species importance values) and maximize between group distances (Matthews 1979). A detailed description of DFA will not be presented here, but the interested reader is referred to Rao (1952) for technical details and to James (1971), del Moral (1975), Grigal and Ohmann, (1975), Kessell and Whittaker (1976), and Matthews (1979) for recent ecological applications.

Diversity (H') was estimated by the Shannon-Wiener formula:

$$H' = - \sum_{i=1}^s \left(\frac{Y_i}{N} \right) \log_e \left(\frac{Y_i}{N} \right); H' \geq 0$$

where N is the sampled total density per

stand, s is the number of species in the stand, and Y_i is the density contribution of the i^{th} species. Evenness was calculated as:

$$J' = H'/H_{\max}; 0 \leq J' \leq 1, \text{ and } H_{\max} = \log_e s$$

where J' is evenness, H' is the Shannon-Wiener value, and H_{\max} is the maximum diversity possible for the given number of species and sample size.

Some researchers (Whittaker 1965; Wilhm 1968) have suggested using a biomass measure rather than relative density for calculating diversity because biomass (1) accounts for different sized individuals of the same species, (2) might be a better indication of a species success in a community, and (3) alleviates the difficulty of distinguishing between individuals. Although we felt that these problems did not affect our tree-stratum forest data, the Shannon-Wiener index was calculated using both relative density and relative basal area (the latter as an index of biomass). The resulting values calculated with each measure of importance were highly correlated ($r^2 = 0.76$, $p < 0.001$). Previously, Risser and Rice (1971a) demonstrated this same correlation for the upland forests of Oklahoma. Therefore, all Shannon-Wiener values reported in this study were based on relative density.

Habitat breadth (HB) for each species was determined with importance values by the algorithm of Levins (1968) which again is the Shannon-Wiener formula. In this case Y_i/N is the ratio of the importance value of species i over the sum of its importance values across the study area. The weaknesses of this measure of HB (species range problems, quadrat spacing, and assumption of a linear gradient response) were discussed by Colwell and Futuyma (1971). Since we interpret the HB values strictly in the context of the study area and not in an evolutionary or interactive manner, these criticisms do not detract from the usefulness of our discussion of habitat breadth.

Results. A discussion of the general characteristics of the north central bottomland forests can be found in Rice (1965);

however, a brief summary is presented here. *Ulmus americana* had the highest importance value in 33 of the 50 stands, and was common throughout the north central forests (Table 1). Other species such as *Fraxinus pennsylvanica*, *Celtis occidentalis*, and *C. laevigata* were widely distributed although not often dominant (average and maximum IV, Table 1). *Quercus macrocarpa*, *Q. shumardii*, *Carya illinoensis*, *Ulmus rubra*, *Platanus occidentalis*, and *Cercis canadensis* were abundant only in the central and eastern counties. *Celtis reticulata* and *Maclura pomifera* were more abundant in the western counties.

Habitat breadth and average importance value (Table 1) are indications of the constancy of occurrence and variation of a species importance value across the study area. High HB values (>3.0) suggest a continuous or broad occurrence in these north central bottomland forests. Species with

high IV and HB values such as *Ulmus americana*, *Celtis occidentalis*, *C. laevigata*, *Sapindus drummondii*, and *Fraxinus pennsylvanica* are typically floodplain dominants. High HB values may occur even if the average importance value of a species is low, e.g. *Morus rubra*, *Juglans nigra*, *Bumelia lanuginosa*, and *Gleditsia triacanthos* which are secondary species in the bottomland forests. Those species with limited occurrences (*Quercus stellata*, *Celtis reticulata*) have a low HB, low average IV, and a narrow range of importance values. These species can be considered "tertiary" in that their occurrence in floodplains is inconsistent or random. Interestingly, successional taxa (*Populus* spp., *Salix nigra*, and *Acer negundo*) have moderate to high HB (2.93-3.01) and were present in most stands even though the data set was designed to sample mature stands. However, the importance values of these

Table 1. The 28 most common bottomland forest species, constancy, percent distribution in each region, average and maximum importance value (IV), and habitat breadth (HB).

Species	Constancy ¹	Percent Distribution ²			Max IV	Ave IV	Habitat Breadth
		West (17)	Cent (15)	East (18)			
<i>Acer negundo</i>	74	29	100	94	131.5	12.6	3.53
<i>Bumelia lanuginosa</i>	84	82	80	89	52.3	6.8	3.04
<i>Carya cordiformis</i>	16	0	7	39	15.6	1.3	1.50
<i>C. illinoensis</i>	38	0	47	67	86.4	9.0	3.35
<i>Catalpa</i> spp.	14	0	20	22	6.6	0.4	1.27
<i>Celtis laevigata</i>	92	82	100	94	65.3	21.2	3.77
<i>C. occidentalis</i>	82	53	93	100	83.0	22.0	3.45
<i>C. reticulata</i>	22	41	13	11	46.0	2.6	1.91
<i>Cercis canadensis</i>	30	6	20	61	11.9	1.4	2.93
<i>Diospyros virginiana</i>	16	12	27	11	9.4	0.4	1.67
<i>Fraxinus pennsylvanica</i>	82	47	100	100	86.4	24.4	2.98
<i>Gleditsia triacanthos</i>	36	6	60	44	31.0	1.8	1.62
<i>Gymnocladus dioica</i> s	68	47	73	83	37.4	7.0	2.18
<i>Juglans nigra</i>	80	59	87	94	74.4	15.1	2.01
<i>Maclura pomifera</i>	20	35	7	17	8.1	0.6	1.33
<i>Morus rubra</i>	84	71	87	94	52.2	8.7	2.65
<i>Morus</i> spp.	22	0	27	39	9.7	0.9	3.33
<i>Plantanus occidentalis</i>	26	0	0	72	25.7	1.8	2.58
<i>Populus</i> spp.	96	100	93	94	245.7	20.6	2.46
<i>Quercus macrocarpa</i>	58	18	67	89	61.7	12.8	3.09
<i>Q. marilandica</i>	14	0	7	33	8.6	0.4	1.76
<i>Q. muehlenbergii</i>	24	0	20	50	42.4	1.7	3.09
<i>Q. shumardii</i>	24	0	0	67	67.0	4.4	1.75
<i>Q. stellata</i>	22	0	20	44	28.6	1.7	1.99
<i>Salix nigra</i>	66	65	53	78	67.7	7.6	3.01
<i>Sapindus drummondii</i>	80	71	100	72	156.9	24.7	3.32
<i>Ulmus americana</i>	100	100	100	100	190.3	80.6	3.13
<i>U. rubra</i>	52	12	67	78	47.5	5.9	2.23

¹Percent of total stands in which a species occurred.
²Values in a region are the percentage of occurrences of a species in that region of the study area. Numbers in parentheses are the number of stands sampled in each region.

taxa were quite variable among the different stands and little can be said from this data set about their overall distribution in all north central bottomland forests.

If the 50 stands are compared to each other with a PO-RA stand ordination, an east to west compositional gradient emerges (Fig. 2). The gradient between east and central stands is weak; however, a separation of western stands from the other two regions is obvious. In fact, no overlap occurs in ordination space between the east-central stands and western stands. Thus an abrupt compositional change occurs in this biogeographic region of the bottomland forests of north central Oklahoma.

A second pattern appears within this ordination. Stands located within a county often are not located together in the ordination (Fig. 2). This indicates that although a general east to west pattern exists in the study area, the composition of stands within a geographic area the size of a county is quite heterogeneous, especially in the western counties. Thus, relatively small environmental differences, along with other stochastic properties (e.g., seed dispersal), can alter the geographic pattern of stands within a portion of the gradient. The within-county variation of stands is largely manifested in the second ordination axis where separation of stands is due to the presence or absence of secondary species such as *Juglans nigra*.

It is possible to provide a quantitative representation of the distribution and importance of the north central bottomland forest tree species along the first axis of the ordination (Table 2). A general pattern or coenocline appeared in this ordination. *Maclura pomifera* and *Celtis reticulata* were two species which showed prominent western distributions (Table 1). *Salix nigra* and *Populus* spp. occurred throughout the area, as previously mentioned. The next twelve species (*Sapindus drummondii* through *Quercus macrocarpa*) were the species characteristic of mature bottomland forests in north central Oklahoma. Many of these species increased in importance from east to west primarily due to the decreasing species richness along this gradient. *Acer negundo* was another widely

occurring successional taxon in the bottomland areas. The following seven species (*Gleditsia triacanthos* through *Carya cordiformis*) were eastern species which rarely occurred in western counties. Finally, the oak species (*Quercus*) are indicative of increasing xeric conditions. Two of these oaks, *Q. stellata* and *Q. marilandica*, are characteristic species of the upland forests of this region (Rice and Penfound 1959).

In the bottomland forests, higher diversity and evenness are found in the eastern counties and these values decrease westward. That is, the average number of species, average diversity, and average evenness per county show an east to west gradient (Table 3). Therefore, the compositional change noted in the ordination of Fig. 2 is also a diversity gradient. A uniform pattern emerges if H' is plotted along axis 1 of the PO-RA ordination (Fig. 3). A sharp break in diversity does not appear in this plot; thus, diversity decreases uniformly across the region whereas species composition changes more abruptly.

Cluster analysis was performed as a means of arranging the stands into an objective classification based upon overall similarity rather than simply comparing the leading dominants. The cophenetic correlation coefficient ($r = 0.886$) indicates that the dendrogram (Fig. 4) explains 78% of the variance in the Euclidean distance resemblance matrix (Sneath and Sokal 1973).

The clustering procedure produced five general groups (Fig. 4). Group 1, by far the largest, contains stands of moderate to high diversity and which are characterized by *Ulmus americana*, *Celtis* spp., and *Fraxinus pennsylvanica*. Thus, group 1 represents the typical bottomland forests of this region (Society of American Foresters 1954; Teskey and Hinckley 1977) and the southern floodplain forests in general (Braun 1950). The eight high diversity stands in group 2 have eastern species such as *Celtis occidentalis* and *Carya illinoensis* as dominants and *Ulmus americana* is of lesser importance. Group 3 is composed of western stands mostly dominated by *Sapindus drummondii* and *Ulmus americana*. Other common species are *Quercus*

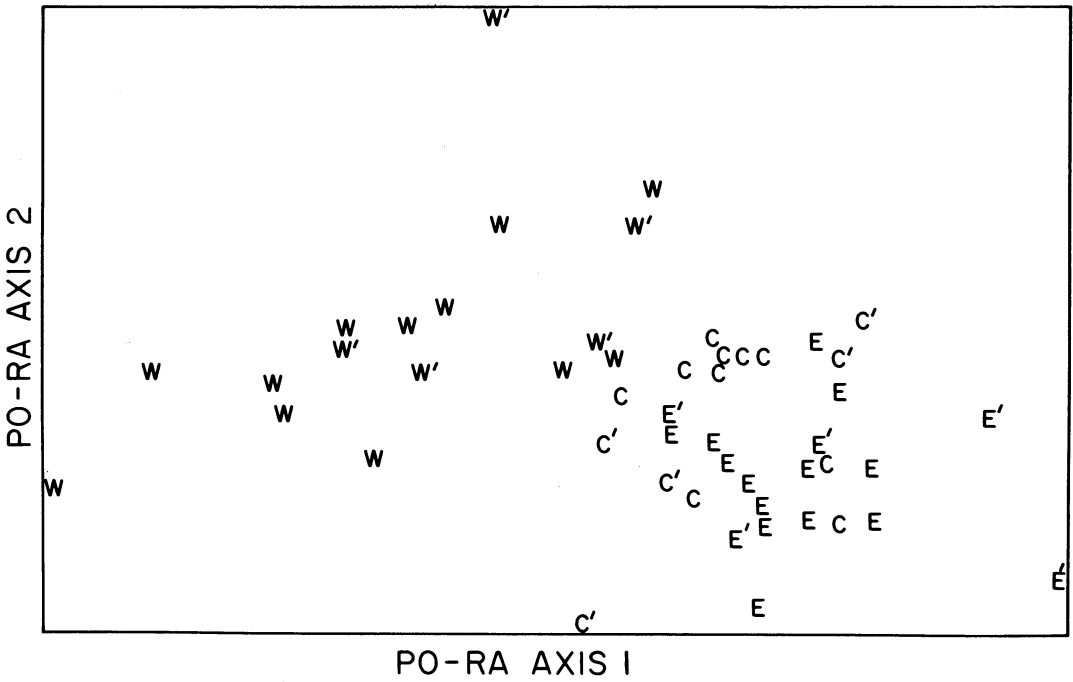


Fig. 2. A PO-RA ordination of the bottomland forest stands showing the location of stands by counties in each geographic section. E = Lincoln, Payne, Creek; E' = Pawnee; C = Oklahoma, Logan; C' = Noble; W = Garfield, Canadian; W' = Kingfisher.

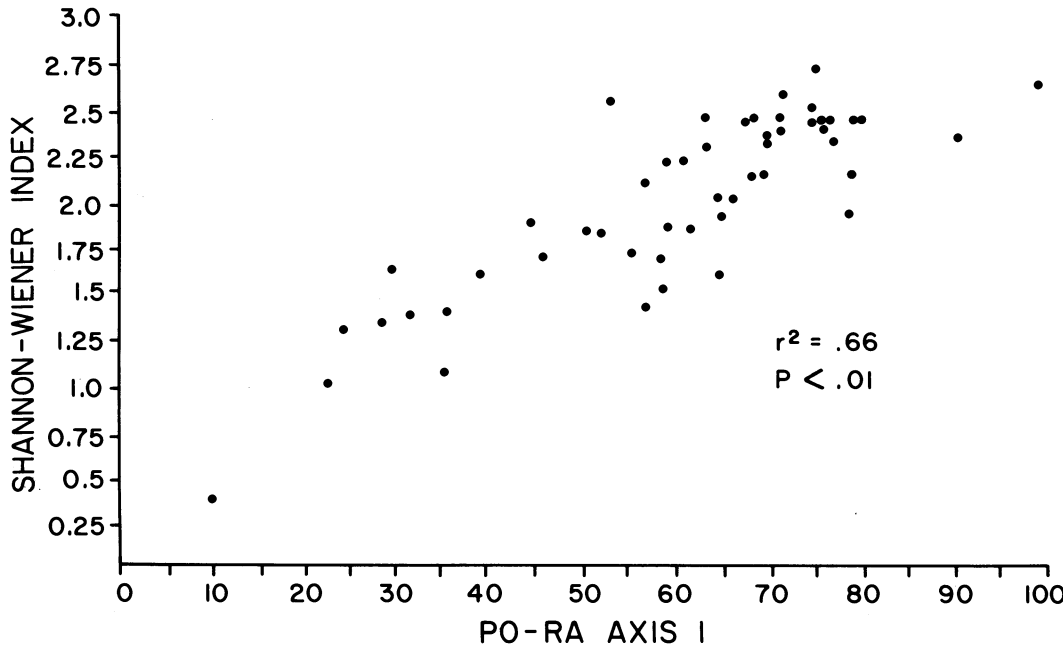


Fig. 3. A plot of the Shannon-Wiener index (H') in relation to the first PO-RA axis.

Table 3. The number of stands, average number of species, total number of species, and average diversity (H') and evenness (J') for each county in the study area.

County	Number of Stands	Average No. of Species	Total No. of Species	$\bar{X} H'$	$\bar{X} J'$
Canadian (W)	7	7.3	18	1.36	0.75
Garfield (W)	5	7.2	15	1.32	0.69
Kingfisher (W)	5	8.6	13	1.56	0.73
Logan (C)	5	11.4	16	1.99	0.85
Nobel (C)	5	11.4	20	2.16	0.90
Oklahoma (C)	5	14.6	24	2.25	0.88
Creek (E)	3	17.0	29	2.44	0.93
Lincoln (E)	5	15.4	27	2.40	0.90
Pawnee (E)	5	14.8	26	2.49	0.91
Payne (E)	5	15.2	24	2.40	0.92

macrocarpa, *Populus* spp., *Celtis reticulata*, and *Fraxinus pennsylvanica*. Group 4 is a cluster of six mostly western, low diversity stands strongly dominated by *U. americana*. Minor taxa include *Celtis laevigata*, *Morus rubra*, and *Fraxinus pennsylvanica*. Often, the importance value of *U. americana* was twice that of the second most important species in a stand. Lastly, group 5, showing weak clustering, contains the successional stands dominated by *Populus* spp., *Salix nigra*, and *Acer negundo* (Hefley 1937).

The five groups from the cluster analysis were restructured by discriminant function analysis (DFA). The first two axes of the DFA accounted for 54.3 and 31.5 percent of the variance, respectively (Fig. 5), and provided good separation of the five groups. Six taxa were entered in a stepwise fashion into the discriminant function: *Ulmus americana*, *Sapindus drummondii*, *Populus* spp., *Acer negundo*, *Celtis reticulata*, and *C. laevigata* (Table 4). All F-values were significant at the 0.01 level. Therefore, the above six species can separate the 50 stands into the five groups described by the cluster analysis. Only 4 stands were reclassified by the DFA (3 from group 1 to group 2, and 1 from group 2 to group 1) substantiating the accuracy of the original cluster analysis.

To determine whether or not the groups display a pattern across the east to west gradient, the five groups have been plotted on the PO-RA ordination (Fig. 6). This is the same ordination as Fig. 2; however, the stands are now represented by their group affiliation. In general, the stands are ar-

ranged by groups in the ordination, and a gradient of community-types is evident. Groups 1 and 2 are very similar, thus their close proximity in the ordination. The difference between the two groups is not due to a change in species composition, but rather it results only from a change of importance values among the species. All stands in group 3 and all but 1 stand in group 4 are located in the western counties. The outlying member of group 4 is heavily dominated by *Ulmus americana*, as are the other group 4 members, however, this stand includes a large number of subordinate species typical of group 1.

The one stand of group 5 which is located in the center of the ordination was the only stand dominated by *Acer negundo* and *Juglans nigra*. Since this stand is equally dissimilar from the four end stands it is placed in the center of the figure (Gauch *et al.* 1977).

Three stands from group 1 occur in the top center of the ordination and away from the main cluster of this group. The upper two of the three stands are *Ulmus-Juglans* stands. The third member, simply misclassified, is dominated by *U. americana* and

Table 4. Species and F-values used to discriminate between the five bottomland forest groups. All F-values are significant at $P = .01$.

Step	Species	F-value
1	<i>Ulmus americana</i>	48.5
2	<i>Sapindus drummondii</i>	23.0
3	<i>Populus</i> spp.	16.4
4	<i>Acer negundo</i>	13.8
5	<i>Celtis reticulata</i>	8.2
6	<i>Celtis laevigata</i>	4.2

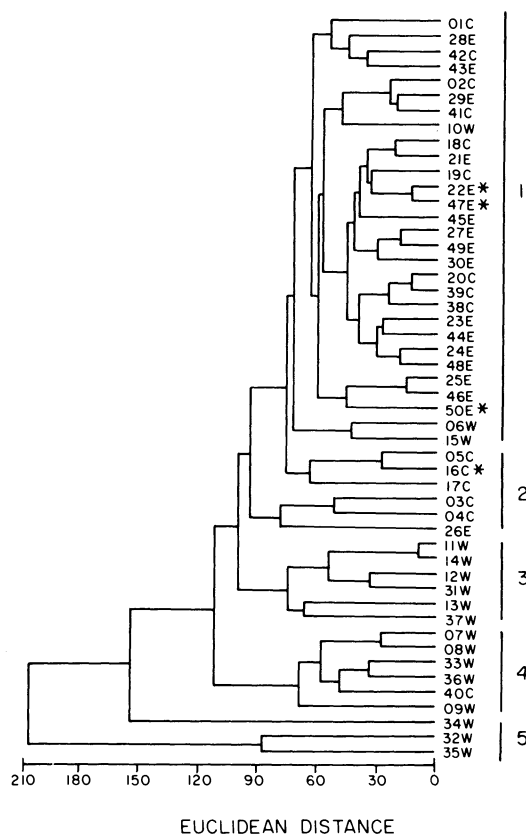


Fig. 4. An unweighted pair-group cluster analysis (UPGMA) of the 50 bottomland stands based upon species importance values. Euclidean distance was used to calculate the resemblance matrix. The dendrogram is divided into 5 general groups as described in the text. * indicates the stands reclassified by the DFA. Stands 22E, 47E, and 50E were moved to group 2; stand 16C was moved to group 1.

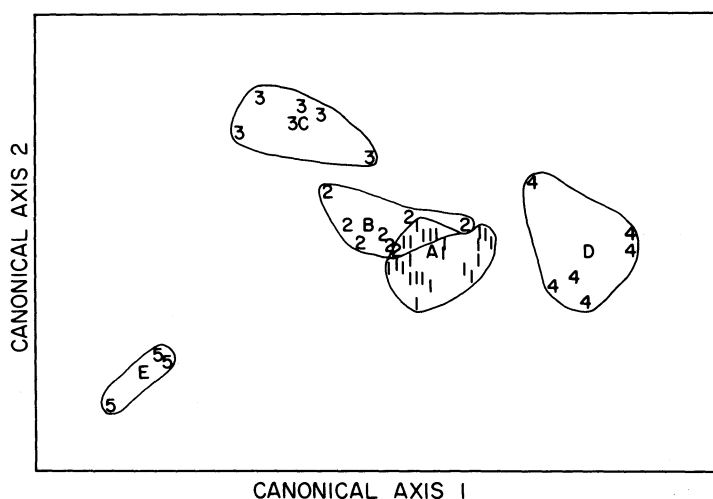


Fig. 5. The first two canonical axes of a multiple discriminant analysis (DFA) of the 5 groups identified in the cluster analysis. The first 2 axes account for 54.3 and 31.5% of the variance, respectively. The letters indicate the location of the group means.

Sapindus drummondii, thus it should be considered a member of group 3.

Dominance-diversity curves (Whittaker 1965) can be constructed as a final analysis of the composition and structure of the five groups. As noted earlier, a general east to west trend of community-types can be found in the north central bottomland forests (Figs. 2,6). The coenocline consists of high diversity *Ulmus-Celtis-Fraxinus* stands in the east to low diversity *Ulmus-Sapindus* and *Populus-Salix* stands in the west. This pattern of group structure can be seen in Fig. 7. Groups 1 and 2 have the greatest diversity and evenness, along with a well defined log-normal distribution of species importance values. Groups 4 and 5 have a geometric series distribution characteristic of high dominance-low evenness communities. Group 3 is intermediate. Species richness does not show a clear pattern between groups, although diversity decreases from east to west (groups 1 to 5). Thus, the diversity change is a result of increasing dominance (low J') particularly by *Ulmus* and *Populus*, rather than decreasing species richness.

Discussion. Clearly, a compositional change along a geographic gradient has been demonstrated in the mature floodplain forests of north central Oklahoma. The high degree of variability of stands within a county suggests that microenvironmental factors along with stochastic variables such as propagule dispersal and topography bring about compositional differences within these geographic areas. However, the within-county differences did not mask the overall east to west regional coenocline. The distribution of species in the study area suggests that this coenocline is due to the elimination of species in the western regions rather than a change of stand composition across the gradient.

The floodplain forests of north central Oklahoma are located to the west of the eastern deciduous forest boundary (Braun 1950). Studies within the eastern deciduous forests have shown that bottomland environments have a lower tree species richness than adjacent upland forests (Gemborys and Hodgkins 1971; Robertson *et al.* 1978).

In Oklahoma, however, the riparian forests of the central counties have a much higher average species diversity than the adjacent upland forests (upland $H' = 0.94$ (Risser and Rice 1971a), bottomland $H' = 2.68-1.67$, Fig. 7). These upland forests represent a transition from mesic eastern forests to dry grasslands and shrublands in the west (Risser and Rice 1971b). The increased species richness of the bottomlands is an indication of the ameliorating conditions found in the mesic riparian microclimate. However, these mesic conditions are not consistent across the region. Rice (1965) noted that flooding of Oklahoma lowland forests occurred primarily in May and June. During the remainder of the growing season, most of the available soil water in these bottomland communities comes from precipitation. An annual precipitation gradient of 70 cm in the west to 94 cm in the east exists across the region. Due to lower rainfall, western floodplain terraces contain less soil moisture than the floodplains of eastern counties. Those riparian species which require a consistently high soil moisture content may not be able to survive the more xeric western floodplain environment.

Rice (1965) analysed other environmental factors in each stand including soil texture, percent organic carbon, total nitrogen and phosphorus, and pH. No consistent east to west trends were found in any of these factors. Therefore, of those environmental variables measured, the precipitation gradient best explains the change in species composition of the forests across the north central counties.

In conclusion, it appears that the overall mesic conditions of the bottomland habitat provides an environment conducive to high tree species richness in contrast to the adjacent upland forests and grasslands. However, conditions change across the study area becoming more xeric in the western counties. This trend parallels that in upland habitats in Oklahoma, but the bottomland environment results in the western distribution of high diversity forests typical of the eastern deciduous regions. As the available soil moisture contributed by precipitation decreases, species

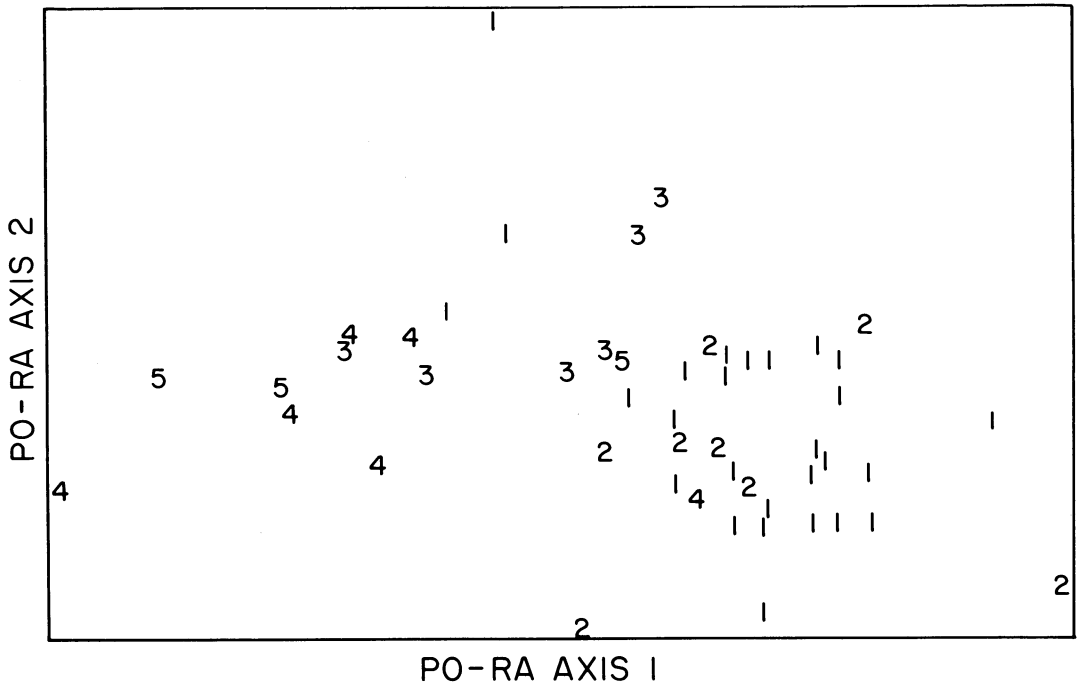


Fig. 6. A PO-RA ordination of the groups from the cluster analysis after reclassification by DFA. This is the same ordination as Fig. 2; however, stand location is now indicated by group affiliation.

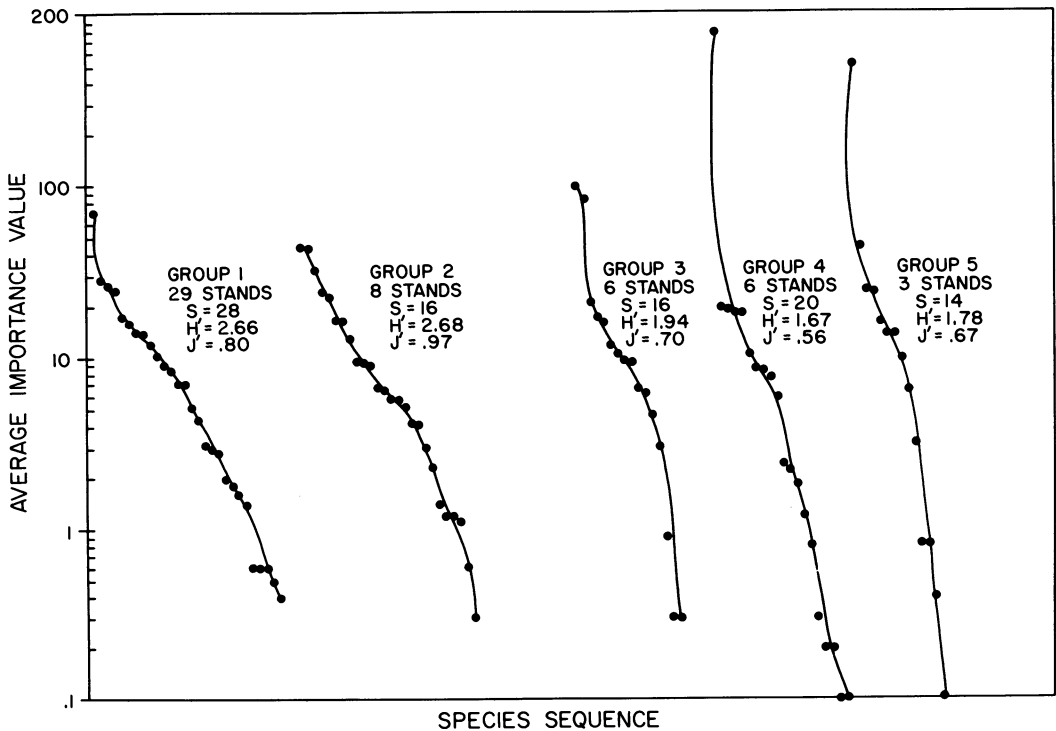


Fig. 7. Dominance-diversity curves for each group defined by the UPGMA-DFA classification.

dominance patterns are altered by the elimination of the more mesic species. The decrease in importance of these species results in a higher percentage of importance for the remaining species which is expressed by a decrease in evenness and diversity across the precipitation gradient. Thus, there are definite trends of stand composition and relative importance of species across this geographic region in north central Oklahoma. In spite of these trends, it is possible to describe the five well-defined community-types which represent relatively homogeneous units of the landscape.

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