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DESCRIPTION AND DYNAMICS OF SOME WESTERN OAK FORESTS IN OKLAHOMA

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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

DESCRIPTION AND DYNAMICS OF SOME WESTERN OAK FORESTS IN OKLAHOMA

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

By

KAREN DOOLEY

Norman, Oklahoma

1983

DESCRIPTION AND DYNAMICS OF SOME

WESTERN OAK FORESTS IN OKLAHOMA

A DISSERTATION

APPROVED FOR THE DEPARTMENT OF BOTANY AND MICROBIOLOGY

By

PREFACE

This study examines western oak forests of the Wichita Mountains Wildlife Refuge, located in southwestern Oklahoma. The dissertation has been written in manuscript form for publication. Chapter I, "Ordination and classification of western oak forests in Oklahoma," will be submitted to the American Journal of Botany. Chapter II, "Dynamics of western oak forests in Oklahoma," will be submitted to the Journal of Ecology.

I would like to thank my major professors, Dr. Paul Risser and Dr. Linda Wallace for their support and guidance throughout my doctoral program. The other members of my committee, Dr. James Estes, Dr. Gordon Uno, Dr. Forrest Johnson and Dr. Frank Sonleitner, provided many helpful comments. I am especially indebted to Dr. Scott Collins for his advice, encouragement and analytical expertise.

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ORDINATION AND CLASSIFICATION OF WESTERN OAK FORESTS IN OKLAHOMA

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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. Cluster analysis based on species composition of the tree size class produced 3 general community types: (1) stands codominated by *Quercus stellata* and *Q. marilandica*, (2) stands dominated by *Q. stellata* and (3) mesophytic forests. A polar-reciprocal averaging ordination (PO-RA) produced a gradient of vegetation that corresponded to a moisture gradient. Many of the high diversity forests were located on loamy drainageway soils or north facing slopes. Tree species diversity (H') was inversely related to the importance of *Q. stellata*. Cluster analysis based on species composition of the seedling size class produced 4 general seedling community types: (1) stands dominated by *Q. marilandica*, (2) stands codominated by *Q. marilandica*, *Q. stellata* and *Juniperus virginiana*, (3) high diversity stands dominated by *Ulmus americana*, *Celtis reticulata* and *Bumelia lanuginosa* and (4) stands dominated by *Acer saccharum*. 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 a differential response to the moisture gradient.

INTRODUCTION

In Oklahoma, the eastern deciduous forest reaches its western limit in the central portion of the state where it takes the form of oak forest and oak savannah. West of this area, woody vegetation is chiefly confined to streambeds. Forests also occur in sandstone canyons of Caddo County and in the Wichita Mountains of Comanche County. 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).

The Wichita Mountains Wildlife Refuge covers approximately 24,000 hectares in southwestern Oklahoma. Established as a forest reserve in 1901, the area became part of the National Wildlife Refuge System in 1935 for the purpose of preserving and maintaining populations of buffalo, longhorn cattle, deer and elk.

The vegetation of the Refuge is a mosaic of grasslands and forests with the forests primarily found along streambeds, in protected valleys and on mountain slopes. 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 being of 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.

Ordination and classification methods represent an improvement on vegetation descriptions based on leading dominants. Multivariate analysis performed on a data base of all species is a useful tool in examining relationships between vegetation and environment. Ordination and classification have been used in descriptions of other Oklahoma forests (Risser and Rice 1971b, Collins *et al*. 1981). No attempt has been made to use these techniques on the forests of the Wichita Mountains Wildlife Refuge. The 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.

THE STUDY AREA

The Wichita Mountains are located in southwestern Oklahoma (approximately 98° 43' W longitude, 34° 44' N latitude). The range covers about 96.5 km 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. The Wichita Mountains Wildlife Refuge encompasses the eastern and central portions of the range. Mount Scott, located at the eastern edge of the Refuge, is the highest peak, with an elevation of 756 m and a base to peak height of 340 m. 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 approximately 200. The average yearly precipitation totals 731 mm with about half occurring from April through July (NOAA 1980).

METHODS

The 46 forest stands used in this study had previously been examined by Buck (1964). He selected undisturbed sites that represented five geologic formations, four soil types and various slope exposures.

In each stand, I determined the composition of the tree size class by use of 20 randomly placed 0.01 ha circular quadrats (in a few 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) were censused in a 0.004 ha circular quadrat centered within each larger quadrat. Importance percentages for trees were calculated as ½ the sum of relative density and relative basal area. Relative density was used as a measure of seedling importance.

Stand relationships were determined using an unweighted pair group cluster analysis (UPGMA, Sneath and Sokal, 1973) derived from a distance matrix of unstandardized importance percent data. The analysis was accomplished using NT-SYS (Rohlf, Kishpaugh and Kirk 1974).

Community gradients were analyzed by polar ordination (PO, Bray and Curtis 1957), reciprocal averaging (RA, Hill 1973) and detrended correspondence analysis (Hill and Gauch 1980). All ordinations were conducted on importance percentage data which had been subjected to log 10 transformation, a treatment which reduces dominance effects and improves normality (del Moral and Watson 1978). Because of the small number of species (19 tree, 23 seedling), all species were included. 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 an RA ordination were used as end stands for the first PO axis. This combined PO-RA ordination has been used successfully on bottomland forests in Oklahoma (Collins et al. 1981). The PO-RA ordination gave the most interpretable results, corresponded well with the cluster analysis and is the only one presented here (van der Maarl 1980).

Diversity was measured by the Shannon-Weiner formula: $H' = -\sum_{i=1}^{S} pi \ln pi$ where s is the number of species and pi is the proportion of the total number of individuals consisting of the ith species. Evenness was calculated as: $J' = H'/H_{max}$, $H_{max} = \ln S$.

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 illinoinensis, 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.

Three general groups of stands were defined by the cluster analysis (cophenetic correlation coefficient, r = 0.9). The first type consisted of low diversity forests that were codominated by Q. stellata and Q. marilandica. These species had a combined importance of 60 to 99% in this group. 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. Juniperus virginiana was important in stands 21 through 26, with an average importance of 20%. The third type was an artificial cluster of nine stands that differed from type 1 and 2 stands by the presence of mesophytic species. Quercus stellata shared dominance with J. rupestris in stands 10 and 42 with Q. shumardii in stand 32 and was less important in the remaining stands. Stands 14 and 35 were similar in the abundance of J. virginiana, but A. saccharum and Q.

shumardii were important in the former while C. illinoinensis and U. americana were important in the latter. Juniperus virginiana was also important in stand 27 where it shared dominance with Q. stellata and Q. muehlenbergii. Juglans rupestris was common in stands 17, 45, and 22 and shared dominance with D. virginiana and C. illinoinensis in stand 17, with U. americana in stand 45, and with A. saccharum in stand 22. Stand 22 differed from all others by the absence of Q. stellata. Three community types can therefore by defined, (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. 2), as would be expected, the mesophytic forests did not group together. Stands of this group defined both axes and thus 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 was negatively correlated with species diversity ($r = -0.53$, $p < 0.01$). 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 forests, members of the artificial group, occur on loamy drainageway soils (Fig. 3). This relationship was not reciprocal, however, as this soil type also supports low diversity, Q. stellata dominated forests.

In order to clarify the 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. 4). The 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 of the second type were Q. stellata, Q. marilandica and Juniperus virginiana. Three subtypes were evident. 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 important seedling in stands 9 through 16. In the third seedling type, the seedling size class was dominated by C. reticulata, U. americana, and B. lanuginosa. 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 seedling. Acer saccharum was the dominant seedling in the fourth type. Therefore the four seedling types were: (1) Q. marilandica, (2) Q. stellata- Q. marilandica-J. virginiana, (3) U. americana-C. reticulata-B. lanuginosa and (4) A. saccharum.

In forests where the seedling layer was dominated by Q. marilandica, Q. stellata and Q. marilandica were the dominant trees (Fig. 4).

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 a PO-RA ordination (Fig. 5). 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 on the ordination. The secondary importance of U. americana, C. reticulata and B. lanuginosa in type 2 forests resulted in the overlap of type 2 and 3 forests. Unlike the tree ordination, the first axis of the PO-RA seedling ordination was not significantly correlated with the importance of post oak seedlings ($r = -0.14$, $p = 0.36$).

Seedling strata that were 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 ($r = 0.49$, $p < 0.01$) and between evenness and the first axis ($r = 0.4$, $p < 0.01$). 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 better than was the case for trees (Fig. 6). The most diverse seedling type, dominated by C. reticulata, U. americana and B. lanuginosa, occurred almost exclusively on loamy drainageway soils. With few exceptions, these 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 coefficient, r = 0.12). Stands that were similar in terms of tree layer composition may not have had similar seedling layers. When each stands' first axis coordinate from the seedling ordination was compared with that from the tree ordination (Fig. 7), a reordering of stands was apparent. The reordering was partly a result of the scattering of the artificial group of 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 forests had seedling layers dominated by Q. stellata, Q. marilandica and J. virginiana, while those located on loamy drainageways 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 are representative of several Oklahoma forest types. The most numerous forests of 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 of precipitation annually, and presumably were more savannah like prior to the advent of heavy grazing and fire suppression. 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 forests, such as *Celtis* spp., *Ulmus americana*, *Bumelia lanuginosa*, *Carya illinoinensis* and *Quercus macrocarpa* (Bruner 1931, F. Johnson, personal communication). Many of the mesophytic forests have components that are typically found in eastern Oklahoma. The most notable example is the presence of *Acer saccharum* in some Refuge forests. The continuous range of *A. saccharum* extends westward as far as the eastern counties of Oklahoma (Fowells 1965). Disjunct populations are located in sandstone canyons of Caddo and Canadian Counties, Oklahoma (Little 1939, Rice 1960) and on some north facing slopes of the Wichita Mountains. The Wichita populations have been identified by some as

A. grandidentatum (Eskew 1938, Little 1944) and by others as A. saccharum (Buck 1964, Dent 1969). 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 Wichita Mountains (Little 1976). Thus the forests containing A. saccharum are not equivalent to those in eastern Oklahoma. Other species not usually found in southwestern Oklahoma are Q. shumardii, Q. muehlenbergii and Diospyros virginiana.

The forests of the Wichita Mountains Wildlife Refuge are characteristically of low diversity and richness. Risser and Rice (1971a) reported an average Shannon-Weiner Index of 0.8 and a total of 12 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, personal communication). 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 layer diversities are greater than those of the tree layers in Refuge forests, as is true for other forests in Oklahoma (F. Johnson, personal communication) and elsewhere (Adams and Anderson 1980).

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. It has been reported that Q. marilandica is the more xeric of the two (Bruner 1931, Johnson and Risser 1972). The occurrence of Q. marilandica on xeric sites may not result from greater drought tolerance, however. 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 comprise a variety of mesic conditions: north facing slopes dominated by A. saccharum, stream bordering forests in which U. americana, J. rupestris and Carya illinoinensis are important, and protected valleys and canyons where Q. shumardii and Q. muehlenbergii are prominent.

The gradient of seedling composition may be interpreted similarly. The Q. marilandica seedling type occupies the xeric end of the gradient. Three stands in this group had been burned prior to sampling as part of the Refuge's prescribed burning program. The average Q. marilandica seedling density in these forests was 308 stems/ha as compared to 234 stems/ha in the unburned members 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, C. reticulata and B. lanuginosa on loamy drainageway soils.

The basis for the implied moisture gradient is probably not edaphic. Lawton loam, granite cobbly land and loamy drainageway soils are generally deep, while the stony rock land soils are variable in depth. The soil types do not differ significantly from one another in terms of soil texture. Since water holding capacity is a function of soil texture, these soils are most likely similar in their potential water holding capacity. Nevertheless, the soils may differ in moisture content, at least seasonally, 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 when the 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 indicators of variation 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, the interaction of topographic variables has produced more mesic conditions where other species achieve importance, if only in the seedling layer.

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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	AVE IP	TREES	CONSTANCY	MAX IP	AVE 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 illinoinensis	9	19	12				

Table 1. Continued.

SEEDLINGS	CONSTANCY	MAX RD	AVE RD	SEEDLINGS	CONSTANCY	MAX RD	AVE 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 triancanthos	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 illinoinensis	9	4	2	Viburnum prunifolium	2	<1	<1
Q. muehlenbergii	9	3	2	Cercis canadensis	2	10	10
Q. shumardii	9	36	16				

Figure 1. An unweighted pair group cluster analysis of the 46 stands based upon tree species importance percentages. Euclidean distance was used as a measure of similarity.

TREES

Figure 2a. A PO-RA ordination of the tree composition of the 46 stands. Stands are represented by the tree community type defined by cluster analysis. 1 = *Quercus stellata-Q. marilandica*, 2 = *Q. stellata*, 3 = mesophytic forests.

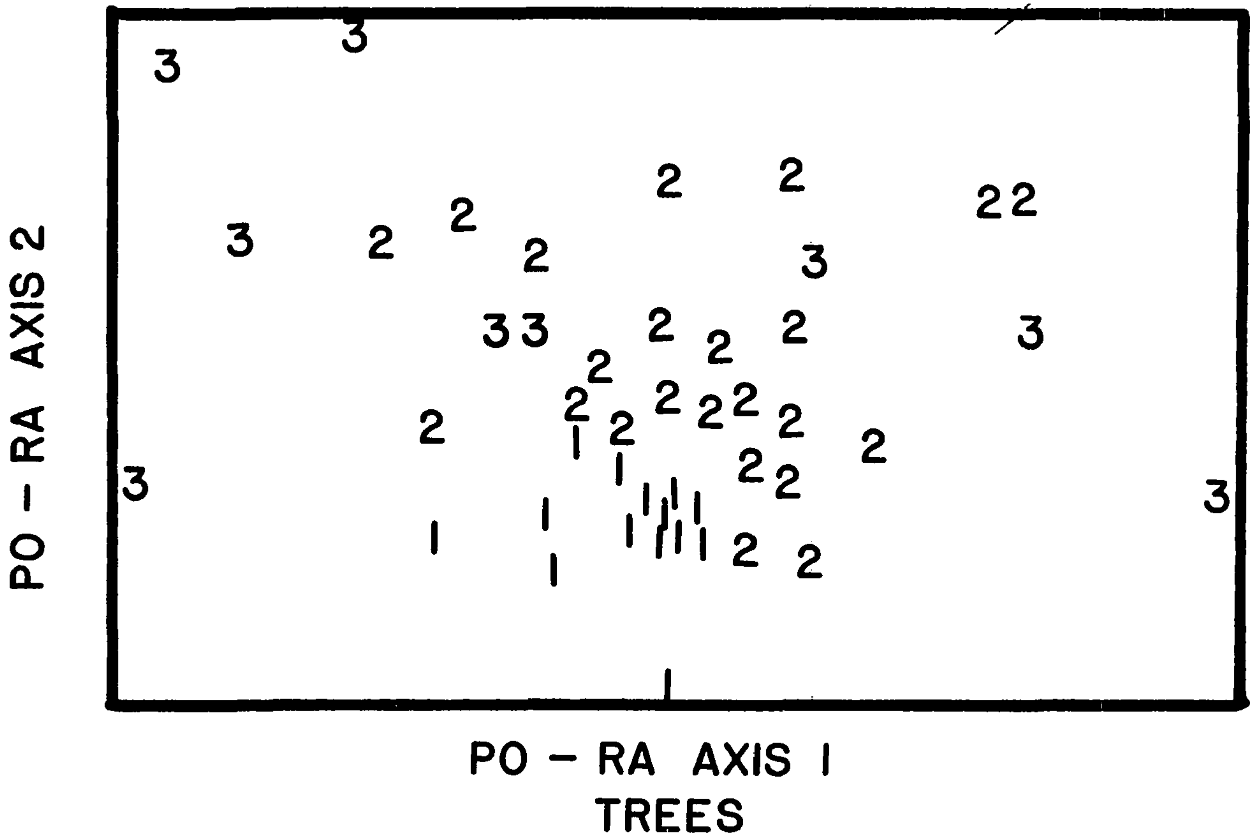

PO – RA AXIS 2
PO – RA AXIS I
TREES

Figure 2b. A PO-RA ordination of tree composition of the 46 stands with stands represented by soil type.

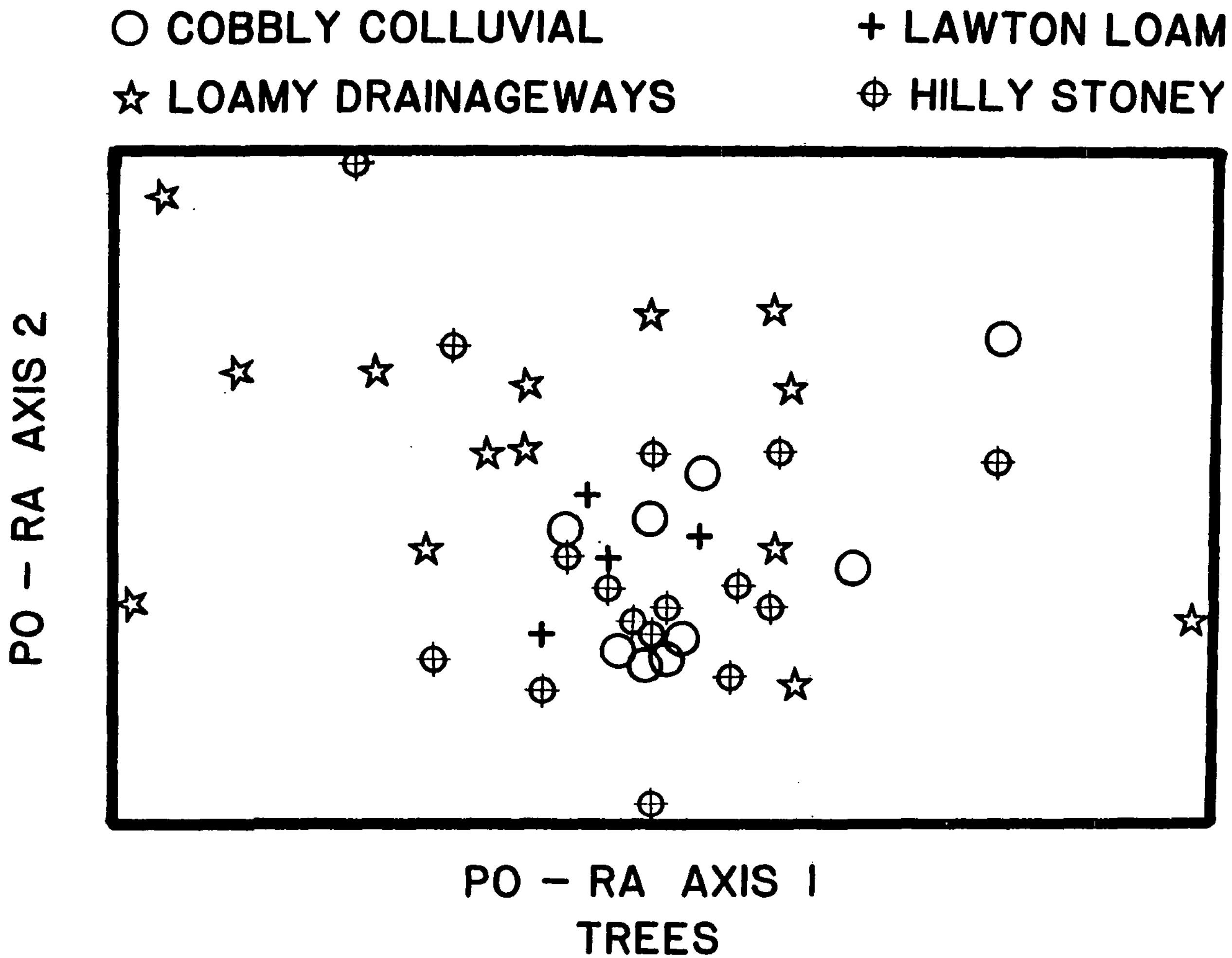
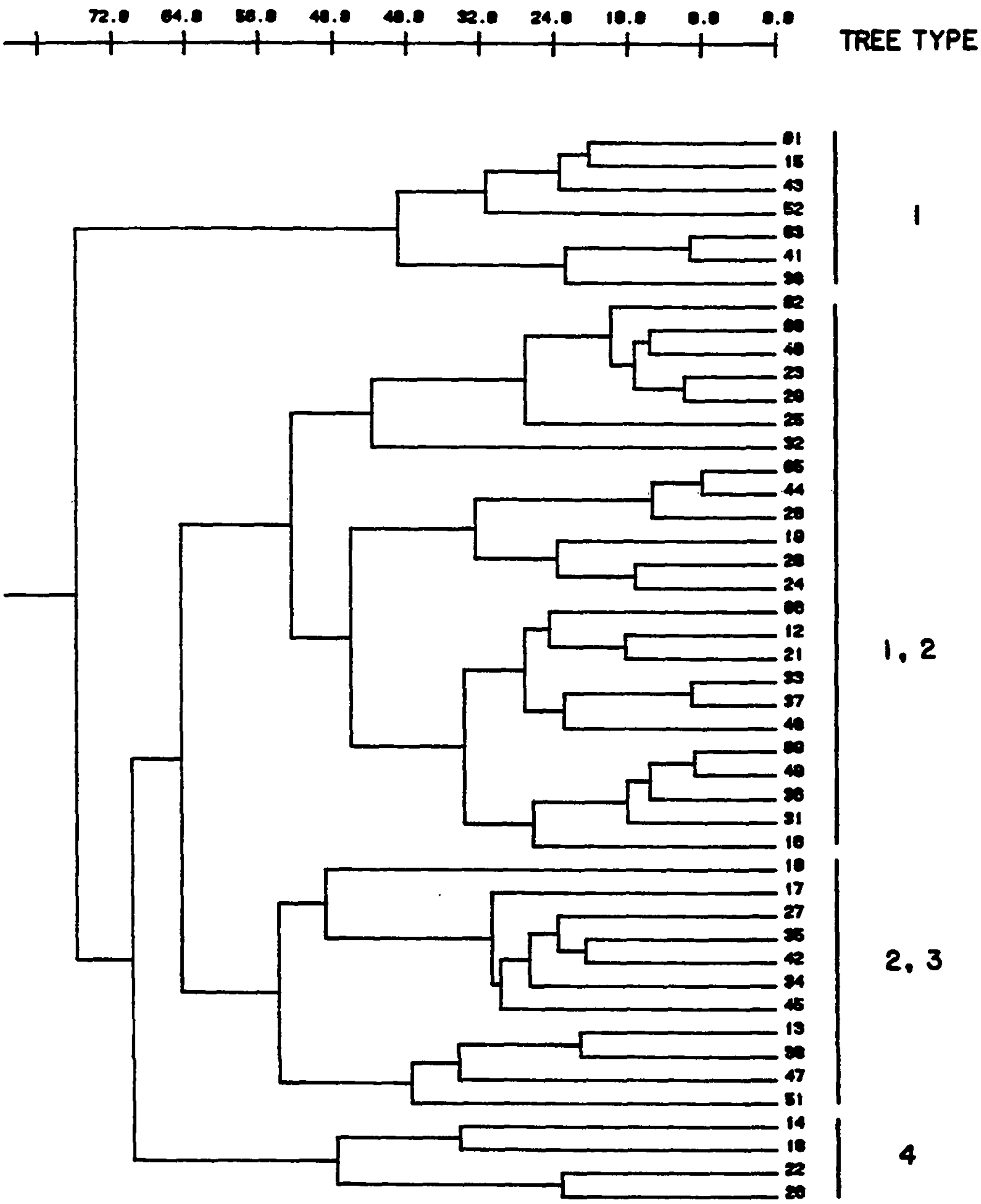
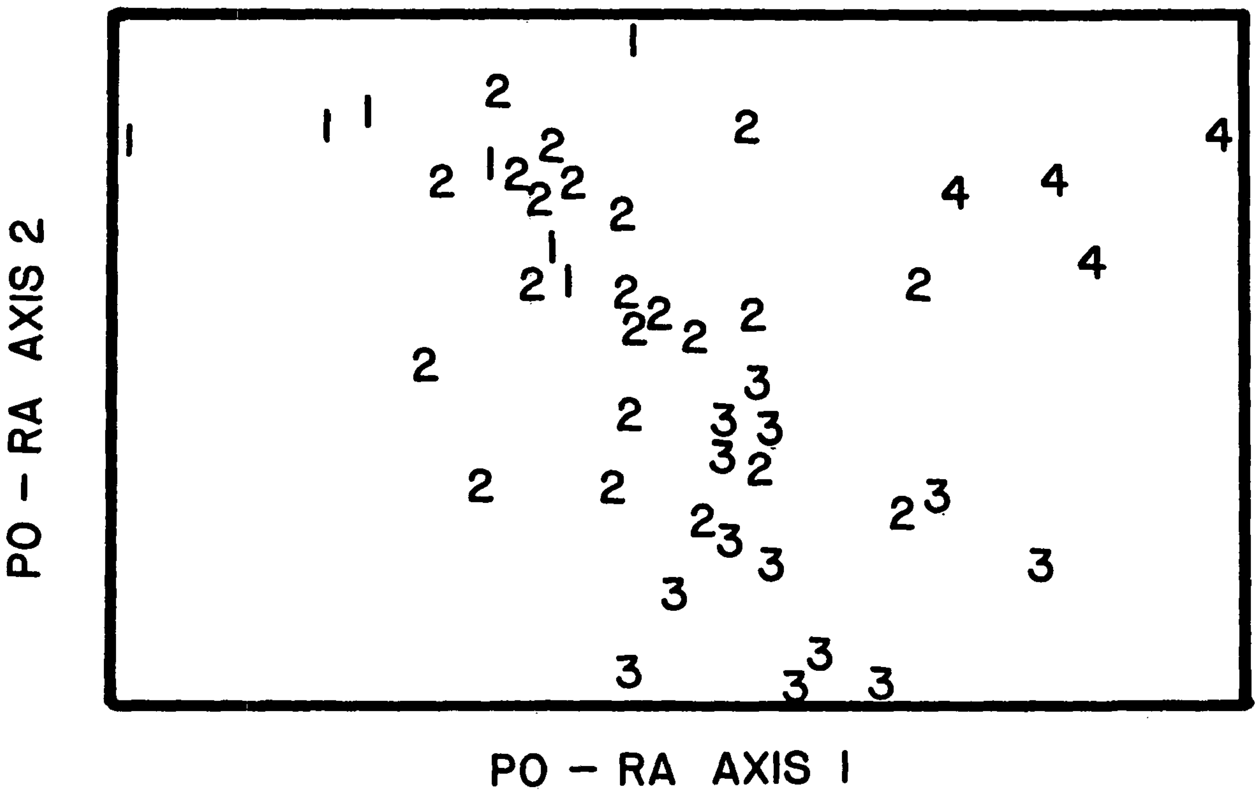

○ COBBLY COLLUVIAL
+ LAWTON LOAM
☆ LOAMY DRAINAGEWAYS
⊕ HILLY STONEY
PO – RA AXIS 2
PO – RA AXIS I
TREES

Figure 3. An unweighted pair group cluster analysis of the 46 stands based upon seedling species importance. Euclidean distance was used as a measure of similarity.



SEEDLINGS

Figure 4. A PO-RA ordination of seedling composition of the 46 stands. Stands are represented by the seedling community types defined by cluster analysis. 1 = *Quercus marilandica*, 2 = *Q. stellata-Q. marilandica-Juniperus virginiana*, 3 = *Ulmus americana-Celtis reticulata-Bumelia lanuginosa*, 4 = *Acer saccharum*.



SEEDLINGS

Figure 5. A PO-RA ordination of the seedling composition of the 46 stands represented by soil type.

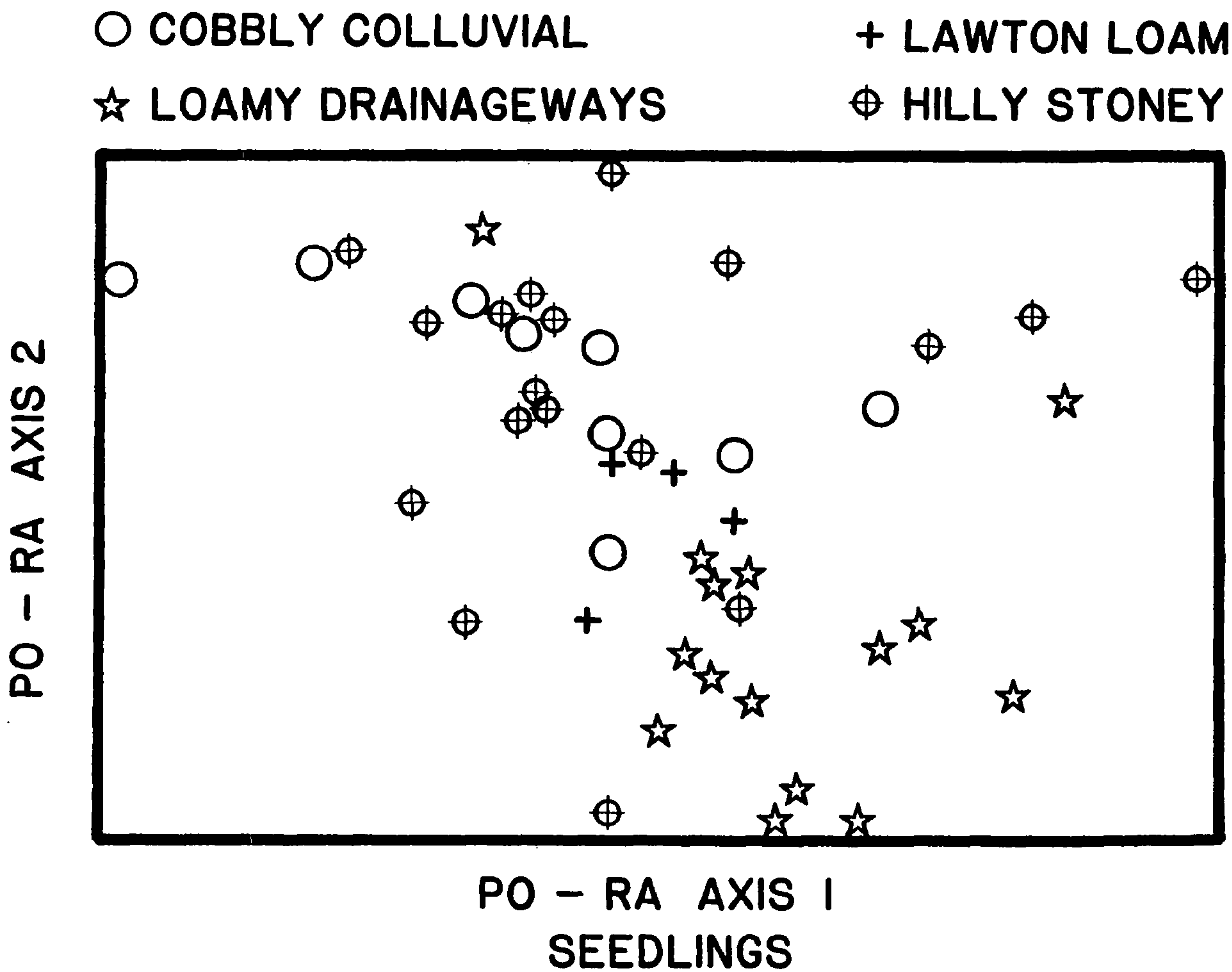
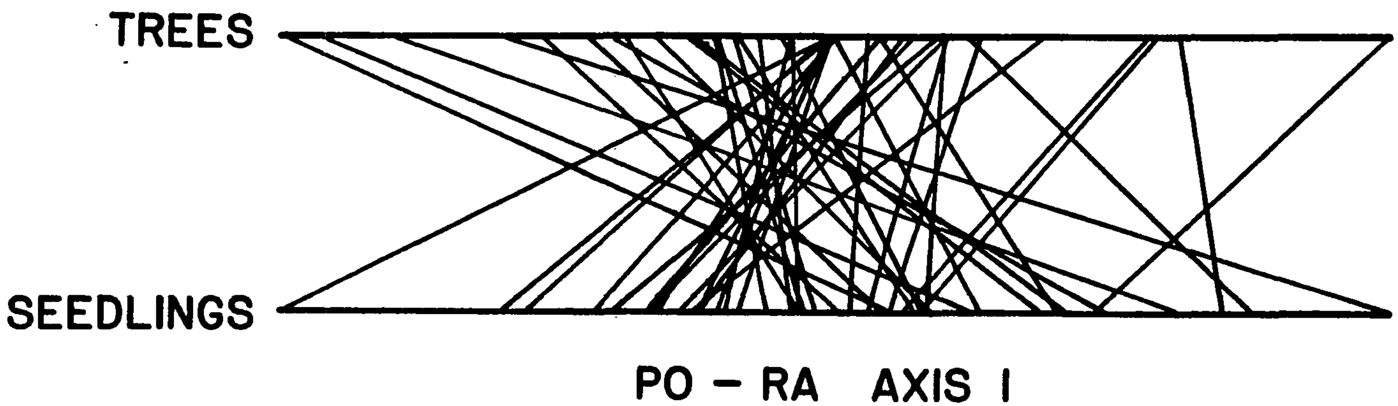

COBBLY COLLUVIAL
LAWTON LOAM
LOAMY DRAINAGEWAYS
HILLY STONEY
PO - RA AXIS 2
PO - RA AXIS I
SEEDLINGS

Figure 6. Comparison of stand position on the first axis of the seedling PO-RA ordination with position on the first axis of the tree PO-RA ordination.


TREES
SEEDLINGS
PO – RA AXIS I

CHAPTER II

DYNAMICS OF WESTERN OAK FORESTS IN OKLAHOMA

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ABSTRACT

Of forty three forest stands in the Wichita Mountains Wildlife Refuge that had been surveyed in 1961, twenty seven stands had the same relative species composition and nine had only slight changes twenty years later. Seven stands, mostly mesic, differed with respect to minor species. The stands that showed the least changes were the least diverse. On the whole, Refuge forests were less diverse in 1981. *Quercus stellata*, the most important tree in Refuge forests, ranged in age from 32 to 270 years with most individuals being between 60 and 80 years old. These ages coincide with the establishment of the Refuge and probably indicate the conversion of savannahs to forests. Size is a poor predictor of age for *Q. stellata* trees in Refuge forests, especially for small trees. Twelve stands had nonsignificant regressions of basal area on age. Size differences in these forests must result from differential growth rates.

INTRODUCTION

Much attention has been devoted to the dynamics of seral communities. Analyses of previously surveyed plant communities have provided important information on the nature of secondary succession. An examination of 19 year changes in a *Pinus taeda* stand in eastern Maryland revealed a strong successional trend to hardwoods (Little and Escheman 1976). Analyses of permanent plots permitted calculation of transition probabilities and analysis of Markovian properties of forest succession (Waggoner and Stephens 1970), and demonstrated that pattern of overstory trees changed from random to regular, total species diversity (H') decreased, and pattern diversity (Dp) increased during climax forest maturation in the North Carolina Piedmont (Christensen 1977). Peet and Christensen (1980) showed that for forests of the North Carolina Piedmont, mortality was a driving force of change in some stages of forest development while establishment was more important in a hurricane disturbed forest.

Comparatively few such analyses have been conducted for mature forests. A study of ten year changes in an old growth beech-maple forest in Indiana revealed only slight changes in importance of the leading tree species but differential mortality among species and size classes (Abrell and Jackson 1977). Analyses of 20 year differences of a permanent forest plot in southern Indiana suggested a gradual change of forest type from mixed mesophytic to beech-maple (Schmelz *et al*. 1975). Examination of short term changes such as these has proven useful in predicting long term community dynamics.

An alternative approach in investigating the long term dynamics of plant communities involves an examination of age and size class structures of component tree populations. Nicholson *et al*. (1979) predicted long term increases in hemlock in some Adirondack forests based on sapling:tree ratios. Successional trends were predicted by age class analysis for virgin spruce-fir and hardwood forests (Leak 1975) and by size association analysis for Wisconsin forests (Zedler and Goff 1973) and Ohio fen vegetation (Collins *et al*. 1979).

This paper examines the dynamics of oak forests of the Wichita Mountains Wildlife Refuge with two objectives: (1) to assess short term changes by reexamining forests that were previously surveyed in 1961 by Buck (1964) and (2) to assess the long term dynamics of the most important tree species, *Quercus stellata*, through use of age and size class analyses.

THE STUDY AREA

The Wichita Mountains are located in Comanche County, southwestern Oklahoma (approximately 98° 43' W longitude, 34° 44' N latitude). The range covers about 96.5 km 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. The Wichita Mountains Wildlife Refuge is located on the eastern and central portions of the range. Mount Scott, located at the eastern edge of the Refuge, is the highest peak, with an elevation of 756 m and a base to peak height of 344 m. 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 lands presently encompassed by the Wichita Mountains Wildlife Refuge were part of the Kiowa-Comanche Territory. When the area was opened for settlement in 1901, a portion was set aside as the Wichita Forest Reserve. The area became part of the Wildlife Refuge system in 1935 with the purpose of preserving and maintaining populations of buffalo, longhorn cattle, deer and elk.

The vegetation of the Refuge is a mosaic of grasslands and forests with the latter occurring along streambeds, on mountain slopes and in protected valleys. The forests, described in more detail elsewhere

(Dooley 1983), are dominated chiefly by Quercus stellata (post oak), Q. marilandica (blackjack oak) and Juniperus virginiana (eastern red cedar). Mesophytic forests occupy some protected valleys, north facing slopes and areas bordering streambeds. Important species in these forests include Acer saccharum (sugar maple), Q. shumardii (Shumard's oak), Q. muehlenbergii (chinkapin oak), Juglans rupestris (western walnut) and Ulmus americana (American elm).

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 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 approximately 200. The average yearly precipitation totals 731 mm with about half occurring in the months of April through July (NOAA 1981).

METHODS

In 1961, Buck (1964) surveyed 52 forest stands in the Refuge to examine relationships between the woody vegetation, soil type and geologic formation. He selected disturbed sites that represented five geologic formations, four soil types and various slope exposures. He determined stand composition by use of the augmented variable radius method (Rice and Penfound 1955).

I resampled forty three of these forests in 1981. In each stand, composition of the tree size class was determined by use of 20 randomly placed 0.01 ha circular quadrats (in a few 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 $\leq$ 2.5 cm) and saplings (2.5 cm $<$ dbh $<$ 10 cm) were censused in a 0.004 hectare circular quadrat centered in each larger quadrat. Importance percentages for trees were calculated as $\frac{1}{2}$ the sum of relative density and relative basal area. Relative density was used as a measure of seedling and sapling importance.

Community gradients were analysed by polar ordination (Bray and Curtis 1957). The ordinations were conducted on importance percentage data which were subjected to log 10 transformation, a treatment which reduces dominance effects and improves normality (del Moral and Watson 1978). Because of the small number of species (21 in 1961, 19 in 1981), rare species were included. Percentage similarity was used as a measure of distance. The ordinations were produced by Cornell Ecology Program CEP-25 (Gauch 1977).

The relative species composition of each stand was compared to its 1961 state by calculating a percentage similarity (PS, Whittaker 1975: 152). To account for sampling error stands that had a PS of 80 or greater were interpreted as unchanged (Curtis 1959: 76).

Diversity was estimated by exp(H') and Simpson's index. The index exp(H'), more interpretable than the Shannon-Weiner index, is sensitive to changes in rare species while Simpson's index is more sensitive to changes in common species (Peet 1974). Evenness was estimated by a modified Hill's ratio (Alatlo 1981).

Quercus stellata is the most important tree species in the Refuge forests (Buck 1964, Dooley 1983). This species occurred in all but one of the stands studied by Buck (1964) and ranged in relative importance from 6 to 95 percent. In order to assess the long term dynamics of this species, 20 stands were selected for age structure analysis. I selected stands that covered the range of *Q. stellata* importance and site conditions. In each stand, 10 *Q. stellata* individuals that represented the range of tree sizes for the species in the stand were bored to determine age based on tree ring analysis. Relationships between age and tree size were determined by regression analysis.

To examine further *Q. stellata* population structure, the size distributions of *Q. stellata* in 40 refuge forests were examined by regression analysis. Polynomial equations from linear to third degree were derived for the density-basal area and log of density-basal area distributions. The polynomial of lowest degree that had an alpha value of 0.05 or less was chosen as the best equation (Goff and West 1975).

RESULTS

Twenty Year Changes

I found 27 of the 43 stands to have PS of 80 or greater (Table 1). Nine stands showed slight differences, primarily as a result of reciprocal changes in the relative importance of *Quercus stellata*, *Q. marilandica* and *Juniperus virginiana*. Changes in the relative importance of minor species resulted in greater differences in the relative species composition of 7 stands. In general, these changes did not follow predictable trends. For example, *Q. muehlenbergii* increased in one forest and decreased in another as did *Ulmus americana*. However, *Juglans rupestris* decreased in relative importance in five forests. Percentage similarity was negatively correlated with 1961 species diversity, as measured by the Shannon-Weiner Index ($r = -0.5$, $p < 0.01$, $n = 43$). The least diverse forests showed the smallest differences in relative species composition.

Quercus stellata showed decreased basal area by more than 20% in 4 stands and so tree density must have decreased as well. *Quercus stellata* basal area remained approximately the same in 15 stands and increased by more than 20% in 21 stands. In the latter group, *Q. stellata* tree density most likely did not change. None of the *Q. stellata* trees were younger than 32 years. Thus, density of *Q. stellata* trees could only have decreased or remained the same. In forests where basal area did not change, either tree density decreased or remained the same. If density remained the same, individuals of Q. stellata grew at a slower rate than those in forests that showed an increase in basal area. An estimate of overall growth rate was calculated as basal area/age. Growth rates of trees in forests that increased basal area did not differ significantly from those in forests that showed no change in basal area (mean growth rates: 5.1 sq. cm/year, n = 102, 4.3 sq. cm/year, n = 45, respectively).

Quercus marilandica basal area decreased by more than 20% in 11 stands, remained the same in 13 and increased by more than 20% in 7 stands. In central Oklahoma, Q. stellata and Q. marilandica have comparable growth rates (Johnson and Risser 1973). Thus, corresponding density changes may be interpreted as for Q. stellata, with density remaining unchanged in the latter two groups.

Species diversity (exp(H')) and richness of the Refuge forests have decreased significantly since 1961 (Table 2). Much of the decrease may be attributed to the reduction of minor species relative importance, since exp(H') is sensitive to changes in rare species (Peet 1974). Simpson's index, more sensitive to differences in common species, was unchanged. Also, evenness did not differ.

Comparison of stand order on the first axis of a polar ordination for 1961 with 1981 (Figure 1) revealed that stands have become more similar, indicating that there has been a decrease in beta diversity. Both the 1961 and 1981 ordinations separated stands along the first axis by the degree of Q. stellata dominance. On the 1981 ordination, stands strongly dominated by Q. stellata comprise a large cluster on the first axis. Thus, the decrease in beta diversity is probably attributable to the reduction of minor species importance.

Quercus stellata Age Analysis

Quercus stellata tree ages ranged from 32 to 270 years, with a mean age of 84 years (Fig. 2). Most of the trees occurred in the 50-90 year age classes, with the majority (62%) being between 60 and 80 years old. Regression showed a significant relationship of basal area to age (Fig. 3, r2 = 0.62, p <0.01, n = 176). For small trees the relationship was weaker (trees with basal area $\leq$1290 sq. cm, r2 = 0.35, p <0.01, n = 165; trees with basal area $\leq$645 sq. cm, r2 = 0.28, p <0.01, n = 146). Small trees (basal area $\leq$645 sq. cm) accounted for 76% of the stems in the 20 forests used for age analysis. Thus size is a poor predictor of age of most individuals of *Q. stellata* in the Refuge forests.

Twelve of 20 stands had non-significant regressions of basal area on age. Within these stands, variation in basal area must be attributable to differences in growth rates and site conditions rather than age. Most of these forests occurred on seasonally mesic sites: north facing slopes and loamy drainageway soils. With two exceptions, forests that had significant regressions of basal area on age were located on other soils and locations.

Basal area was significantly correlated with diameter at 20 years of age (r = 0.35, p <0.01, n = 142). This correlation suggests that large trees had greater diameters when young than did trees which did not attain large size.

Size Class Analysis

Of the 40 stands, 28 had *Q. stellata* size class distributions that fit the negative exponential equation (Fig. 4). The size class distributions in 2 stands were best described by a linear regression of density on basal area and by a 2nd degree polynomial in 2 others (Fig. 5). None of the equations fit the size class distributions of *Q. stellata* in 8 stands.

Although seedlings of *Q. stellata* were generally numerous, saplings were scarce. *Quercus stellata* saplings had an average density of 11 stems/ha and were absent in over half the forests (Table 3). Low sapling densities were characteristic of the other species with the exception of *Acer saccharum*.

DISCUSSION

Based on percentage similarity of relative composition, over half the forests of the Wichita Mountains Wildlife Refuge have experienced few changes since Buck's (1964) survey in 1961. Nine stands showed slight changes in the relative abundance of the most important species, *Quercus stellata*, *Q. marilandica* and *Juniperus virginiana*. Only 7 forests showed marked changes, primarily in the importance of minor species. It should be noted, however, that percentage similarity estimates were based on relative values and so may not be indicative of changes in absolute numbers. The minor species were usually not abundant and may have been under or overrepresented in the census as a result of sampling error. Large differences in relative importance, on the other hand, are probably reflective of actual changes. In particular, *Juglans rupestris* exhibited large decreases in several forests. Since it is unlikely that tree densities increased since 1961, reductions in relative importance are probably indicative of actual decreases rather than increases in other species.

With the exception of one stand that had burned, the forests that showed the greatest changes occurred on mesic sites, one on a north facing slope and the rest on loamy drainageway soils. These sites presumably experience greater year to year fluctuations in soil moisture content than do drier sites. As a result, these forests might be more subject to change, particulary among the minor species.

The diminished importance of minor species may be a cyclic trend. Prolonged dry periods, common to southwestern Oklahoma (Risser *et al.* 1981), would presumably favor more xeric species such as *Q. stellata*, *Q. marilandica* and *J. virginiana*. Precipitation totals at least 13 cm below average occurred seven times between 1961 and 1981. Particulary dry years occurred from 1963 to 1967 (NOAA 1981). Alternatively, the reduction in relative importance may be a continuing trend for some species, most notably *J. rupestris*, which approaches the easternmost extension of its range in the Wichita Mountains (Little 1976). Like other species, *J. rupestris* was poorly represented in the sapling size class but was even less abundant in the seedling layer (maximum relative density, 13%, average relative density, 4%).

Dale (1914) described the mountains as being for the most part almost bare of timber with a thin fringe of trees along streams. Blair and Hubbell (1939) described a *Q. stellata*-*Q. marilandica* association of open growth with numerous glades on the lower hills and south facing slopes. It is likely, then, that many of the present-day oak forests of the Wichita Mountains Wildlife Refuge were formerly savannahs.

The majority (80%) of *Q. stellata* trees examined were between 50 and 90 years old, with most of these (83%) aged 60 to 81 years. These ages coincide with the establishment of the Wichita Forest Reserve in 1901. During the early years of the Forest Reserve, grazing by privately owned cattle was permitted. The number of domestic livestock was conservatively estimated at 5,000 from 1906 to 1910 and then decreased until 1937 when grazing leases were cancelled (Halloran and Glass 1959). Like all national forests, fire suppression was an integral part of the early management history of the Refuge (Dana 1956). The combination of intense overgrazing and fire suppression has been credited with the conversion of oak savannah to oak forest in Oklahoma (Rice and Penfound 1959, Johnson and Risser 1975) and in Texas (Dyksterhius 1948).

Density of Q. stellata greatly increased since the creation of the Wichita Forest Reserve. In the future, the forests might not be converted back to savannah, even with the present management policy of controlled burning. Johnson and Risser (1975) found that Q. stellata-Q. marilandica forests in Central Oklahoma are resistant to the effects of fire following canopy colsure.

Analyses of size class distributions provide valuable information on population structure and long term community dynamics when size is a good indicator of age. In a very general context, the size of Q. stellata trees may be used to predict age. Trees that are large (basal area greater than 645 sq. cm) are old (mean age = 134 years, n = 30); small trees are mostly between 60 and 80 years old. Many forests have an age distribution of many young (small) trees and fewer old (large) trees. But eight forests had essentially even distributions of individuals across size classes.

For small trees, size is a poor predictor of age in Q. stellata. In many stands basal area was not significantly related to age. In these forests, differences in size of Q. stellata trees can not be attributed to differences in age and so must result from different growth rates, with large trees growing more rapidly than small trees. The majority of these forests occur on mesic sites, loamy drainageway soils and north facing slopes. Differential growth rates of small and large trees could result from environmental heterogeneity within stands or between years.

Density diameter curves of stable, undisturbed tree populations have been reported to be of a negative exponential form (Meyer 1952). Goff and West (1975) reported that for small stands where overstory-understory interactions are important, density diameter curves are of a rotated sigmoid form. Nearly two thirds of the forests examined had size class distributions that were described by negative exponential equations. None had distributions that fit the rotated sigmoid form.

Differences in size class distributions of Q. stellata could not be attributed to soil type or to xeric or mesic condition. Stands where Q. stellata is important have significantly more individuals in the small size classes. The forests which had a decrease in Q. stellata basal area (and thus in density) had fewer individuals in the small size classes, suggesting that small trees have experienced greater mortality rates than large trees.

An interesting aspect of size distribution of Wichita Mountains tree species is the scarcity of saplings. Sapling densities were low at the time of Buck's (1964) study and have remained low to the present. Low sapling densities may be a consequence of grazing and/or trampling pressures by the buffalo and longhorn cattle, periodic fires, or the "saturation" of the forests following their conversion from savannahs.

In about half the forests, the basal area of Q. stellata increased by more than 20% over the twenty year period. Under steady state conditions, basal area would be expected to remain approximately the same over time. Thus, the Q. stellata-Q. marilandica forests of the Wichita Mountains Wildlife Refuge have not yet reached maturity.

The relationship between biological diversity and community stability has received much attention (MacArthur 1955, Odum 1969 , Goodman 1975). McNaughton (1967) and Mellinger and McNaughton (1975) have reported a positive relationship between species diversity and community stability. In contrast, May (1972) and Pimm (1979) have demonstrated with mathematical models that increasing species diversity may result in decreased stability. Percentage similarity can be used to assess the structural stability of a community through time. For Refuge forests, those with the lowest species diversity experienced the least change and may be interpreted as being the most stable.

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Table 1. Percentage similarity of stands to their relative species composition in 1961.

Stand	PS	Stand	PS
1	89.2	2	74.4
3	84.4	8	74.2
5	93.8	12	75.8
6	84.0	17	70.8
10	85.4	18	72.0
15	89.7	21	70.2
16	83.9	29	77.8
19	87.7	48	74.0
20	88.0	51	79.2
22	89.0		
23	94.8		
24	82.2		
25	82.3	13	66.4
26	82.4	14	52.1
28	86.2	30	34.5
31	89.7	35	61.3
32	83.6	38	64.8
33	98.8	42	58.7
34	87.4	45	56.7
37	93.4		

Table 1. Continued.

Stand	PS	Stand	PS
41	93.8		
43	84.5		
44	85.8		
47	89.0		
49	91.8		
52	87.5		

Table 2. Comparison by paired t-test of mean species diversity indices and evenness for 1961 and 1981.

	exp (H')*	Simpson's+	N	Evenness#
1961	3.07	0.48	6.65	0.70
1981	2.63	0.52	4.48	0.74
t	-2.99	1.72	-6.23	-1.12
pr > |t|	0.01	0.09	0.01	0.27

* exp(H'), H" $-\sum_{i=1}^{S}$ pi lg pi, where S is the number of species and pi is the relative importance of species i.

+ Simpson's Index $=\Sigma[n_i(n_I-1)]/[N(N-1)]$ where n_i is the number of individuals in species L, N is the total sample size.

evenness = $(N_2-1)/(N_1-1)$ where N_2 is 1/Simpson's, N_1 = exp(H').

Table 3. Sapling species present in forests of the Wichita Mountains Wildlife Refuge. Constancy is the percent of stands in which the species occurred as a sapling.

Species	Maximum Density stems/hectare	Average Density stems/hectare	Constancy
Juniperus virginiana	73	14	76%
Quercus marilandica	117	29	50%
Quercus stellata	52	11	45%
Acer saccharum	110	82	11%
Bumelia lanuginosa	16	5	13%
Celtis reticulata	10	5	11%
Carya illinoinensis	4	4	4%
Juglans rupestris	6	6	4%
Ulmus americana	2	2	4%

Figure 1. Comparison of stand order on the first axis of a polar ordination (PO) for 1961 and 1981.

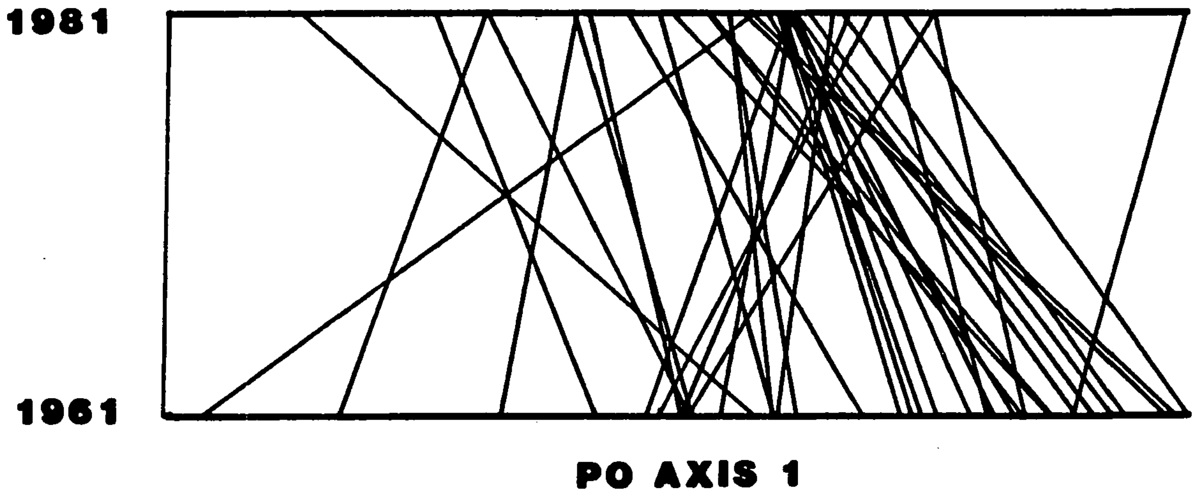

1981
1961
PO AXIS 1

Figure 2. Distribution of age classes for 176 *Quercus stellata* trees. Age classes correspond to 20 year increments (e.g., age class 40 is trees 30 to 59 years of age).

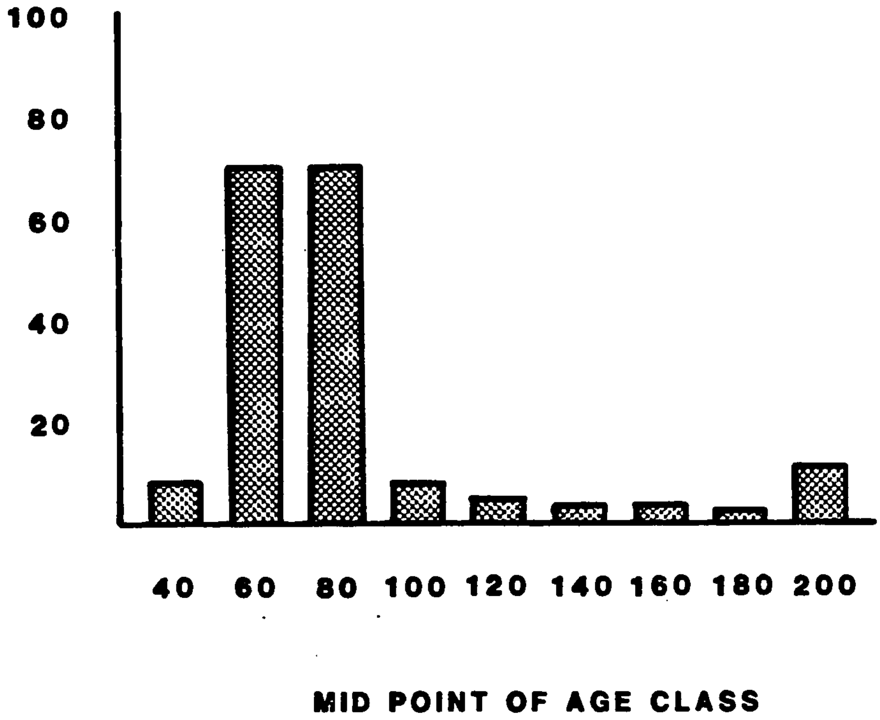

100
80
60
40
20
40 60 80 100 120 140 160 180 200
MID POINT OF AGE CLASS

Figure 3. Regression of basal area on age for 176 _Quercus stellata_ trees.

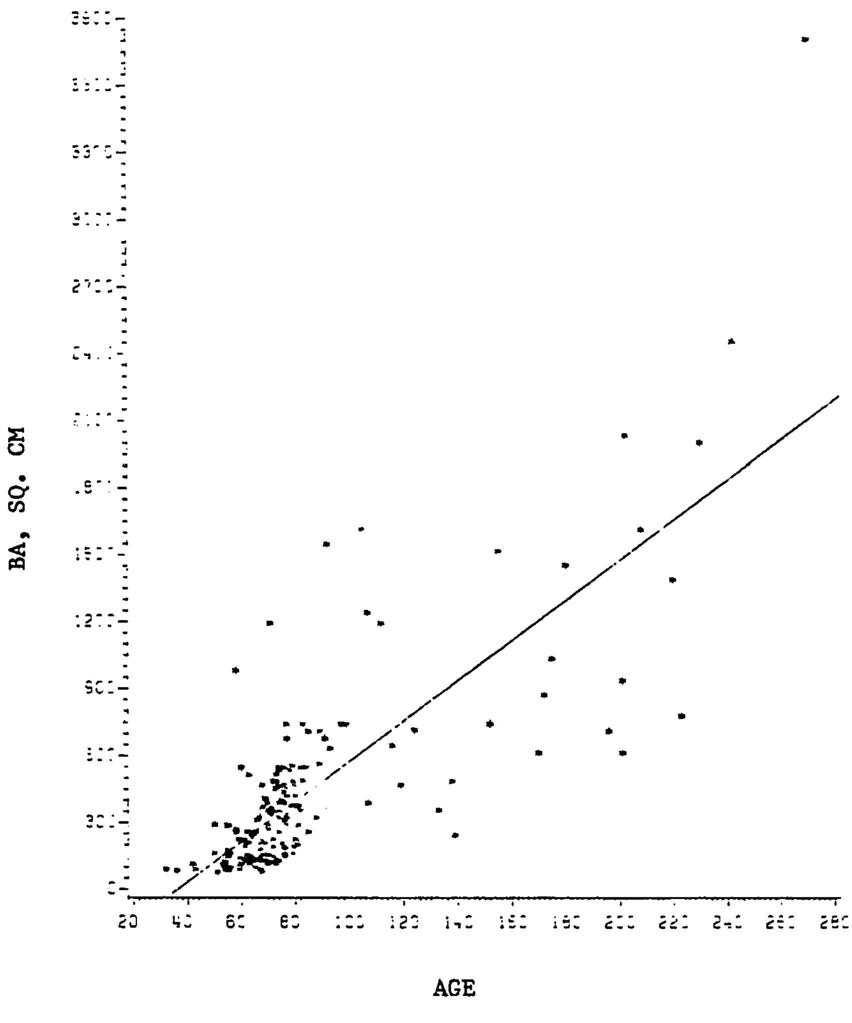

BA, SQ. CM
AGE
20
40
60
80
120
280

Figure 4. Size class distribution of *Quercus stellata* in stand 12. The negative exponential distribution is representative of *Q. stellata* size class structure of 28 Refuge forests.

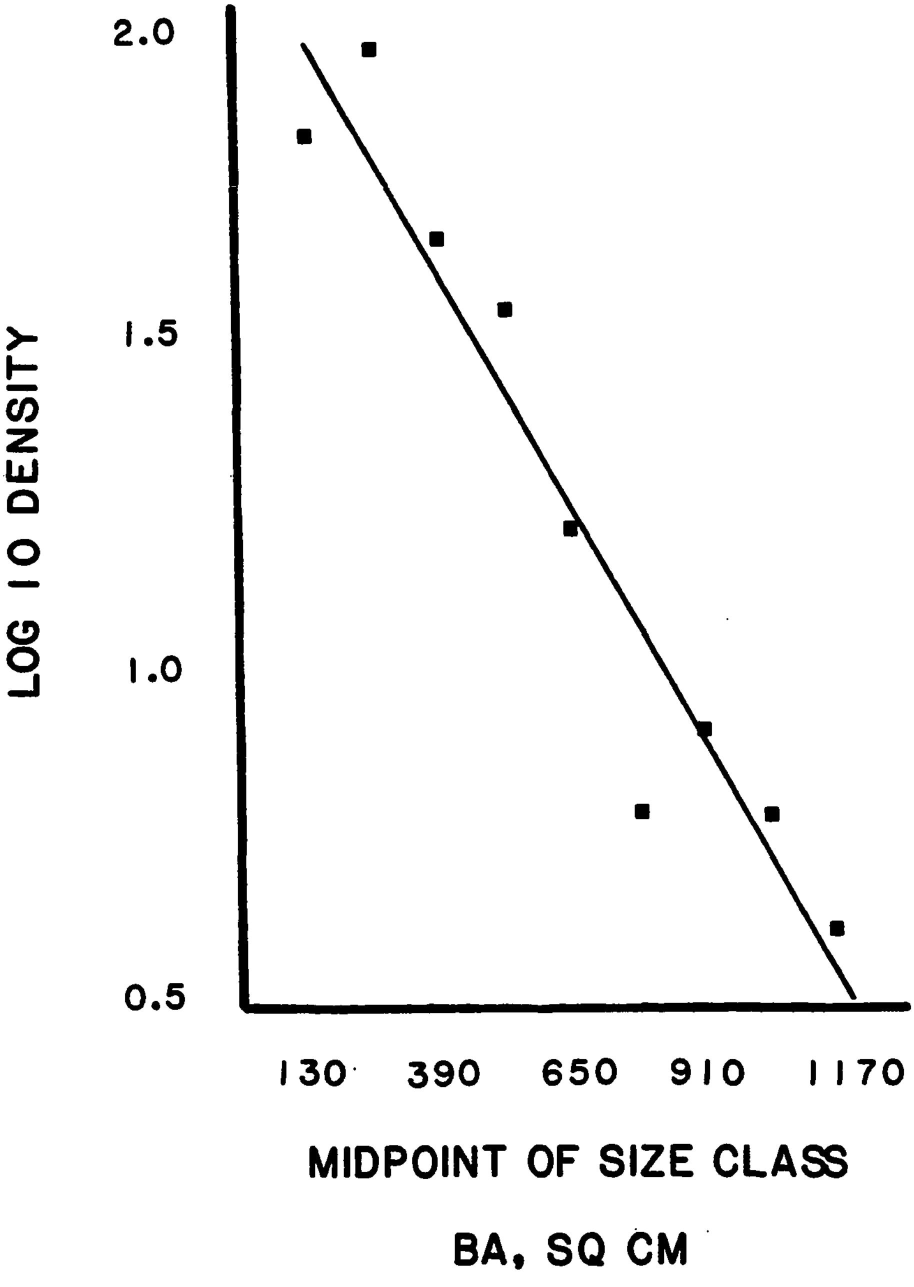
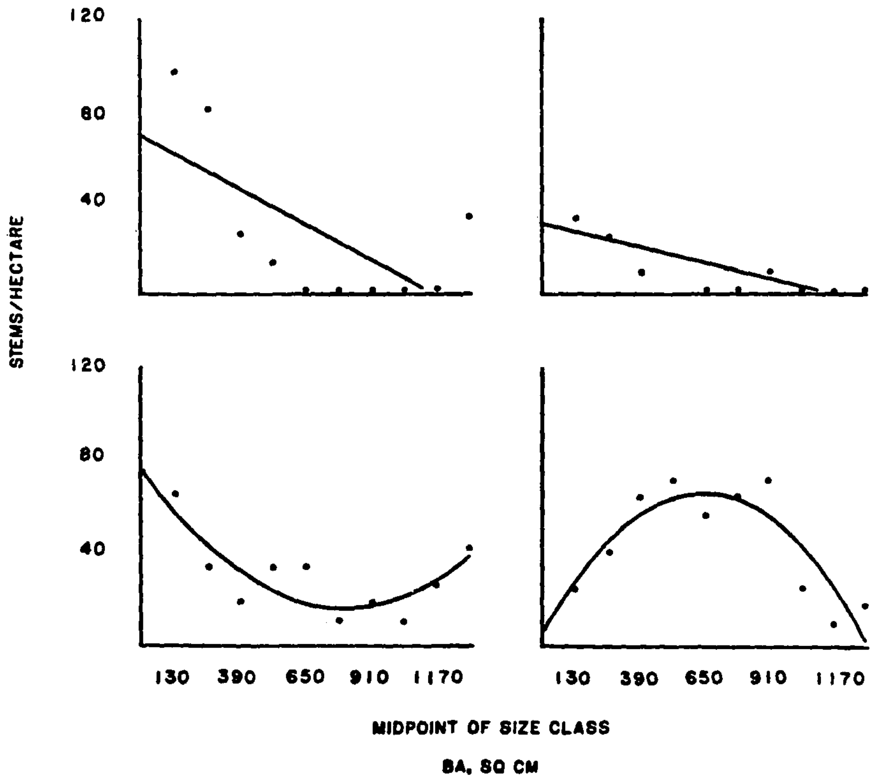

2.0
1.5
1.0
0.5
LOG 10 DENSITY
130
390
650
910
1170
MIDPOINT OF SIZE CLASS
BA, SQ CM

Figure 5. Size class distribution of *Quercus stellata* in 4 Refuge forests.



120
80
40
STEMS/HECTARE
120
80
40
130 390 650 910 1170
130 390 650 910 1170
MIDPOINT OF SIZE CLASS
BA, SQ CM