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THE UPLAND FORESTS OF OKLAHOMA[1]

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INTRODUCTION

Objectives

A series of investigations on the deciduous forest frontier was inaugurated in 1953 at the University of Oklahoma. Initially it was planned to confine the studies to the blackjack-post oak forest, the major forest type of the forest-prairie ecotone. Subsequently it became necessary to include all of the upland forest types throughout the state. This report includes analytical data, obtained in the summer months from 1953 through 1957, from 208 upland forest stands. Objectives comprised the identification and distribution of all relatively undisturbed forest types and a quantitative description of each stand based on the woody species. No data were obtained on herbaceous plants because of the necessary variation in time of sampling and the unequal amount of grazing in the diverse stands. During the last two years of the investigation, data were secured on the death of trees caused by the extended drought (1952-1956).

Nature of Oklahoma forests

The upland forests of Oklahoma constitute a westward extension of the oak-hickory association of the deciduous forest formation. According to Braun (1947) the oak-hickory forest developed ". . . from the mixed forest of the tertiary or from the quaternary representative . . . as a result of increasing aridity in Pliocene time, which eliminated the more mesophytic genera . . . from much of the area west of the Appalachian plateau." In 1950, Braun indicated that "To the south and west of the Interior Highlands is an area occupied by oak-hickory forest, oak and oak-hickory savannah, and in part by prairie." Braun thus recognized an east-west cline of oak-hickory forest, oak-hickory savannah, and oak savannah. These savannahs apparently were much more open than they are today. Evidence of the open nature of these forests in Oklahoma are the labels which have been applied: oak forest, oak openings, scrub oak forest, forest range, forest-prairie ecotone, cross timbers, woodland, pigmy woodland, woodland range, savannah forest, savannah, and chaparral.

Forest studies in adjoining states

Several upland forest investigations have been reported from neighboring states. In Arkansas, Turner (1935) described six upland forest communities, all of which occur in Oklahoma. In a survey of scrub oak forests in the Chautauqua Hills, Kansas, Hale (1955) reported the following percentages of trees: post oak, 56; black oak, 22; and blackjack, 21. He remarked that black oak and blackjack ". . . probably occupy the opposite poles of an ecological gradient in the Chautauqua Hills," since they were never found together. In the Missouri Ozarks, Liming (1942) analyzed 100 blackjack stands. Of the total number of trees, the following percentages were found to occur: blackjack, 52.7; post oak, 16.9 and black oak, 11.5. He remarked that "Natural improvement of the

[1] Contribution of the Oklahoma Biological Survey, Dr. Carl D. Riggs, Director.

composition of these stands through relatively high mortality of blackjack oak is now progressing rather rapidly. . . ." In discussing the vegetation of Texas, Tharp (1926) indicated that transition from pine-oak to oak forest merely meant a gradual decrease of pine until it had entirely disappeared. He indicated that "Contact with the prairie is generally through an ecotone in which the forest proper gives way at its edge to mottes of timber scattered over grassland." In his study of the western cross timbers of Texas, Dyksterhuis (1948) found that the overstory consisted primarily of post oak (63%) and blackjack (29%), although ten other species were encountered.

Forest studies in Oklahoma

According to Phillips, Gibbs, and Mattoon (1950), "Approximately 10,300,000 acres or about 24% of the State's area is covered with forest growth." In his monograph on the vegetation of Oklahoma, Bruner (1931) reported a well-developed, deciduous forest on the rugged topography of the Ozark Plateau and magnificent forests of towering shortleaf pine in the Ouachita Mountains. Westward, however, he found that "The forest gradually becomes poorer in species and dwarfed in stature, and scrub and grassland become more and more abundant." He reported that blackjack and post oak, in the climax oak-hickory forest, often reached heights of 75 feet whereas they rarely exceeded 40 feet in the oak-hickory savannah. He indicated that blackjack was the dominant tree on dry; exposed hillsides and that post oak occurred in more mesic sites. It was reported also that "Communities dominated by either species alone are infrequent, that is, consocies are not well-developed." In 1943, Duck and Fletcher published a very useful map delineating the game (vegetation) types of Oklahoma, and in 1945 they described these game types more completely. They described five upland forest types and pointed out that the post oak-blackjack oak type included 17,628 square miles with a total area greater than all the other forests (12,253 sq. mi.) in Oklahoma. They encountered this type in 65 of the 77 counties in the state.

Several investigations in Oklahoma have been concerned with limited areas. Little and Olmsted (1931) described the upland forests in the Southeastern Oklahoma Protective Unit. In this report they described a dwarf oak association from the tops of the higher mountains in the northern part of the Ouachitas and an oak-hickory sprouts association which had been caused by severe fires. Eskew (1938) referred to the upland forest of the Wichita Mountains Wildlife Refuge as a mixed oak association with blackjack as the dominant. In 1938, Little described the vegetation of Muskogee County and pointed out that the oak-hickory forest is less luxuriant westward with ". . . crooked, low-spreading trees averaging 25 to 40 feet high and up to 1 foot or more in diameter. . . ." Luckhart and Barclay (1938) described an oak-hickory woodland in the vicinity of Tulsa. They noted that post oak was the dominant but that there were more blackjacks on south-facing slopes. In 1939, Little described a dwarf oak woodland on the upland adjacent to Caddo County Canyons. He indicated that blackjack was the dominant species with eastern red cedar and post oak as important secondary species. In 1947, Barclay reported that post oak was the dominant tree in the upland forest, Bear's Glen, near Tulsa. Dale (1956) stated that woodland communities varied considerably in the Arbuckle Mountains. He observed that post oak and blackjack were always ". . . the most important dominants on the dry, upland soils where the parent materials are granite or porphyry." In preparation for this investigation Rice and Penfound (1955) made a complete census of a blackjack-post oak forest and developed the augmented variable-radius method as the method of choice in sampling the 208 upland forest stands, upon which the current report is based.

General Description

Physical features

Oklahoma is a land of surprising diversity: in geology, in physiography, in topography, in climate. The state slopes southeastward from an elevation of 4,978 feet in the Panhandle to 324 feet in the southeastern corner of the state. The Panhandle and the northwestern corner of the state belong to the Great Plains province (Fenneman, 1938). The Redbed Plains, primarily Permian in age, occupy most of the remainder of the state except the eastern border. Included in the Redbeds Plains region are the Arbuckle Mountains and Wichita Mountains, of Paleozoic age. Superimposed on the Redbeds Plains are many recent dune deposits. The eastern border includes portions of the Ozark Plateaus, Boston Mountains, Arkansas Valley, Ouachita and Gulf Coastal Plain provinces (Fenneman, 1938).

The state of Oklahoma is especially interesting for the study of forest vegetation since it is a border state between the cold temperate north and the warm temperature south and between the arid west and the humid east. It is a state in

which the vegetation types, and especially their floral components, are conditioned largely by the north-south cline in temperature and by the east-west gradient in precipitation. The Eastern section is heavily timbered (Figs. 1, 2), the Central section is occupied by savannah-like forest (Fig. 1, 3), and the Western section is primarily grassland, with tongues of upland timber on the sand dunes along the streams and on outcrops of sandstone (Figs. 1, 6).

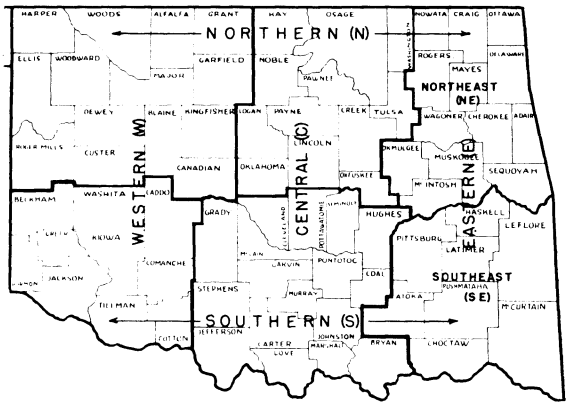

FIG. 1. Sections of Oklahoma referred to in text.

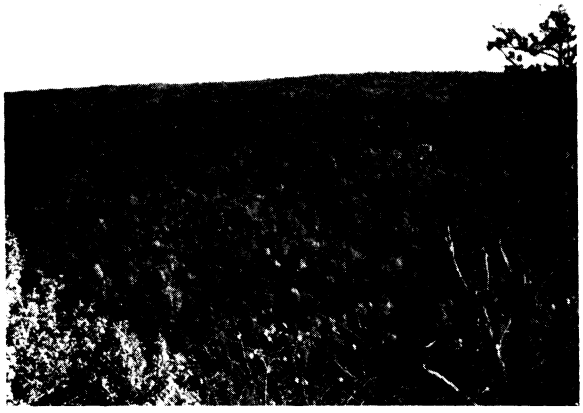

FIG. 2. Extensive oak-hickory-pine forest in southeastern Oklahoma.

Climate

The average annual temperature at Oklahoma City is 60.5° F. However, the mean annual temperature varies from 59.4° F. near Woodward to a mean of 63.7° F. at Idabel in the southeastern corner. The western portion of the state is characterized by greater extremes of temperature than the Central and Eastern sections. The number of days in the average growing season varies from about 200 at Woodward to 240 at Idabel.

The average, annual precipitation varies from about 25 in. at Woodward, in the northwest, to approximately 45 in. at Idabel. Throughout the state, the spring season is the period of greatest

FIG. 3. Typical oak-hickory savannah in central Oklahoma, with scattered trees in grassland.

rainfall, with summer, autumn, and winter exhibiting decreasing amounts of precipitation, in that order. According to Bruner (1931), the rainfall decreases westward "at the approximate rate of one in. for each twenty miles." Furthermore, the rainfall becomes more torrential westward and less evenly distributed throughout the year. As a result, the conditions are progressively unfavorable for forest development. During the period of our observations (1953 through 1957), the average annual precipitation was 30.25 in. as compared to the normal for that period of 30.70 in. Nevertheless this period constituted one of the worst droughts on record. In 1952 the annual rainfall was only 23.29 in. at Oklahoma City. Inches of precipitaion at Oklahoma City for the actual period of investigation, were as follows: 1953, 31.41; 1954, only 17.84; 1955, 37.42; 1956, only 22.56; and 1957, 42.04. From the above data, it should be noted that the investigation was initiated after a year of subnormal rainfall and that the period of study included two years of very low precipitation. As a result, thousands of native upland trees died, especially in the western part of the state.

Original forests

The upland deciduous forests of Oklahoma belong to the oak-hickory forest association in the sense of Weaver and Clements (1938). Well-developed oak-hickory forests occur in the Eastern section but are progressively more open westward. According to Marbut (1911), Beilmann and Brenner (1951) and other authors, many of the original arborescent stands were really savannahs, with large trees scattered throughout a grassy landscape. Further evidence of the open, savannah-like nature of many of the original forest stands has been obtained from descriptions of the cross timbers (Foreman, 1947). The name is de-

rived from the fact that these timber belts were disposed across the line of east-west travel of the pioneers (Fig. 6). According to Foreman (1947), "A large part of the cross timbers is included within the counties of Stephens, Grady and Caddo, Oklahoma. . . ." They are composed primarily of blackjack and post oak. Apparently the open nature of these early forests was produced as follows. In the course of a few years the herbaceous vegetation under the trees developed a considerable quantity of litter. When fires started under such conditions all of the seedlings, many of the saplings, and even small trees were destroyed. The result was an open stand of timber, with relatively large trees dispersed throughout a grass-covered terrain (Figs. 3, 4).

FIG. 4. Heavily grazed oak savannah showing pendant branches of blackjack oak.

Not all of the original stands of timber were savannah-like, however. In many cases, the pioneers literally had to hack their way through the cross timbers, especially in southcentral Oklahoma. Foreman (1947) quotes almost as many travelers as having a difficult time getting through the cross timbers as those who drove wagons through without any trouble. Apparently the answer to the riddle lies in the species of trees which were present. In post oak (*Quercus stellata*)[2] the branches are disposed horizontally and upward whereas in blackjack (*Quercus marilandica*) the tough branches arch downward and remain on the tree for several years after they die (Fig. 4). When blackjack trees are growing in a closed stand, progress, especially with wagons, is incredibly difficult.

[2] Nomenclature follows Waterfall's Catalogue of the Flora of Oklahoma (1952) except for several varieties which were not separated in the present report and one variety for which the authority is given in Table X. Common names in Table II.

Present forests

In the early history of Oklahoma, the forests were reduced drastically by lumbering and by clearing for cultivation. By 1931, Bruner indicated that ". . . All the best and most accessible timber has been cut and to find undisturbed primeval forests one must travel far from the highways." It is probable also that thousands of upland trees in Oklahoma were destroyed by extended droughts in the early thirties and fifties. Many upland trees in Kansas succumbed to desiccation during the dust-bowl days (Albertson 1940, Stiles and Melchers 1935). In Texas, large numbers of trees were killed by the drought of 1949-1954 (Young 1956). On the other hand, there has been considerable invasion of forest trees into areas that were formerly savannah or grassland. This was noted in Arkansas and Missouri by Marbut as early as 1911. In the Missouri Ozarks, Beilmann and Brenner (1951) believed that the encroachment of forests into the ancient prairies had been very rapid, and that our present forests are of relatively recent origin. In Texas also, a pronounced increase of (red cedar) trees into grassland, was observed by Buechner (1944). A considerable extension of forests has taken place in Oklahoma through the production of ravines in grassland by accelerated erosion, and subsequent invasion by trees. Many trees have been planted in cities, around farmsteads, and in shelterbelts. When all of the evidence is examined, it seems probable that there are more trees today than at any other time in the history of Oklahoma.

Bruner (1931) described the following upland forest associations in Oklahoma: *Quercus-Carya* association, *Pinus echinata* consocies, and *Quercus-Carya* savannah. According to Duck and Fletcher (1945) the upland forests of Oklahoma comprise the following types: loblolly pine, oak-pine, oak-hickory, and post oak-blackjack. According to both authors the post oak-blackjack forest (*Quercus-Carya* savannah) extended westward almost to the border of the main body of the state where it gave way to shinnery (Fig. 5). This shrubby community, which does include some trees, occurs mainly in southwestern Woodward, Central Ellis, western Roger Mills, Beckham, and northern Harmon counties. No samples were obtained in this vegetation type because of the shrubby nature of the stands. Duck and Fletcher (1943, 1945) also listed the stabilized dune type for northwestern Oklahoma. This forest type occurs primarily along the north banks of the following rivers: South Canadian, North Canadian, Cimarron, and Salt Fork of the Arkansas. It

consists of savannah-like stands of American elm (*Ulmus americana*), western hackberry, (*Celtis reticulata*), and chittamwood (*Bumelia lanuginosa* var. *oblongifolia*). Apparently these trees are the first invaders of the relatively stabilized dunes and are replaced later, at least in part, by blackjack and post oak. No samples were taken in this forest type because of the fragmentary nature of the stands.

FIG. 5. Contact of oak savannah, shinnery, and grassland in western Oklahoma.

Some of the present upland forests, particularly in the Central and Western sections of Oklahoma, still retain the savannah-like nature of some of the original stands. There is general agreement, however, that the current upland forests possess a greater arborescent cover than the primeval stands. This is especially true in the oak-hickory and oak savannahs. Many heavily grazed and cut-over forest areas have tremendous numbers of saplings and young trees of blackjack and black hickory. Such disturbed stands are so dense that they are virtually impenetrable. According to Dyksterhuis (1957) and according to our own observations and information obtained from early settlers in Oklahoma, heavy grazing and the absence of fire result in the dominance of woody species. It is apparent that these two factors work together to favor trees, shrubs, and woody vines. Heavy grazing weakens the grassland dominants and lowers the fire hazard. Even if fires do get started, they do little damage to the woody components. The result is a continuing increase in arborescent cover and timber volume in areas which were formerly occupied by savannah or grassland. Interdigitation of grassland and oak savannah presents the appearance shown in Figure 6.

In the oak-hickory forest, Oosting (1956) states that "*Quercus alba, Q. rubra, Q. velutina, Q. stellata, Q. marilandica, Carya cordiformis, C. ovata, C. tomentosa* and *C. laciniosa* are species

FIG. 6. Interdigitation of oak savannah and prairie in central Oklahoma.

that may be found in the climax anywhere." This is certainly not the case in Oklahoma, although all of the above species were encountered in our study except *C. laciniosa*. Of the above species *Quercus marilandica, Q. stellata, Q. velutina, Carya tomentosa,* and *C. cordiformis* were found in central Oklahoma and only the first two of these were sampled in the western part of the state.

METHODS

Field methods

The selection of stands of upland forests in Oklahoma was accomplished according to the following pattern. The vegetation type for a given county was determined by the aid of the Game Type Map of Duck and Fletcher (1943). In the field at least three stands per county were selected by means of county road maps, possible undisturbed stands being located by noting areas with few or no roads. Care was taken also to locate these stands with reference to the vegetation types of adjacent counties. Once the stand was decided upon, data concerning it were entered on an appropriate form. These items included the stand number, location (with included map), past history (including cutting, burning, and grazing), a presence list of trees, shrubs, and woody vines and other miscellaneous data.

An augmented variable-radius method was chosen for analysis of the selected stands. This consisted of the variable-radius technique for determining basal area, supplemented by 40 arms-length rectangles of 0.01 acre each for procuring data on frequency and density (Rice and Penfound 1955). In practice, basal area was obtained at 40 evenly spaced points by means of an angle gauge. Frequency and density were determined by 40 arms-length rectangles between these points. In limited stands only 20 or 30 points were uti-

TABLE I. Average importance percentage (I.P.) of trees in stands where indicated species were the leading dominants. Two hundred and two stands

No of stands	Leading dominant (With highest I.P.)	Q.m.	Q.s.	C.te.	Q.v.	U.a.	C.to.	P.e.	Q.a.
65	Quercus marilandica, Q.m.	*62.8*	22.3	6.9	8.4	0.7	4.7	6.6	3.0
103	Quercus stellata, Q.s.	20.4	*58.7*	8.5	4.1	3.1	6.7	4.7	0.1
7	Carya texana, C.te.	3.8	11.9	*33.2*	15.5	4.0			1.4
9	Quercus velutina, Q.v.	14.0	18.3	7.8	*38.9*				4.7
2	Ulmus alata, U.a.	11.6	20.7	7.9	17.9	*26.3*	8.0		
1	Carya tomentosa, C.to.	2.3	1.4			0.2	*32.6*	11.6	22.9
10	Pinus echinata, P.e.	3.0	22.7			0.7	5.7	*49.2*	4.9
5	White oak, Q.a.	0.7	4.8			0.9	9.5	2.8	*29.8*

lized. Field data on both trees and saplings were entered on appropriate forms for later analysis.

Compilation methods

After the field notes were brought into the laboratory the following data on each species were entered on a prepared form: number of saplings and trees, frequency of trees, and basal area of trees per sample. From these data the following compilations were made for each species: number of saplings and trees per acre, basal area per acre, relative frequency, relative density, relative basal area, and importance percentage. The importance percentage is calculated by adding the relative data on frequency, density, and basal area and dividing by three. It is equivalent to one-third of the importance value or DFD index of Curtis and McIntosh (1951). The importance percentage has the advantage of being directly comparable to relative frequency, relative density, or relative basal area. Dominants were designated as those species having an importance percentage (I.P.) of 25 or more. Further compilations comprised an ordination of dominants with reference to mesophytism, a table of association-segregates or faciations, a list of upland forest communities and their dominants and several compilations on number, basal area, and importance percentages. In addition, presence lists for all woody species and constance percentage tables for important species were compiled for all sections of the state.

The sections of the state utilized in this investigation were patterned after those of Kelting and Penfound (1953). Changes include a transfer of Canadian, Kingfisher, Garfield, and Grant Counties to the Western section and a shift of Tulsa and Washington Counties to the Central section (Fig. 1).

FOREST TYPES

The forest continuum

Of the total number of arborescent taxa (74) encountered in this investigation, the numbers in the various sections were as follows: Western, 25; Central, 46 and Eastern, 65. This increase of species eastward indicated the possibility of a forest continuum. In order to test this possibility the importance percentages were calculated for each dominant species. Then the stands were arranged into groups, each dominated by one of the eight major species, according to the method of Curtis and McIntosh (1951), but with the xeric stands at the top. When this was done each taxon reached its optimum development at a given point along the series. However, no group of species achieved their peaks in the same stands, and *Quercus stellata* and *Q. marilandica* were fairly prominent in most stands (Table I). Thus no discrete communities could be delineated on the basis of the leading dominants in the stands. This demonstrates that the upland forests of Oklahoma form a vegetational continuum in which a definite gradient is exhibited from the relatively xeric stands to the more mesic stands (Table I).

In discussing the question of the relation of the continuum to the classification of plant communities, Oosting (1956) states that "This leads to the question of the propriety of grouping these communities into units of any system of classification, the argument being that such discrete units do not exist and that it is improper to set up a system with categories whose limits are arbitrarily set. . . ." Despite the obvious fact that the upland forests of Oklahoma do constitute a vegetational continuum, it is relatively easy in the field to recognize distinct stands. Furthermore, at the ends of the continuum an almost completely different group of species is present, e.g. shin oak or western walnut stands in the Western section as against shortleaf pine or loblolly pine communities in the Eastern section. It has, therefore, seemed desirable to sub-divide the oak-hickory forest association into association-segregates or faciations.

Faciations

According to Oosting (1956), "A geographical variant with two or more, but less than the total

number, of associational dominants is termed a faciation." Using this definition we have divided the oak-hickory association in Oklahoma into five faciations: oak-loblolly pine, oak-hickory-pine, oak-hickory forest, oak-hickory savannah, and oak savannah (Table II). Since each of these faciations includes several stands or concrete communities, perhaps they should be designated as community-types as recommended by Whittaker (1956). Except for the oak-loblolly pine faciation, the number of dominants decreased westward.

TABLE II. Dominants in upland forest communities of Oklahoma. Species arranged in order of increasing mesophytism (top to bottom). Communities arranged from west to east (left to right)

Species	Oak savannah	Oak-hickory savannah	Oak-hickory forest	Oak-hickory-pine	Oak-loblolly pine
Quercus Havardi (Shin oak)	x				
Juniperus virginiana (Red cedar)	x				
Quercus marilandica (Blackjack)	x	x	x		
Quercus stellata (Post oak)	x	x	x	x	x
Juglans microcarpa (Western walnut)	x				
Carya texana (Black hickory)		x	x		
Quercus velutina (Black oak)		x	x		
Ulmus alata (Winged elm)			x		
Carya tomentosa (Mockernut)			x	x	
Pinus echinata (Shortleaf pine)				x	
Quercus Shumardii (Shumard's oak)			x		
Quercus alba (White oak)			x	x	
Quercus rubra (Northern red oak)				x	
Pinus Taeda (Loblolly pine)					x
Quercus Muhlenbergii (Chinquapin oak)	x		x		
Acer saccharum (Sugar maple)			x		

Only four dominants were present in the oak-hickory savannah (Table II). Typically only two dominants, post oak and blackjack, were present in the oak savannah, although shin oak, red cedar and western walnut were dominant or codominant in three stands (Table III).

The sixteen species listed as dominants were so designated only if they exhibited an importance percentage of 25 or above in at least one stand (Table II). When they were arranged into groups according to the method of Curtis and McIntosh (1951) a reasonable ordination according to increasing mesophytism was accomplished (Table II). This scheme was supplemented by observing which groups of dominants occurred most often together. When this was done a more satisfactory arrangement was achieved. Since several species were dominant in only one or two stands, however, the position of certain species should be regarded as tentative. This group includes western walnut, winged elm, mockernut and loblolly pine.

TABLE III. Upland forest communities in Oklahoma, arranged in approximate order of increasing mesophytism (top to bottom)

Type of stand	Number of Stands			
	Western	Central	Eastern	Total
Shin oak	1			1
Blackjack-red cedar	1			1
Western walnut	1			1
Blackjack-post oak	10	42	19	71
Blackjack	16	7	6	29
Post oak	6	25	21	52
Blackjack-black oak			6	6
Post oak-black hickory		3	3	6
Post oak-black oak		2	3	5
Black hickory-black oak		2	4	6
Black hickory			2	2
Black oak		1	3	4
Winged elm			1	1
Winged elm-post oak			1	1
Mockernut			1	1
Shortleaf pine			5	5
Shortleaf pine-post oak			5	5
Shortleaf pine-white oak			1	1
Shortleaf pine-red oak			1	1
Loblolly pine			1	1
White oak-black oak			1	1
White oak-Shumard's oak			1	1
White oak			4	4
Chinquapin oak	1			1
Chinquapin oak-maple			1	1
Total stands	36	82	90	208

Type of stands

Each of the above faciations includes several types of stands or concrete communities. The oak savannah, which is characteristic of the Western section of Oklahoma (Fig. 4) includes seven different types of stands (Table III). These stands are comparable to the forest cover types of the Society of American Foresters (1932). Each is a distinct community which would be designated as associations by Braun-Blanquet (1932). The more xeric communities included shin oak and red cedar whereas the most mesic community was the chinquapin oak stand on a north-facing slope in the Wichita Mountains. The only really important species in the Western section were blackjack and post oak, since they were dominant in 33 of the 36 stands sampled. It should be emphasized that blackjack and post oak occur as sole dominants in many stands and may contribute 90 per cent or more of the total arborescent cover. This is not in agreement with the statement of Bruner (1931) that "Communities dom-

inated by either species above are infrequent, that is, consocies are not well developed."

The oak-hickory savannah is characteristic of the Central section of the state (Fig. 3). This faciation comprises only four dominant species but several combinations of dominants are represented, as well as numerous single-dominant stands (Table III). As is quite apparent, blackjack and post oak are the principal species, being dominant in 79 of the 82 stands.

The Eastern section of the state comprises all faciations of the oak-hickory forest association in Oklahoma and an extended list of dominants (Table III). The oak savannah and oak-hickory savannah are confined to less favorable sites such as south-facing slopes and ridge tops. The oak-hickory forest is characteristic of the better sites, especially in the Northeast section; the oak-hickory-pine subclimax is more abundant in southeastern Oklahoma; and the oak-loblolly pine faciation is limited to the Gulf Coastal Plain in the southeast corner of the state. In the Eastern section, 21 aborescent communities and 12 dominant tree species were encountered. Of these species, blackjack or post oak was dominant in 64 of the 90 stands sampled. It should be observed, however, that these 2 species were less important, relatively, in the Eastern section, than they were in the Western and Central sections.

Comment should be made here about the arbitrary policy of designating dominants as those species having an importance percentage of 25 or above. When this was done, all stands had one or 2 dominants, except for 3 stands with none and 3 stands which had 3 dominants each. In such cases the stands were designated by the 2 species having the highest importance percentages. In the Eastern section there were 4 white oak stands and one white oak-Shumard's oak community. Usually these 2 species occur together on north-facing slopes and form a distinctive aggregation. In the 5 stands listed, white oak exhibited an average I.P. of 29.5 and Shumard's oak had a mean I.P. of 18.4. Since the average importance percentages of the 2 species were similar, it might appear more logical to include all 5 stands as white oak-Shumard's oak communities. These facts indicate the difficulty that is faced when an inflexible system of classification is utilized. On the other hand, even greater problems are encountered if a more subjective system is employed.

When all types of stands and all sections of the state are considered, blackjack and post oak are the only really important species. Either blackjack or post oak was dominant in 9 of the 25 types of stands. Even more important was the ascendancy of one or the other of these species in 176 of the 208 stands sampled (Table III). Only blackjack and post oak were found to be dominant in every section of the state. Next in importance were black hickory and black oak. These species do not occur in the Western section although they may be prominent in both the Central and Eastern sections. Black hickory or black oak was found to be dominant in seven out of the 25 types of stands and in 29 out of the 208 stands encountered (Table III). Although the remaining species were dominant in 16 out of the 25 types of stands they were prominent in only 27 of the 208 stands investigated (Table III). As a group, therefore, they were of minor importance in the upland forest types of Oklahoma.

Dominants

Number of trees

The number of trees per sample, or per acre, did not vary greatly in the various sections of the state, although a somewhat greater number occurred in the Central section (Table IV). For the state as a whole, the average number was 166 trees per acre, a figure similar to values reported for the oak-hickory forest association elsewhere. The number of saplings (one to three inches DBH) was found to be surprisingly high in all sections of the state (Table IV). Furthermore, saplings of the dominant species were found in every type of community throughout the state. This signifies that all communities were reproducing themselves adequately. This was notably true for the blackjack-post oak forest. For individual stands the range was 0 to 840 saplings per acre, but the average amplitude per section was similar to that given in Table IV. These findings do not agree with the statements of various authors that oak-hickory forests do not reproduce themselves satisfactorily.

Table IV. Number of saplings and trees per acre, and basal area in square feet per acre, in upland forests of Oklahoma

	Western	Central	Eastern	Northern	Southern	State
Saplings	188	207	203	184	218	202
Trees	166	181	152	159	173	166
Basal area	36.0	48.6	55.3	47.3	51.1	49.2

According to Weaver and Clements (1938) the Cross Timbers ". . . have usually been regarded as portions of the oak-hickory forest . . . They are

composed almost wholly of post oak and blackjack . . . which are usually not true climax dominants . . . In this prairie climate, the oaks constitute a post climax, since the climax forest would return in the event of a shift to a wetter climate." As far as climate in Oklahoma is concerned, the blackjack-post oak forest occurs in areas with precipitation ranging from 25 to 45 inches. Typically it occurs on the better sites (usually stabilized sand dunes) in the western part of its range and on the poorer sites (south-facing slopes and ridge tops) in the eastern part of its spread. In general, it is separated from the main body of the oak-hickory forest by the oak-hickory savannah, which comprises black oak and black hickory in addition to blackjack and post oak. With increased grazing and protection from fire, the above savannahs are rapidly returning to forest stature. In view of the above facts it is our belief that the oak savannah and oak-hickory savannah are portions of the oak-hickory forest and that their major components should be regarded as climax dominants.

Basal area

The average basal area of the upland forests of Oklahoma was 49.2 square feet per acre. This is much lower than that of good upland timber stands to the east of Oklahoma. Basal area, in square feet per acre, was very low in the Western section, low in the Central section, and only moderate in the Eastern section (Table IV). There was no significant difference between the Northern and Southern sections in this respect. The absolute range in basal area per stand, in square feet per acre, varied from 7.0 in Western Oklahoma to 115.0 in the Eastern section. Typical ranges in basal area, in the various sections, were as follows: Western, 15-40; Central, 30-60; Eastern, 45-75 (Fig. 7).

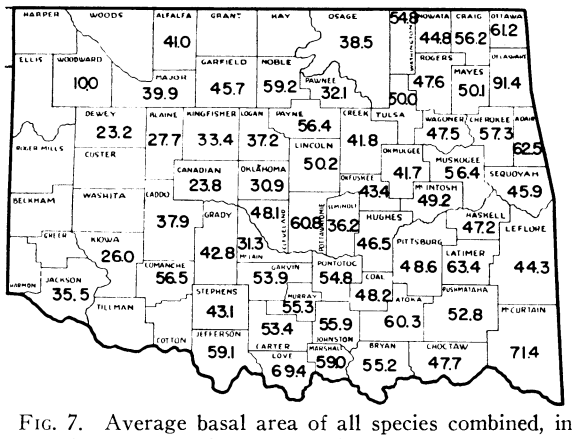

FIG. 7. Average basal area of all species combined, in square feet per acre, in counties of the state.

It will be observed that there is considerable variation in basal area, even in adjacent counties (Fig. 7). This is a reflection of the kinds of stands available for sampling as well as the variation in habitat types. In the southwestern corner of the state, for example, the average basal area is relatively low, whereas that in Comanche County is above the average for the state (Fig. 7). This is due to the fact that two of the stands on favorable sites had very high basal areas. As expected, the lowest average basal areas per county were encountered in the Western section, and especially in the northwestern corner of the state. The average basal area per county increased gradually to the eastern border (Fig. 7). The highest volume was observed in Delaware County, where the basal areas, per stand, were 84.75, 115.00, and 74.55 square feet per acre, respectively. In general, the basal area was highest in the Northeast section, which was adjudged to be the most mesic section of the state.

Of the average basal area per acre (49.2), eight species contributed 90.3 per cent. Major contributions were by post oak (40.8%) and blackjack (26.8%). Together, these two species accounted for 67.6 per cent of the total basal area (Table V). By comparison, all other species were minor components, with black oak and black hickory being the most prominent. The second division included shortleaf pine, mockernut, winged elm and white oak, none of which contributed significantly to the total basal area.

TABLE V. Relative basal area and average importance percentage per stand. Arranged according to decreasing importance percentages

Species	Relative Basal Area	Importance Percentage
Post oak	40.8	39.1
Blackjack	26.8	30.5
Black oak	8.1	6.5
Black hickory	4.9	6.4
Shortleaf pine	4.5	3.7
Mockernut	1.8	1.9
Winged elm	1.2	1.9
White oak	2.2	1.7
Other species	9.7	8.3
Total	100.0	100.0

The relative prominence, as indicated by basal area, is portrayed graphically in the following figures (Figs. 8, 9, 10, 11). Attention is called to the fact that post oak is more prominent in the Central section whereas blackjack is more impressive in the Western section. All the other dominants were confined to the Central and Eastern sections but augmented the total basal area

only slightly (Figs. 8, 9). When the Northern and Southern sections are considered, it will be observed that post oak exhibited a higher basal area in the Southern division, whereas blackjack was more prominent in the Northern section (Fig. 10). Black oak, black hickory, and white oak also possessed a higher basal area in the Northern section. All of the other dominants were more prominent in the Southern section (Figs. 10, 11).

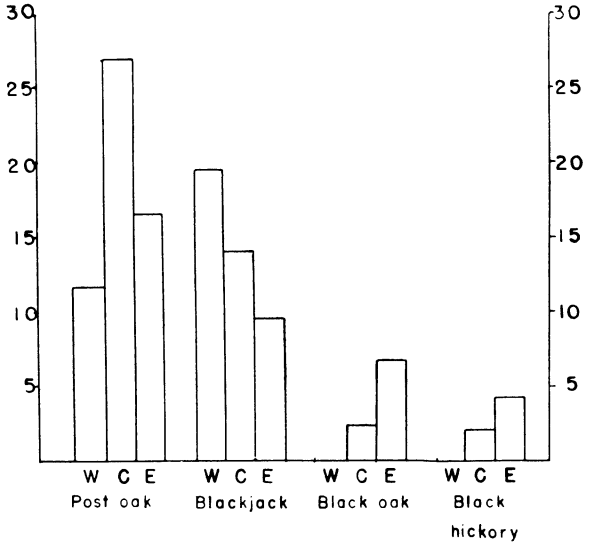

FIG. 8. Average basal area, in square feet per acre, of four leading dominants in Western (W), Central (C), and Eastern (E) sections of Oklahoma.

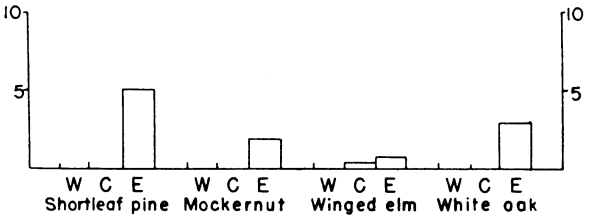

FIG. 9. Average basal area, in square feet per acre, of minor dominants in Western (W), Central (C), and Eastern (E) sections of the state.

The basal area, in square feet per acre, was also determined for the eight leading dominants in each county of the state. Reference to the basal area data on post oak (Fig. 12) indicates that this species was relatively unimportant in the counties of the northwestern portion of the state, whereas it was impressive in the southwestern corner. Blackjack, on the other hand, was more prominent in the northwestern corner, but subordinate in the southwestern portion (Fig. 13). The basal area values, for both post oak and blackjack, were highest in the Central section but decreased eastward, presumably due to competition with the more mesic species of eastern Oklahoma.

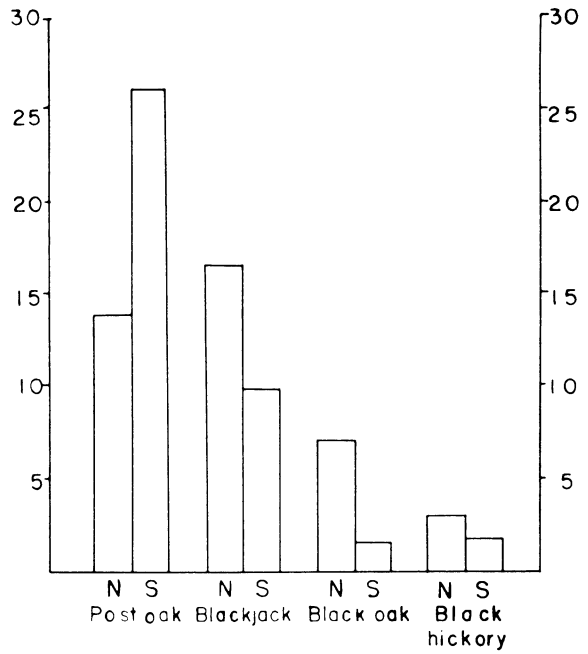

FIG. 10. Average basal area, in square feet per acre, of four leading dominants in the Northern (N) and Southern (S) sections of the state.

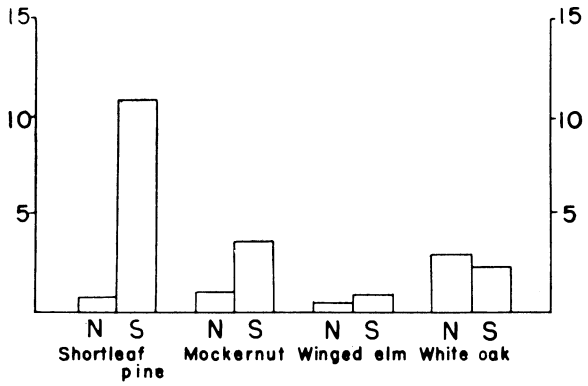

FIG. 11. Average basal area, in square feet per acre, of minor dominants in the Northern (N) and Southern (S) sections of Oklahoma.

It should be noted that the basal area of post oak was about twice that of blackjack in the Eastern section, which suggests that post oak is a better competitor than blackjack (Figs. 12, 13).

Of the next pair of dominants, black oak was relatively prominent in the counties of the Northeastern subsection whereas black hickory was evenly distributed throughout the counties of the Central and Eastern sections (Figs. 14, 15). In many counties of Eastern Oklahoma black oak exceeded both post oak and blackjack in volume (Figs. 12, 13, 14). The second quartet of dominants (shortleaf pine, mockernut, winged elm and white oak) was sampled primarily in the Eastern section. As a group they contributed only a small

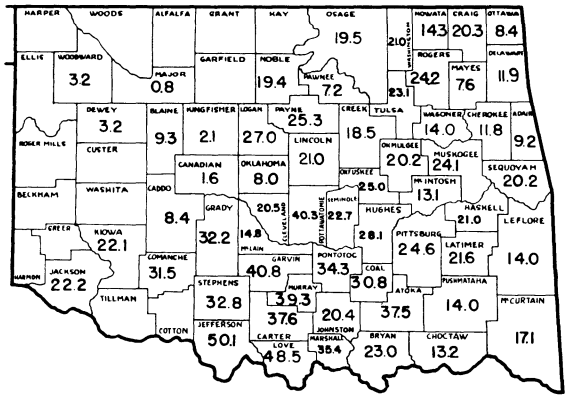

FIG. 12. Average basal area per county, in square feet per acre of post oak.

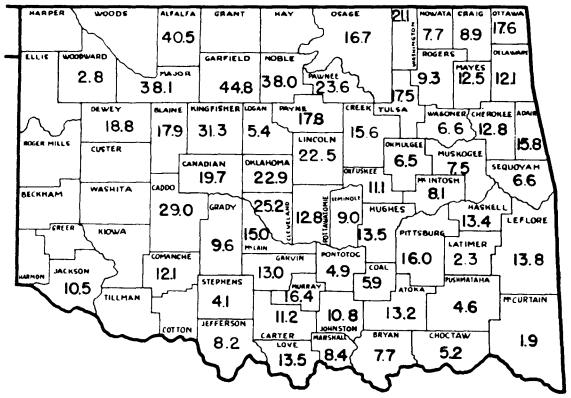

FIG. 13. Average basal area per county, in square feet per acre, of blackjack oak.

percentage (9.7) of the total basal area. Of these species, shortleaf pine contributed the greatest basal area (4.5%), although it was sampled largely in the counties of the Southeastern subsection.

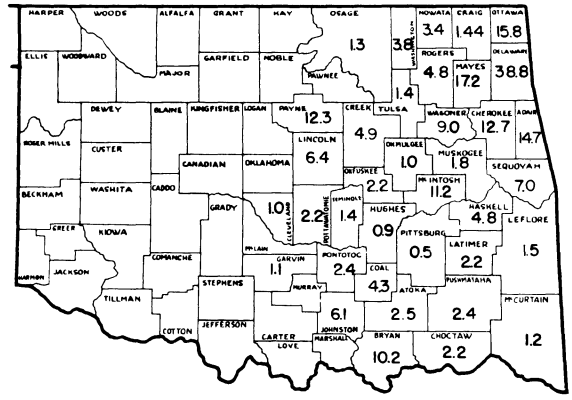

FIG. 14. Average basal area per county, in square feet per acre, of black oak.

On a collective basis, the other three minor dominants contributed only meager basal area (5.2%), although distributed rather evenly throughout the Eastern section.

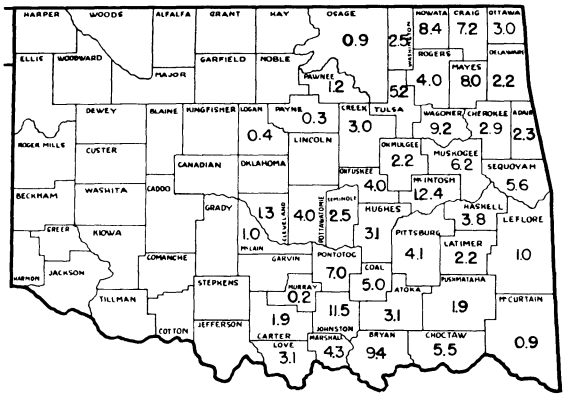

FIG. 15. Average basal area per county, in square feet per acre, of black hickory.

Importance percentage

The importance percentage (I.P.) was calculated for all 74 tree species, but the importance percentages for the eight major species only are presented here (Table VI). For the state as a whole, the species may be divided into three groups on the basis of importance percentages: post oak-blackjack, black oak-black hickory, and shortleaf pine-mockernut-winged elm-white oak.

TABLE VI. Average importance percentage per stand in sections of Oklahoma, arranged in order of decreasing importance percentages for the state. Sections: W, Western; C, Central; E, Eastern; N, Northern; S, Southern

Species	W	C	E	N	S	State
Post oak	30.7	52.9	29.8	29.3	48.3	39.1
Blackjack	56.4	32.2	18.5	39.3	22.2	30.5
Black oak		4.3	11.2	9.7	3.5	6.5
Black hickory		6.6	8.8	7.4	5.5	6.4
Shortleaf pine			8.7	0.6	6.8	3.7
Mockernut			4.4	1.0	2.8	1.9
Winged elm		2.0	2.5	1.5	2.3	1.9
White oak			3.9	2.0	1.4	1.7

The post oak-blackjack group had high I.P. values and contribtued 69.6 of the total importance percentage (Table VI). The black oak-black hickory group exhibited moderate I.P. values and accounted for 12.9% of the total. The other four species, mostly eastern in distribution, yielded only 9.2 of the total importance percentage (Table VI).

When post oak and blackjack are compared, it will be observed that post oak had lower I.P. yields in the Western section than blackjack, but higher I.P. values in the Central and Eastern sections (Table VI). On a north-south basis, postoak exhibited higher I.P. values in the Southern section, but lower values in the Northern section, when compared with blackjack (Table VI). Other significant differences on a north-south

basis occurred also in black oak, which was very prominent in the Northeastern subsection, and shortleaf pine, which was predominant in the Southeastern subsection (Table VI).

When the relative basal areas and importance percentages are compared, it is evident that they are very similar (Table V). They are almost identical in post oak, whereas the relative basal area is somewhat lower than the importance percentage in blackjack (Table V). This indicates that the DBH was somewhat higher in post oak than in blackjack. This was true also for black oak, shortleaf pine and white oak. The data suggest that either compilation is adequate in determining dominance and importance in the upland forests of Oklahoma.

Effect of Drought

It may be recalled that this investigation occurred during one of the worst droughts on record. Some trees died during the dry summer (17.84 in. of rainfall) of 1954 but widespread death of trees did not occur until 1956 (Fig. 16). Our records, therefore, include the summers of 1956 and 1957 only, and do not comprise many stands, especially in the Central section (Fig. 17). Data were obtained on the death of trees in 79 stands distributed unequally over the state. The results indicate that destruction of trees through desiccation was highest in the Western section, moderate in the Central section, and least in the Eastern section (Table VII).

Fig. 16. Death of blackjack trees from drought in oak savannah, western Oklahoma.

The greatest number of trees died in Woodward County in the northwestern corner of the state (42.3%). The number of dead trees in other counties of the Western section was much lower, however (Fig. 17). Destruction of trees by drought in Eastern Oklahoma was much less than in the Western section, no dead trees being encountered in three stands in the Eastern section (Fig. 17). Although our data are meager in the Central section, it seems probable that there was a gradual decrease in number of dead trees from the Western border eastward.

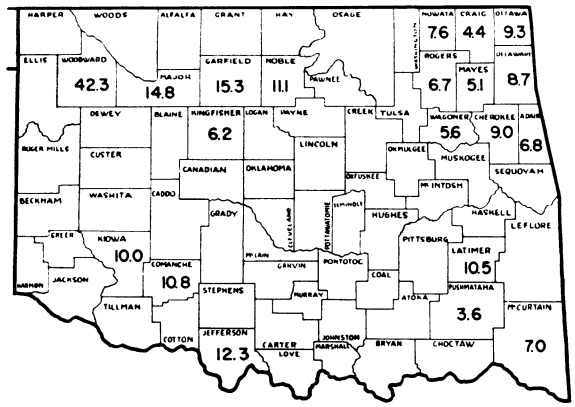

Fig. 17. Average per cent mortality of trees from drought. From data obtained in 1956 and 1957 only.

Table VII. Per cent dead trees as determined from stands sampled in the summers of 1956 and 1957

Section	No. of stands	Per cent dead trees
Western	13	14.6
Central	11	11.8
Eastern	55	6.6
Northern	48	9.3
Southern	36	10.8

In stands that included both blackjack and post oak, more blackjacks than post oaks were killed by desiccation (Fig. 16). In one stand in Jefferson County 81.5% of all blackjack trees were dead while only 8.5% of the post oak trees were dead. This is contrary to the prevailing opinion that blackjack is the more xeric of these two associates. From the available evidence it appears that blackjack may occur on less favorable sites than post oak but is not as drought-resistant. It seems probable, also, that blackjack has a narrower range of ecological amplitude than post oak.

Status of Savannahs

From the western boundary of the main body of the state eastward, the major vegetation types are as follows: grassland, oak savannah, oak-hickory savannah, oak-hickory forest. It appears that the oak savannah would metamorphose into an oak-hickory savannah in the event of a shift to a wetter climate and that it would change to grassland in the event of a change to a drier climate. This latter shift was almost accomplished in 1956-1957 and would certainly have occurred had the

drought continued for a few more years. Similarly, the oak-hickory savannah presumably would be converted into oak-hickory forest with an increase in available moisture and would be transformed into an oak savannah with cumulative desiccation. It should be emphasized that oak savannahs and oak-hickory savannahs occur throughout the main body of the state, with a precipitation range from 25 to 45 in. With the exception of the extreme eastern part of the state, the savannahs occur on soils of fairly course texture derived largely from sandstones or granites. Fine textured soils derived largely from limestones or shales support grassland vegetation. This means that almost all of Oklahoma is a broad ecotone between forest and grassland. Actually, the climate throughout the ecotonal area cannot be said to be either a true grassland or forest climate. The deciding factor is the soil texture, apparently through its effect on water relations.

According to Dyksterhuis (1957) "A savannah type should be regarded as normal, or climax, only on a savannah site." In other words a savannah type should be regarded as climax only in a savannah climate. It seems logical and appropriate to designate the climate in the broad ecotonal zone described above as a savannah climate. In fact, since there are two distinct types of savannah in Oklahoma, it appears logical to postulate two kinds of savannah climates. The oak savannah climax would occur throughout a range of about 25 to 32 inches of rainfall and the oak-hickory savannah climax would extend throughout an area having about 32 to 40 inches of precipitation. Since these savannahs are relatively stable, except during major climatic shifts, and since they are reproducing adequately, it is felt that they should be considered as climax communities and that their major components should be designated as climax dominants.

Distribution

Presence

The number of woody taxa encountered in this investigation was 134. This list comprised 74 trees and 60 shrubs and woody vines. Five additional varieties were identified but were not included in the tables because of the difficulty of recognizing these taxa in the vegetative condition. The number of woody species was lowest in the Western section and increased continuously eastward in the state (Table VIII). The number of woody taxa from west to east were as follows: Western, 54; Central, 86; Eastern, 116. Surprisingly, there was a slightly greater number of species in the Northeastern subsection than in the Southeastern portion (Table VIII).

Table VIII. Number of woody species per section in the upland forests of Oklahoma based on sampling data. W, Western; C, Central; E, Eastern; NE, Northeastern; SE, Southeastern

	W	C	E	NE	SE	State
Number of stands	36	82	90	50	40	208
Shrubs and vines	29	40	51	42	37	60
Tree species	25	46	65	58	52	74

A complete list of trees and their distributions are presented in Table IX. The distribution of several species was extended considerably when herbarium specimens from the Bebb Herbarium, at the University of Oklahoma, were included. In all discussions which follow concerning the restriction of woody species to any section or subsection, data from the herbarium sheets have been included even though all herbarium specimens were not necessarily from upland forests. Distribution data on all woody taxa, including a record of herbarium specimens, were spotted by counties on maps of the state. When this was done, many records for counties were blank where it was felt certain that the species occurred. These maps, therefore, have been omitted, but are available for study at the University of Oklahoma. If, and when, sufficient additional records are obtained, it is hoped that these distributional maps may be included in a later publication.

On the basis of data from samples and herbarium specimens, certain tree species were found to be confined to one section only (Table IX). *Juglans microcarpa* and *Quercus virginiana* were limited to the Western division, no tree species were exclusive to Central Oklahoma, but 15 species were restricted to the Eastern section. *Aesculus glabra* var. *glabra* and *Fraxinus quadrangulata* were confined to the Northeastern subsection, and *Ilex opaca* and *Pinus Taeda* were limited to the Southeastern subdivision. The remaining species (11) occurred in both subsections.

The compilation of total woody species comprised 41 shrubs and 19 vines (Table X). A few species, such as *Menispermum canadense* and *Passiflora lutea,* which are generally essentially herbaceous above ground have been included here as woody vines. As was true for the trees, some were confined to one section, some were limited to two sections, and a few more were present in all three divisions of the state. The following shrubs and vines were present in a very high percentage

TABLE IX. Presence and distribution of tree species in the upland forests of Oklahoma. W, Western section; C, Central; E, Eastern; x, in stands; h, in Bebb herbarium (not always from upland forests)

Taxa	W	C	E	Taxa	W	C	E
Acer rubrum			x	Morus rubra	x	x	x
Acer saccharum	x		x	Nyssa sylvatica			x
Aesculus glabra var. glabra			x	Ostrya virginiana			x
Amelanchier arborea		x	x	Pinus echinata			x
Bumelia lanuginosa var. oblongifolia	x	x	x	Pinus Taeda			x
Carpinus caroliniana			x	Platanus occidentalis		x	x
Carya cordiformis		x	x	Populus deltoides		x	h
Carya illinoensis	h	x	x	Populus Sargentii	x	h	h
Carya ovata		h	x	Prosopis juliflora var. Torreyana	x	x	h
Carya texana		x	x	Prunus mexicana	x	x	x
Carya tomentosa		x	x	Prunus serotina		x	x
Castanea ozarkensis		h	x	Quercus alba		h	x
Catalpa speciosa	x	h	h	Quercus falcata		h	x
Celtis laevigata (mostly var. texana)	x	x	x	Quercus Harvardi	x	x	
Celtis occidentalis	h	x	x	Quercus macrocarpa	h	h	x
Celtis reticulata	x	x	x	Quercus marilandica	x	x	x
Cercis canadensis	x	x	x	Quercus Muhlenbergii	x	x	x
Cornus florida	h	x	x	Quercus nigra			x
Crataegus crus-galli	x	x	x	Quercus palustris		h	x
Crataegus Marshallii		x	x	Quercus Phellos			x
Crataegus mollis		x	x	Quercus rubra			x
Crataegus Reverchoni var. discolor			x	Quercus Shumardii	x	x	x
Crataegus spathulata			x	Quercus stellata	x	x	x
Crataegus viridis	x	x	x	Quercus velutina		x	x
Diospyros virginiana	h	x	x	Quercus virginiana	x		
Fraxinus americana	h	x	x	Rhamnus caroliniana		x	x
Fraxinus pennsylvanica	h	x	x	Robinia Pseudo-Acacia	h	x	x
Fraxinus quadrangulata			x	Salix caroliniana	x	h	h
Gleditsia triacanthos	h	x	x	Salix nigra	h	x	x
Gymnocladus dioica	h	x	x	Sapindus Drummondii	x	x	x
Ilex opaca			x	Sassafras albidum		x	x
Juglans microcarpa	x			Sophora affinis		x	h
Juglans nigra	x	x	x	Tilia americana			x
Juniperus virginiana	x	x	x	Ulmus alata		x	x
Liquidambar Styraciflua		h	x	Ulmus americana	x	x	x
Maclura pomifera	h	x	x	Ulmus crassifolia		x	x
				Ulmus rubra	x	x	x
				Viburnum rufidulum	h	x	x

TABLE X. Presence and distribution of shrubs and woody vines in upland forests of Oklahoma. W, Western section; C, Central; E, Eastern; x, in stands; h, in Bebb herbarium (not always from upland forests)

Taxa	W	C	E	Taxa	W	C	E
Aesculus glabra var. arguta (Buckl.) Robinson	x	x	h	Passiflora lutea var. glabriflora	h	h	x
Amorpha canescens	x	x	x	Ptelea trifoliata	x	x	h
Amorpha fruticosa	x	x	x	Prunus angustifolia	x	x	x
Ampelopsis arborea		x	x	Prunus gracilis	x	x	x
Artemisia filifolia	x	h		Prunus Monsoniana			x
Ascyrum Hypericoides		x	x	Prunus virginiana	x		
Asimina triloba		h	x	Quercus prinoides	x	x	x
Berchemia scandens		x	x	Rhododendron canescens			x
Brunnichia cirrhosa			x	Rhus aromatica var. aromatica	x	x	x
Callicarpa americana		x	x	Rhus aromatica var. pilosissima	x	x	h
Campsis radicans		x	x	Rhus copallina var. latifolia	x	x	x
Ceanothus americanus var. Pitcheri	h	x	x	Rhus glabra	x	x	x
Ceanothus herbaceus	x	h	x	Rhus radicans	x	x	x
Celastrus scandens	x	x	x	Ribes odoratum	x	h	x
Cephalanthus occidentalis	x	x	x	Rosa carolina var. villosa		x	x
Cissus incisa	x	x	x	Rosa foliolosa		x	x
Clematis versicolor			x	Rosa setigera		x	x
Cocculus carolinus	x	x	x	Rubus spp.	x	x	x
Cornus Drummondii	x	x	x	Sambucus canadensis	h	x	x
Corylus americana			x	Smilax Bona-nox	x	x	x
Euonymus spp.	h	x	h	Smilax rotundifolia	x	x	x
Forestiera pubescens var. pubescens	x	h	h	Staphylea trifolia		h	x
Hypericum densiflorum var. lobcarpum			x	Symphoricarpos orbiculatus	x	x	x
Hypericum frondosum			x	Vaccinium arboreum		x	x
Hypericum spathulatum			x	Vaccinium stamineum var. neglectum			x
Ilex decidua		x	x	Vitis spp.	x	x	x
Ipomoea sp.	h	x	h	Xanthoxylum americanum		x	x
Lonicera albiflora	x	h		Xanthoxylum Clava-Herculis		x	x
Lonicera sp.		x	x				
Lyonia ligustrina var. salicifolia			x				
Menispermum canadense	h	h	x				
Parthenocissus quinquefolia	x	x	x				

of the stands sampled in every section of the state: *Rhus radicans, R. glabra, Symphoricarpos orbiculatus, Smilax Bona-nox, Parthenocissus quinquefolia,* and *Vitis* spp. Of the shrubs and woody vines, only one species was confined to the Western section and none to the Central section, based on data from samples and herbarium specimens. On the other hand, 10 taxa were limited to the Eastern section.

Constance

Constance percentages were determined for all arborescent species encountered in the study. A comparative compilation of the constance data, on the octette of major species, is presented in Table XI. On a state-wide basis, post oak and blackjack were each present in over 90% of the stands, black oak and black hickory occurred in over 50% of the samples, where the other dominants occurred in a relatively small percentage of the stands. The constance percentages indicate again the wide

TABLE XI. Constance percentages of important upland trees in sections of Oklahoma. Arranged according to decreasing importance percentages

Species	Western	Central	Eastern	State
Post oak	69.4	98.7	97.7	93.2
Blackjack	83.3	100.0	93.3	94.2
Black oak		46.3	83.3	54.3
Black hickory		52.4	85.5	57.6
Shortleaf pine			31.1	13.4
Mockernut			67.7	29.3
Winged elm		29.2	45.5	31.2
White oak			27.7	12.0

distribution and prominence of post oak and blackjack in the upland forests of Oklahoma. With reference to constance percentages, both species had the lowest values in the Western section and the highest in the Central division (Table XI). Of all the species, only blackjack was sampled in every stand of a given (Central) section of the state. When compared with post oak, blackjack exhibited a higher constance percentage in the

Western and Central sections but a lower value in the Eastern division (Table XI).

Summary

1. The upland deciduous forests of Oklahoma extend across the main body of the state from east to west with diminishing number and stature of their woody components. Apparently the present upland forests possess a greater arborescent cover than the original stands because of heavy grazing and the absence of fire.

2. This report is concerned with quantitative, phytosociological analyses of 208 stands during the summers of 1953 through 1957.

3. Presence for all woody species was obtained by reconnaissance. The number of trees and saplings was determined by means of 40 arms-length rectangles and the basal area of trees was calculated by an angle gauge at 40 points in each stand. From these data the following compilations were made for each species: number per acre, basal area per acre, relative frequency, relative density, relative basal area, and importance percentage.

4. When dominants were designated as those species having an importance percentage of 25 or above, there were 25 types of stands. Four of these types were confined to the Western section of the state, none was exclusive to the Central region, but 13 types of stands were limited to Eastern Oklahoma.

5. The upland, deciduous forest of Oklahoma was divided into the following faciations or association-segregates: oak-loblolly pine forest, oak-hickory-pine forest, oak-hickory forest, oak-hickory savannah, and oak savannah. The Eastern section comprised all of the above faciations. Except for a few mesic habitats, the Central region included only the last two faciations and the Western section comprised only the oak savannah.

6. On a state-wide basis, the only important tree species were post oak (*Quercus stellata*) and blackjack (*Quercus marilandica*). This was true whether based on presence, constance, frequency, density, basal area, or importance percentage data. Other prominent species, in order of decreasing importance percentages, were black oak (*Quercus velutina*), black hickory (*Carya texana*), shortleaf pine (*Pinus echinata*), mockernut (*Carya tomentosa*), winged elm (*Ulmus alata*), and white oak (*Quercus alba*). Eight other species were dominants in at least one stand.

7. All types of stands were found to be reproducing themselves adequately, as indicated by the abundant saplings present. This was notably true for the stands in the oak-hickory savannah and the oak savannah. These, and other facts, suggest that these savannahs should be designated as climax communities, and that their major components should be considered as climax dominants.

8. Some trees, in every type of community, were destroyed during the extended drought from 1952 through 1956. The greatest destruction occurred in the Western section and the least along the eastern border. In stands that included both blackjack and post oak, more blackjack than post oak trees were killed by the drought.

9. The upland forests of Oklahoma comprised 74 arborescent species and 60 shrubs and woody vines. Several tree species were confined to certain sections of the state, the sections and their exclusive species being as follows: Western, *Juglans microcarpa* and *Quercus virginiana;* Central, none; Eastern, *Pinus echinata, Pinus Taeda* and 14 other species. Of the shrubs and woody vines, only one species was limited to the Western section and none to the Central section. Ten species were confined to the Eastern section.

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PHYTOSOCIOLOGICAL AND ENVIRONMENTAL CHARACTERISTICS OF OUTBREAK AND NON-OUTBREAK AREAS OF THE TWO-YEAR CYCLE SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA*[1]

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INTRODUCTION

In the most severe outbreak areas in the eastern and western parts of North America, the spruce budworm, *Choristoneura fumiferana* (Clem.) (Tortricidae), maintains a one-year life cycle. Within the Canadian Rocky Mountains, however, the budworm's life cycle lasts two years. The outbreaks are also quite different in character. The two-year cycle budworm is present in most of the spruce-fir stands of this region, but high populations recur only in certain restricted stands within this spruce-fir forest. This would indicate that there are essential habitat differences between the outbreak and non-outbreak areas which affect the ability of the budworm to reproduce and survive. Detailed descriptions were made of the soil, plant, and climatic characteristics of these two habitats from a forest community viewpoint. Differences in the environmental conditions between the habitats led to an evaluation of the factors affecting the favorable development of the budworm. The importance of these factors was investigated by assessing budworm survival under the two sets of environmental conditions.

The study areas were located in Banff, Yoho, and Kootenay National Parks in the Canadian Rocky Mountains. Eight outbreak areas were located from past records, and seven non-outbreak

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