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ORDINATION AND CLASSIFICATION OF WESTERN OAK FORESTS IN OKLAHOMA[1]

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ABSTRACT

Ordination and classification techniques were used to analyze patterns of forest vegetation, species diversity, and soil type in the Wichita Mountains Wildlife Refuge of southwestern Oklahoma. Cluster analysis based on tree species produced three general community types: 1) *Quercus stellata-Q. marilandica* forests; 2) *Q. stellata* forests; and 3) mesophytic forests. A polar ordination produced a gradient of vegetation that corresponded to a moisture gradient. Many high diversity forests were located on loamy drainageway soils or north facing slopes. Tree species diversity (H′) was inversely related to the importance of *Quercus stellata.* Cluster analysis based on species composition of the tree seedlings produced four general community types: 1) *Q. marilandica* type; 2) *Q. marilandica-Q. stellata-Juniperus virginiana* type; 3) *Ulmus americana-Celtis reticulata-Bumelia lanuginosa* type; and 4) *Acer saccharum* type. The third seedling type occurred almost exclusively on loamy drainageway soils. There was no relationship between stand location on the first axis of the tree ordination and the first axis of the seedling ordination suggesting that trees and seedlings respond differently along the moisture gradient.

THE EASTERN deciduous forest reaches its western limit in the central portion of Oklahoma where it takes the form of oak forest and oak savannah. West of this area, woody vegetation is chiefly confined to streambeds (Collins, Risser and Rice, 1981). However, outposts of the eastern deciduous forest occur in sandstone canyons in the west-central part of the state (Rice, 1960), and in the Wichita Mountains of southwestern Oklahoma (Buck, 1964). The presence of forests in these areas has been attributed to climatic fluctuations which favored the western migration of eastern deciduous forest species (Little, 1939; Braun, 1950).

The Wichita Mountains Wildlife Refuge contains approximately 24,000 ha of grasslands and forests (Buck, 1964; Crockett, 1964) with the forests primarily found along streambeds, in protected valleys and on mountain slopes. Although oak savannah was common in western Oklahoma (Rice and Penfound, 1959), most of the forests in the Wichita Mountains now have a closed canopy. Tree age-class distribution (Dooley, 1983) indicates, however, that many of the present forests have recently developed from savannahs with the advent of grazing and fire suppression in the area (Penfound, 1962). Hoffman (1930) reported that these forests were comprised of *Quercus marilandica* and *Juniperus virginiana,* with the former being more abundant. Eskew (1938) characterized the forests as a mixed oak association with *Q. marilandica* dominant. In addition to oak forests, Blair and Hubbell (1939) described mesophytic forests comprised of *Q. shumardii, Ulmus americana, Bumelia lanuginosa, Fraxinus americana,* and *Celtis* spp. bordering streambeds. They also reported the presence of *Acer saccharum* in some protected valleys and canyons. Diehl (1953) distinguished between the mountain forests and those bordering streams. More recently, Buck (1964) found that soil types and geologic formations could not be delineated on the basis of woody species associations. Since these classifications of the refuge vegetation were subjective and primarily based on analysis of leading dominants, we believe a more objective analysis is justified.

Ordination and classification methods represent an improvement on vegetation descriptions based on leading dominants. In addition, multivariate analyses performed on a data base

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of all species are useful tools in examining relationships between vegetation and environment. The specific objectives of this study were to: 1) define refuge forest community types by use of classification techniques; 2) elucidate vegetational gradients and their possible environmental bases by use of ordination; 3) examine species diversity in relation to compositional and environmental gradients; and 4) compare species composition of tree and seedling strata.

MATERIALS AND METHODS—*Study area*—The Wichita Mountains are located in Comanche Co., southwestern Oklahoma (98°43′W longitude, 34°44′N latitude). The range covers about 96.5 km in length and is oriented along an east–west axis with a maximum width of about 40 km. The mountains, composed chiefly of granite and other igneous rocks (Snider, 1917; Hoffman, 1930), rise abruptly from the surrounding redbed plains. Mount Scott is the highest peak, with an elevation of 756 m and a base to peak height of 340 m. The Wichita Mountains Wildlife Refuge encompasses the eastern and central portions of the range. The slopes of many of the mountains are covered by talus composed chiefly of large boulders. The upper slopes of some of the higher peaks are bare rock surfaces.

The drainage of the Wichita Mountains is generally southeasterly to the Red River. Within the Refuge, all streams are intermittent and many have been dammed.

The climate of the Refuge is classified as subtropical humid (Trewartha, 1968). The average January temperature is 2.7 C and the average July temperature is 27.8 C. The number of frost-free days averages 200. The average yearly precipitation totals 731 mm with about half occurring from April through July (NOAA, 1980).

Field methods—The 46 forest stands sampled in this study during 1980–1981 had previously been sampled by Buck (1964). He selected undisturbed sites that represented five geologic formations, four soil types and various slope exposures.

In each stand, the composition of the tree size class was determined in 20 randomly placed 0.01-ha circular quadrats (in nine small stands, only 10 or 15 quadrats were used). All stems with a diameter at breast height (dbh) of at least 10 cm were tallied and basal area recorded. Seedlings (dbh < 2.5 cm) and saplings (≥2.5 cm but ≤10 cm dbh) were censused in a 0.004-ha circular quadrat centered in each larger quadrat. Sampling was carried out after seedling emergence. Importance percentages for trees were calculated as ½ the sum of relative density and relative basal area. Relative frequency was significantly correlated with relative density ($r = 0.94$, $P < 0.01$) and so was not used in the calculation. Relative density was used as a measure of seedling importance. Stems in the sapling size class were extremely rare and were not included in the analyses.

Data analysis: Stand relationships were determined using an unweighted pair-group cluster analysis (UPGMA, Sneath and Sokal, 1973; Rohlf, Kishpaugh and Kirk, 1974) derived from a distance matrix of unstandardized importance percent data. Community gradients were analyzed by reciprocal averaging (RA, Hill, 1973) and polar ordinations (PO, Bray and Curtis, 1957). All ordinations were conducted on importance percentage data which had been $\log_{10}$ transformed, a treatment which reduces dominance effects and improves normality (del Moral and Watson, 1978). Because of the small number of species (19 trees, 23 seedlings), all species were included in the multivariate analyses. For the PO, percentage similarity was used as a measure of distance. An analytical disadvantage of PO is the subjectivity of end stand selection. To overcome this drawback, the first axis end stands from the RA ordination were used as end stands for the first PO axis. This combined PO-RA ordination has been used successfully on bottomland forest data in Oklahoma (Collins et al., 1981). The PO-RA ordination provided good stand separation (see van der Maarel, 1980), and corresponded well with the cluster analyses.

Diversity (H′) was estimated with the Shannon-Weiner index:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i,$$

where s is the number of species and p_i is the proportion of the total number of individuals of species i (Peet, 1974). Evenness (E) was calculated with the index of Alatalo (1981):

$$E = (N_2 - 1)/(N_1 - 1),$$

where N_2 is $1/\Sigma\, p_i^2$ and N_1 is $\exp(H')$.

RESULTS—The most important species in both the tree and seedling strata were *Quercus stellata*, *Q. marilandica* and *Juniperus virginiana* (Table 1). Although not widely distributed, *Ulmus americana*, *Juglans rupestris*, *Acer saccharum*, *Carya illinoensis*, *Q. muehlenbergii*, *Q. shumardii*, and *Diospyros virginiana* achieved importance in some forests. *Celtis reticulata* and *Bumelia lanuginosa* were widespread but abundant only in the seedling layer.

TABLE 1. *The tree and seedling species of the Wichita Mountains Wildlife Refuge, their constancy (percent of stands in which they occurred), maximum and average importance percent (IP) and maximum and average relative density (RD)*

Trees	Constancy	Max. IP	Avg. IP	Trees	Constancy	Max. IP	Avg. IP
Quercus stellata	98	98	64	*Q. muehlenbergii*	9	38	15
Q. marilandica	89	63	17	*Q. shumardii*	6	53	27
Juniperus virginiana	74	48	11	*U. rubra*	4	2	1
Celtis reticulata	28	10	2	*Fraxinus pennsylvanica*	4	4	2
Bumelia lanuginosa	39	6	2	*Morus rubra*	4	2	1
Ulmus americana	24	52	11	*Diospyros virginiana*	2	33	33
Juglans rupestris	20	49	18	*Gleditsia triacanthos*	1	<1	<1
Acer saccharum	13	46	17	*Q. macrocarpa*	2	13	13
Prunus americana	9	1	1	*Crataegus* spp.	2	<1	<1
Carya illinonensis	9	19	12				
Seedlings	**Constancy**	**Max. RD**	**Avg. RD**	**Seedlings**	**Constancy**	**Max. RD**	**Avg. RD**
Quercus stellata	92	93	31	*U. rubra*	11	7	2
Q. marilandica	89	99	22	*Fraxinus pennsylvanica*	9	9	2
Juniperus virginiana	94	49	14	*Morus rubra*	6	2	1
Celtis reticulata	96	53	15	*Diospyros virginiana*	4	3	2
Bumelia lanuginosa	72	31	8	*Gleditsia tricanthos*	4	2	2
Ulmus americana	74	68	12	*Q. macrocarpa*	2	2	2
Juglans rupestris	22	13	4	*Crataegus* spp.	6	2	1
Acer saccharum	15	74	31	*Ptelea trifoliata*	2	4	4
Prunus mexicana	50	6	2	*Sapindus drummondii*	2	<1	<1
Carya illinonensis	9	4	2	*Viburnum prunifolium*	2	<1	<1
Q. muehlenbergii	9	3	2	*Cercis canadensis*	2	10	10
Q. shumardii	9	36	16				

Three general groups of stands were defined by the cluster analysis (Fig. 1, cophenetic correlation coefficient, $r = 0.9$). The first type consisted of low diversity forests that were codominated by *Q. stellata* and *Q. marilandica* which ranged in importance from 37 to 61% and 17 to 63%, respectively. Forests of the second type were of slightly lower diversity and were dominated by *Q. stellata,* which ranged in importance from 55 to 95%. In Stands 2 through 13, *Q. marilandica* was of secondary importance (average IV = 10%). *Juniperus virginiana* was important in Stands 21 through 26, with an average importance of 20%. The remaining stands, which are highly variable in composition, represent forests principally dominated by mesophytic species. Although *Q. stellata* and *J. virginiana* occur in several of these stands, mesophytic species such as *Juglans rupestris, Acer saccharum, Carya illinoensis, Q. muehlenbergii, Q. shumardii,* and *Ulmus americana* are also important within these stands. In summary, three forest community types can be distinguished in the Refuge: 1) *Q. marilandica-Q. stellata*; 2) *Q. stellata*; and 3) mesophytic forests.

When tree compositions of the 46 stands were compared with a PO-RA ordination (Fig. 2A), as would be expected, the mesophytic forests did not group together. Stands of this group defined both axes and this forced Type 1 and 2 stands together. Stand separation along the first axis was related to *Q. stellata* importance. The first axis was significantly correlated with *Q. stellata* relative density ($r = 0.67$, $P < 0.01$). Stand order along the second axis was related to the presence of minor species.

The first axis of the PO-RA ordination was negatively correlated with species diversity ($r = -0.53$, $P < 0.01$) and evenness ($r = -0.38$, $P = 0.05$). The correlation was stronger between the relative density of *Q. stellata* trees and the Shannon-Weiner index ($r = -0.81$, $P < 0.01$). Low species diversity is characteristic of forest overstories on the Refuge; the Shannon-Weiner index is 1.0 or less for approximately half of the forests. Similarly, evenness was negatively correlated with the relative density of *Q. stellata* trees ($r = -0.83$, $P < 0.01$).

Many of the high diversity mesophytic forests occur on loamy drainageway soils (Fig. 2B). This relationship was not reciprocal, however, as this soil type also supports low diversity *Q. stellata*-dominated forests.

In order to compare trends suggested by the tree stratum analyses, patterns in the seedling stratum were also analyzed by ordination and classification techniques. Cluster analysis (cophenetic correlation coefficient, $r = 0.7$) defined four general seedling types (Fig. 3). The

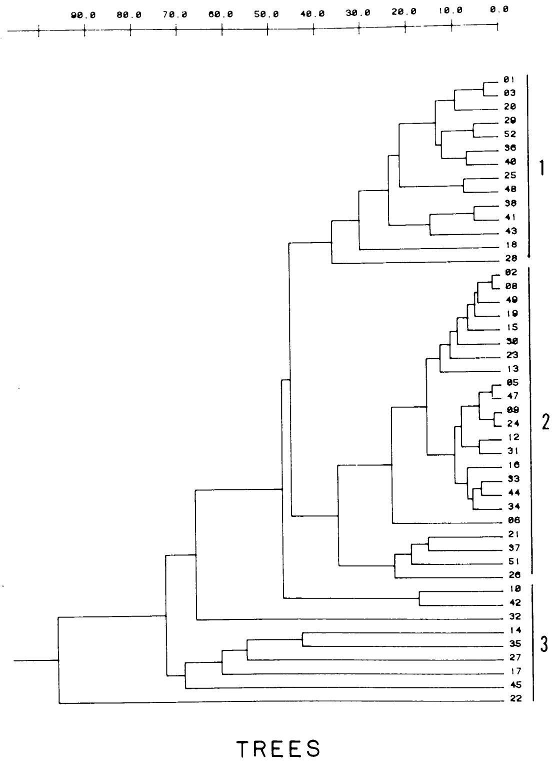

Fig. 1. An unweighted pair-group cluster analysis of the 46 stands based on tree species importance. Euclidean distance was used as a measure of similarity. The groups are: (1) *Quercus stellata-Q. marilandica* forests, (2) *Q. stellata* forests, and (3) mesophytic forests.

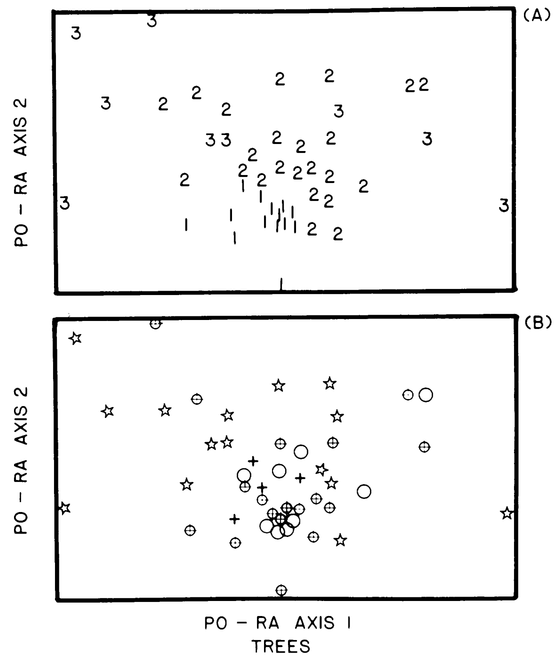

Fig. 2. **A.** A reciprocal averaging-polar ordination of tree species composition in 46 stands. Stands are represented by tree community types defined in Fig. 1. **B.** The same ordination as A with stands represented by soil type. (○) = cobbly colluvial, (☆) = loamy drainageway, (+) = lawton loam, and (⊕) = hilly stoney.

first type consisted of stands in which the seedling layer was dominated by *Q. marilandica.* In Stands 1 through 52, *J. virginiana* was also dominant. The dominant seedlings in Group 2 were *Q. stellata, Q. marilandica* and *Juniperus virginiana.* Three subtypes were evident in this group. In Stands 2 through 32 dominance was shared more or less equally by *Q. stellata, Q. marilandica,* and *J. virginiana.* In Stands 5 through 48, *Q. stellata* and *Q. marilandica* were equally important with *J. virginiana, U. americana, B. lanuginosa* and *C. reticulata* of secondary importance. *Quercus stellata* was the only common species in Stands 9 through 16. In the third seedling group *C. reticulata, U. americana* and *B. lanuginosa* were dominants. *Celtis reticulata* was the most important seedling in Stands 10 through 45 with *B. lanuginosa* and *U. americana* less abundant. In Stands 13 through 51, *U. americana* was the most important species. *Acer saccharum* was the dominant seedling in the fourth group. Therefore, four seedling types are identified: 1) *Q. marilandica*; 2) *Q. stellata-Q. marilandica-J. virginiana*; 3) *U. americana-C. reticulata-B. lanuginosa*; and 4) *Acer saccharum.*

In forests where the seedling layer was dominated by *Q. marilandica, Q. stellata* and *Q. marilandica* were the dominant trees. Forests with seedling layers dominated by *Q. stellata, Q. marilandica,* and *J. virginiana* had overstories dominated by *Q. stellata* alone or *Q. stellata* and *Q. marilandica.* Where *C. reticulata, U. americana,* and *B. lanuginosa* were the dominant seedlings, the important trees were either *Q. stellata* or the mesophytic species. The latter species dominated the overstories of forests where *A. saccharum* was common in the understory.

The seedling composition of the 46 stands was compared using PO-RA ordination (Fig. 4A). Each stand is represented by its seedling type as defined in the cluster analysis. The importance of *Q. marilandica* in Type 1 and 2 forests resulted in some overlap of these in the ordination. The secondary importance of *U. americana, C. reticulata* and *B. lanuginosa* in Type 2 forests resulted in the overlap of Types 2 and 3 in the diagram. Unlike the tree ordination, the first axis of the PO-RA seedling ordination was not significantly correlated with

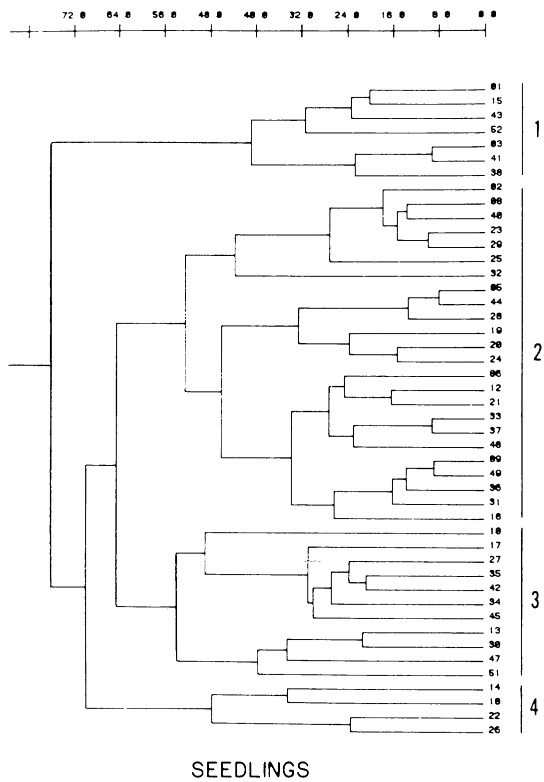

Fig. 3. An unweighted pair-group cluster analysis of the 46 stands based on seedling species density. Euclidean distance was used as a measure of similarity. The groups are: (1) *Quercus marilandica* type; (2) *Q. stellata-Q. marilandica-J. virginiana* type; (3) *Ulmus americana-Celtis reticulata-Bumelia lanuginosa* type; and (4) *Acer saccharum* type.

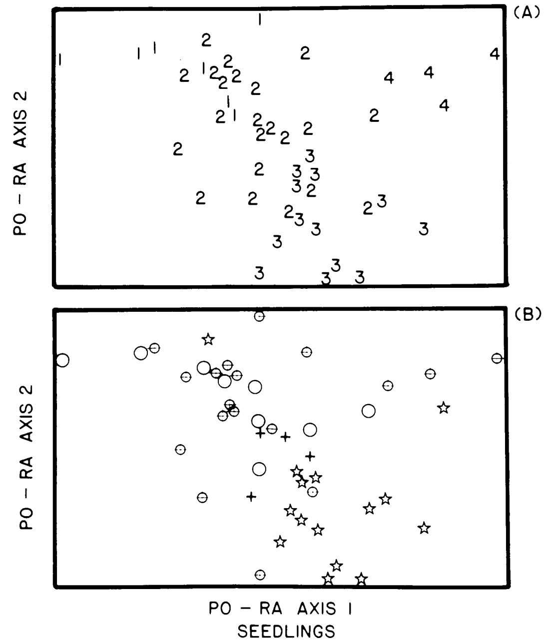

Fig. 4. **A.** A reciprocal averaging-polar ordination of seedling composition of the 46 stands. Stands are represented by the seedling community types defined in Fig. 3. **B.** The same ordination as A with stands represented by soil type. See Fig. 2 for explanation of the symbols.

the importance of *Q. stellata* seedlings ($r = -0.14$, $P = 0.36$).

Seedling strata dominated by *C. reticulata, U. americana,* and *B. lanuginosa* were more diverse than those dominated by other species. There was a significant correlation between species diversity and the first axis of the PO-RA ordination ($r = 0.49$, $P < 0.01$) but not between evenness and the first axis ($r = 0.06$, $P > 0.05$). It is notable that diversity was higher in the seedling layer than in the tree layer. The correlation between the Shannon-Weiner index and the relative density of post oak seedlings was significant but weaker than was the case for trees ($r = -0.32$, $P = 0.05$).

The correlation of seedling community type with soil type was higher than was the case for trees (Fig. 4B). The most diverse seedling type (Group 3) occurred most exclusively on loamy drainageway soils. With few exceptions, the soils did not support the other seedling types.

The correlation between stand position on the first axes of the tree and seedling ordinations was not significant (Spearman's rank correlation, $r_c = 0.12$). Stands that were similar in terms of tree layer composition may not have had similar seedling layers. When the first axis coordinates for stands from the seedling ordination were compared with that from the tree ordination (Fig. 5), a reordering of stands was apparent. The reordering was partly the result of scattering of the mesophytic forests across the tree ordination. For example, four forests had *Acer saccharum* present in the overstory and understory. They were located on the far left of the tree ordination and on the far right of the seedling ordination. However, many forests did have differences in strata. Several *Q. stellata* dominated stands had seedling layers dominated by *Q. stellata, Q. marilandica*

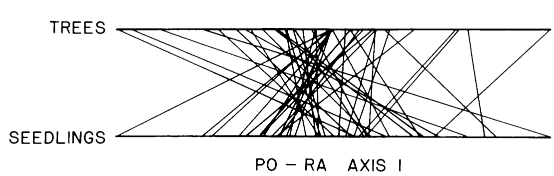

Fig. 5. Comparison of stand position on the first axis of the tree ordination (Fig. 2) with the position on the first axis of the seedling ordination (Fig. 4). $r_c = 0.12$, $P > 0.05$.

and *J. virginiana,* while those located on loamy drainageway soils had an abundance of *C. reticulata, U. americana* and *B. lanuginosa* in the seedling size class.

Discussion—The forests of the Wichita Mountains Wildlife Refuge represent several forest types found elsewhere in Oklahoma. The most numerous forests in the Refuge are the *Q. stellata-Q. marilandica,* and *Q. stellata* types. These types correspond to the oak savannah of western Oklahoma described by Rice and Penfound (1959). The oak savannahs are dominated by *Q. stellata* and *Q. marilandica,* occur in areas receiving 635–813 mm precipitation annually, and presumably were more savannah-like prior to the advent of heavy grazing and fire supression. Although many forests bordering intermittent streams in the Refuge have overstories dominated by *Q. stellata,* seedling layers are often dominated by species typical of western Oklahoma bottomland vegetation such as *Celtis* spp., *Ulmus americana, Bumelia lanuginosa, Carya illinoensis* and *Q. macrocarpa* (Bruner, 1931; F. Johnson, pers. comm.).

Many of the mesophytic forests contain species characteristic of eastern Oklahoma forests, the most notable example of which is *Acer saccharum.* The continuous range of *Acer saccharum* extends westward as far as the eastern counties of Oklahoma (Fowells, 1965). Disjunct populations in Oklahoma are located in sandstone canyons of Caddo and Canadian counties (Little, 1939; Rice, 1960) and on some north facing slopes of the Wichita Mountains. Tree species commonly associated with *A. saccharum* in eastern Oklahoma are generally absent in the Wichita Mountains. In one of the sampled forests, *A. saccharum* codominates with *Juglans rupestris* which approaches the easternmost extension of its range in the Refuge (Little, 1976). Thus, the forests containing *A. saccharum* are not equivalent to those in eastern Oklahoma or elsewhere. Other species not usually found in southwestern Oklahoma are *Q. shumardii, Q. muehlenbergii,* and *Diospyros virginiana.*

The forests in the Refuge are characteristically of low diversity and richness. Risser and Rice (1971) reported an average Shannon-Weiner index of 0.8 and a total of 12 tree species for the upland forests of southwestern Oklahoma. Bottomland forests of the region are more diverse, with an average Shannon-Weiner index of 1.54 (F. Johnson, pers. comm.). Like the refuge forests, the upland forests of Oklahoma achieve their highest diversity when dominated by species other than *Q. stellata* and *Q. marilandica.* Seedling layers are more diverse than tree layers in Refuge forests, as is true for other forests in Oklahoma (F. Johnson, pers. comm.) and elsewhere (Adams and Anderson, 1980).

Based on species composition, the ordinations produced a pattern of vegetation that corresponds to a complex moisture gradient. Forests located at the xeric end of the gradient are codominated by *Q. marilandica* and *Q. stellata.* Although *Q. marilandica* can survive on more xeric sites than *Q. stellata* (Bruner, 1931; Johnson and Risser, 1972), the occurrence of the former on more xeric sites may not result from greater drought tolerance. Rice and Penfound (1959) reported greater mortality for *Q. marilandica* following a severe drought in stands where *Q. stellata* also occurred. It is possible that the dominance of *Q. marilandica* on less favorable sites may be due to greater tolerance of soil infertility (Johnson and Risser, 1972) or increased coppicing following fire (Penfound, 1968). *Quercus stellata*-dominated stands located in the middle of the ordination may be interpreted as corresponding to slightly more mesic conditions. Forests at the mesic end of the gradient occur in a variety of conditions: north-facing slopes dominated by *Acer saccharum,* forests bordering streams in which *U. americana, J. rupestris,* and *Carya illinoensis* are important, and protected valleys and canyons where *Q. shumardii* and *Q. muehlenbergii* are prominant.

The gradient of seedling composition may be interpreted similarly. The *Q. marilandica* community type occupies the xeric end of the gradient. Three stands in this group had been burned prior to sampling as part of a prescribed burning program. The average density of *Q. marilandica* seedlings in these forests was 308 stems/ha as compared to 234 stems/ha in the unburned stands of this group. This suggests that the density of *Q. marilandica* seedlings may increase following fire. On slightly more mesic sites, the seedling layer is dominated by *Q. marilandica, Q. stellata,* and *J. virginiana.* The remaining seedling types represent the most mesic conditions in the Refuge: *A. saccharum* on north-facing slopes, and *U. americana* and *B. lanuginosa* on loamy drainageway soils.

Soil type is probably not the basis for the derived moisture gradient. Lawton loam, granite cobbly land, and loamy drainageway soils are generally deep, while the stony rock land soils are variable in depth. These soil types do not differ significantly from one another in terms of soil texture (Dooley, 1983). Nevertheless, the soils may differ in moisture content, at least seasonally, partially as a result of topographic differences. The mesic end of the gradient is represented by north-facing slopes and loamy drainageway soils. This latter group would presumably experience more mesic conditions in spring and early summer, especially when Refuge streams are flowing.

For Refuge forests, stand ordinations differed for trees and seedlings, suggesting that forest strata may respond differently to environmental gradients. Kennedy (1973) and del Moral and Watson (1978) have reported differential response of forest strata to environmental variables. Presumably, seedlings are more sensitive to variations in environmental conditions than are trees. It is not surprising then, that the correlation of loamy drainageway soils with high diversity stands is better for the seedling size class. On these sites, *U. americana, C. reticulata,* and *B. lanuginosa* flourish in the seedling layer. With the exception of *U. americana* in one stand, these species are never important components of the overstory. The inability of these species to reach the overstory may be a consequence of poorer drought tolerance, grazing and trampling pressures, or fire.

The forests of the Wichita Mountains Wildlife Refuge represent a western outpost of the eastern deciduous forest. The low diversity of the Refuge forests results from the inability of many tree species to tolerate the less than optimal environments of southwestern Oklahoma. Only *Q. stellata, Q. marilandica,* and, to a lesser extent, *J. virginiana* exhibit widespread importance. In some areas, however, the interaction of topographic variables has produced more mesic conditions in which species characteristic of eastern forests may achieve importance. Evidence from the seedling-sapling layer and age distribution data (Dooley, 1983) suggests that the composition of several mesophytic stands may gradually be shifting to a vegetation type more characteristic of drier, western Oklahoma conditions.

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