

THE VEGETATION OF A TRACT OF ANCIENT
CROSS TIMBERS IN OSAGE COUNTY,
OKLAHOMA

By

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CHAPTER I

A COMMUNITY CLASSIFICATION AND GRADIENT ANALYSIS OF A TRACT OF ANCIENT CROSS TIMBERS IN OSAGE COUNTY, OK

ABSTRACT

The Cross Timbers are a mosaic of forests, glades, and savannas located in the forest-prairie transitional zone in Kansas, Oklahoma, and Texas. Because of their noncommercial timber, these forests may contain more extant old-growth than any other eastern deciduous forest. The purpose of the present study was to characterize the patterns of woody vegetation on a tract of ancient Cross Timbers. I sampled the woody vegetation in 85 plots during the growing season of 1997. I defined seven communities on the basis of physiognomy and topographic position: upland savannas, upland forests, upland glades, narrow forest ravines, floodplain community, riparian community, and lakeshore community. I further classified the upland forests into five types based on dominant woody species: *Quercus stellata*-*Q. marilandica*, *Q. stellata*-*Vaccinium arboreum*, *Q. stellata*-*Carya texana*-*Q. velutina*, *Q. velutina*, and *Q. shumardii* stands. Gradient analyses revealed that topographic position, through its influence on soil moisture and nutrient regimes, was important in shaping overall species composition. A rather long gradient separated the uplands from the lowlands and was probably related to soil moisture. Among the upland communities, soil fertility, as indicated by nutrient concentrations, cation exchange capacity (CEC), and organic matter, was an important influence on species composition and separated communities on north-facing slopes from those on west-facing slopes and ridgetops.

INTRODUCTION

The Cross Timbers are a mosaic of forests, glades, and savannas that mark the transition from the eastern deciduous forests to the central grasslands. They extend from southeastern Kansas, through eastern and central Oklahoma, and into north-central Texas (Fig. 1), forming a north-south oriented band of vegetation that dissects the tallgrass prairie vegetation type (Duck and Fletcher 1943; Küchler 1964). In presettlement times, the Cross Timbers may have covered some 7,909,700 ha (Küchler 1964).

The origin of the name “Cross Timbers” is not known, but it may have been coined by the early explorers of the region who crossed these belts of timber on their journey westward (Foreman 1947). Kennedy (1841) wrote: “When viewed from the adjoining prairies on the east or west, it [the Cross Timbers] appears in the distance as an immense wall of woods stretching from south to north in a straight line, the extremities of which are lost in the horizon...”

Due to the dry climate in this region, the trees of the Cross Timbers forests do not attain large sizes and hence have little value for timber production. As a result, the Cross Timbers may contain more extant old-growth than any other eastern deciduous forest type (Stahle 1996). Scientists conducting dendrochronological research over the past 15 years have located hundreds of uncut Cross Timbers forests, particularly in Oklahoma (Stahle *et al.* 1985; Stahle and Cleaveland 1993; Therrell 1996). All of them contain *Quercus stellata* (post oak) in the 150- to 300-year age class, and one site includes the oldest individual of *Q. stellata* ever recorded, over 400 years old.

The vegetation and vegetation-environment relationships of the upland forests of Oklahoma have been thoroughly described by other naturalists (Bruner 1931; Weaver and

Clements 1938; Duck and Fletcher 1943; Barclay 1947; Dyksterhuis 1948; Rice and Penfound 1959; Dwyer and Santelmann 1964; Johnson and Risser 1971; Risser and Rice 1971; Bell and Hulbert 1974; Harrison 1974; K uchler 1974). However, a study with the expressed purpose of describing the vegetation of an *ancient* Cross Timbers site has not been conducted. The purpose of the present study was (1) to describe patterns in woody vegetation and (2) to determine the environmental factors responsible for these patterns on a tract of ancient Cross Timbers.

METHODS

DESCRIPTION OF STUDY SITE

I conducted the study on a tract of ancient Cross Timbers in southern Osage County, Oklahoma (Township 20 N, Range 10 E), generally known to ecologists and conservationists as the “Frank Tract”. Located approximately 10 miles west of downtown Tulsa on U.S. Highway 412 (Fig. 2), the tract comprises approximately 445 ha of the rugged uplands overlooking the Arkansas River (impounded by Keystone Lake) near its confluence with the Cimarron River. Elevation ranges from 323 m on the ridgetops to 229 m in the creek bottoms and on the lakeshore. The average annual precipitation is 93 cm, the average winter temperature is 4° C, and the average summer temperature is 25° C (Oklahoma Climatological Survey 1996). The land is owned by Mr. Irvin Frank of Tulsa, Oklahoma, with the exception of the lakeshore buffer zone which is managed by the U.S. Army Corp of Engineers.

The Frank Tract provided an ideal site for a floristic study of the ancient Cross Timbers primarily because it contains extensive tracts of old-growth forests. During field

tests of a predictive model to locate ancient Cross Timbers in southern Osage County, Therrell (1996) discovered that the steep slopes of the Frank Tract retain uncut forest on at least 90% of the land surface. These slopes are covered with 200- to 400-year-old *Quercus stellata* (Stahle *et al.* 1996). In addition, the site contains many ancient *Juniperus virginiana* (eastern red cedar) in the 300- to 500-year age class, including the oldest *J. virginiana* ever recorded in Oklahoma (over 500 years) (Stahle *et al.* 1996).

In addition to forests, the Frank Tract also contains a broad cross-section of the other communities that characterize the Cross Timbers, including savannas, glades, and a mesic floodplain. The varied topography of this site creates a variety of microhabitats that add to the diversity of the area. The tract contains numerous dissected ridges and includes north, south, east, and west exposures.

Although the forests of the Frank Tract have not been cut, there is anthropogenic disturbance on the site. However, the greatest amount of evidence for disturbance was found on the ridgetops; the forested slopes appear to be relatively undisturbed. Associated with oil exploration, there are several gravel roads, oil wells, and pipelines on the ridgetop. The effects of fire suppression are indicated by numerous thickets of *Rhus glabra* (smooth sumac) and trees of *Juniperus virginiana* that have invaded the ridgetop savannas. It appears that the savannas and parts of the forests have been grazed, as evidenced by manmade ponds and antique barbed wire around trees. In addition, the ruins of two foundations were noted on the ridgetop.

COLLECTION OF DATA

From April to September 1997, I sampled the woody vegetation in 85 plots at the Frank Tract. I subjectively chose the location of each plot because I wanted to represent all major community types at the site. I used a square or rectangular quadrat, depending on topography. On most sites, I set up a 30 m x 30 m plot with a 10 m x 10 m plot in the center. The center plot was designated the “core” and the surrounding area was the “boundary”. On rock outcrops, narrow ravines, and other sites with unusual topography, I used a rectangular 10 m x 50 m plot. For two high bluffs, I modified the rectangle to be an 18 m x 50 m plot. In all cases, the central 10 m x 10 m area of the rectangle was designated the core plot.

In each plot, I identified and measured the diameter at breast height (DBH) of all woody stems taller than breast height and with a DBH greater than 2.5 cm. In the core plot, I also identified and recorded the DBH of all saplings (woody stems taller than breast height with a DBH less than 2.5 cm). Species nomenclature follows Kartesz (1994) for scientific names and Taylor and Taylor (1994) for common names. A complete list of vascular taxa encountered at the tract is included in Appendix A.

In each core plot, I also recorded selected environmental data. I measured percent slope using a clinometer and aspect using a compass. I estimated percent cover of bare ground, rock, understory plants, moss, and water, and, at each corner, I measured the percentage canopy cover using a convex spherical densiometer (Lemmon 1956).

For each core plot, I collected a soil sample to a depth of 10 cm in each corner, composited the four samples into one, air-dried the composite sample, and sent it to Brookside Laboratories, Inc. (New Knoxville, OH). The laboratory analyzed each

sample for cation exchange capacity (CEC), pH (1:1 H₂O), percent organic matter, exchangeable anions (sulfur and phosphorous), exchangeable cations (calcium, magnesium, potassium, and sodium), and trace elements (boron, iron, manganese, copper, zinc, and aluminum). They reported anions, cations, and trace elements in parts per million (ppm).

ANALYSIS OF DATA

To quantify species abundance, I calculated an importance value for each woody species in each plot. The importance value was the average of relative density and relative basal area. I used aspect data to create five dummy variable categories that incorporated both aspect and topographic position: ridgetops, north-facing slopes, east-facing slopes, south-facing slopes, west-facing slopes, and lowlands. For percentage canopy cover, I averaged the four measurements to get one value for each plot.

I subjectively classified each plot into a community type on the basis of its physiognomy and topographic situation. I then used techniques of gradient analysis to subdivide further the upland forests into community types and to elucidate the most important gradients related to species composition.

I used detrended correspondence analysis (DCA), an indirect gradient analysis technique, to determine the important gradients as defined by the species (Hill and Gauch 1980). Axes were scaled in average standard deviations (SD) of species turnover, and complete turnover of species composition was expected to occur in about 4 SD. I then used a complementary direct gradient analysis technique, canonical correspondence analysis (CCA), to reveal the important gradients as defined by the measured

environmental variables (ter Braak 1986). Continuous variables were represented as biplot arrows pointing in the direction of maximum change for that variable, and the length of an arrow was proportional to the strength of the gradient represented by that arrow. Dummy variables were represented as centroids. In DCA and CCA, eigenvalues close to one indicate strong gradients while those close to zero indicate weak gradients (Hill and Gauch 1980; ter Braak 1986).

I performed all gradient analyses using the program CANOCO® (ter Braak 1997). I ran two series of ordinations: one on all plots and one on the upland forest plots. Prior to analysis, importance values were square-root transformed to ensure that dominant species did not have an undue influence on the analysis (Gauch 1982). Also, rare species were downweighted, and a plot containing only one species (encountered in only two plots in the study) was omitted. This was done because rare species often obscure the true results of ordinations (Gauch 1982). Soil element concentrations were log transformed following the recommendation of Palmer (1993). For the CCAs, percent cover of canopy, bare ground, understory plants, and mosses were eliminated from the analysis. These variables are of little value in explaining woody species composition because they were either derived from or strongly influenced by the woody vegetation.

To assist in the interpretation of the gradient analyses, I ran Scheffe's test, a pairwise comparisons procedure, to determine if there were differences in environmental characteristics between communities. Because not all of the data were normally distributed, I performed a log transformation on soil element concentrations and an arcsine transformation on slope and cover values before statistical analysis.

RESULTS AND DISCUSSION

COMMUNITY DESCRIPTIONS

I defined seven communities at the Frank Tract on the basis of their physiognomy and topographic position: upland savannas, upland forests, upland glades, narrow forest ravines, floodplain community, riparian community, and lakeshore community.

Savannas

Savannas cover much of the ridgetops at the Frank Tract. They are open landscapes characterized by low canopy cover and a well developed herbaceous layer (Table 1). Each is similar to a tallgrass prairie dominated by the grass *Schizachyrium scoparium* (little bluestem) and frequently interrupted by clusters of trees and extensive colonies of clonal shrubs. *Quercus marilandica* (blackjack oak), *Prunus angustifolia* (chickasaw plum), and *Rhus glabra* (smooth sumac) were the most abundant woody species in the savanna plots (Table 2). *Q. marilandica* had an importance percentage more than three times that of *Q. stellata* (post oak; Table 2). The reverse was true for a Cross Timbers savanna in central Oklahoma, where *Q. stellata* was more than three times as abundant as *Q. marilandica* (Johnson and Risser 1975).

I believe that the savannas of the Frank Tract were indeed part of the presettlement landscape and were maintained by a combination of edaphic factors. First, soil texture is an important consideration. The savannas are located on sandy, well-drained soils (Bourlier *et al.* 1979). On a similar site in central Oklahoma, Johnson and Risser (1975) studied an upland savanna and an adjacent lower forest and concluded that the lower forest had once been a savanna but had converted to forest in the absence of

fire. They proposed that the upland savanna persisted because of its sandy, permeable substrate. The sandy soil quickly discharged rain water to the lower slopes, making the lower slopes more suitable for tree growth than the adjacent uplands.

Fire also plays a key role in the maintenance of savannas. There is an abundance of evidence that fires in the forest-prairie transitional zone were much more frequent in the presettlement era (Bragg 1971; Cutter and Guyette 1994; Robertson and Heikens 1994). Fires burning in savanna landscapes inflict greater damage to woody plants than those burning in forests, probably because of the greater intensity of heat produced by burning grass litter (Johnson and Risser 1975). Thus, frequent fires in the savannas would have kept woody growth in constant check and thereby helped to maintain an open landscape (Bragg 1971; Schwegmann and Anderson 1984; Robertson and Heikens 1994).

At the Frank Tract, the evidence of woody encroachment is abundant. They are dotted with *Juniperus virginiana* (eastern red cedar), a very fire-sensitive species (Arend 1950). In addition, some of the ridgetops support closed-canopy forests. These ridgetop forests contain some trees with the broad, open crowns that are characteristic of savanna trees, indicating that these areas once supported a savanna landscape and not a forest (Johnson and Risser 1975). With proper management, I believe that these areas could be restored to their presettlement conditions. After just one intense fire in the Spring of 1996, I observed that many of the *Juniperus* individuals scattered throughout the savannas were killed.

Upland Forests

The upland forests of the Frank Tract occur on sideslopes with a variety of aspects and exposures. As noted above, there are also some forested areas on the ridgetops, intermingled with the savannas. In general, the forests were quite open, with an average canopy cover of about 67 percent (Table 1). Also noteworthy is the low cover of understory plants (Table 1). McPherson and Thompson (1972) demonstrated that the litter of *Quercus stellata* and *Q. marilandica*, two of the most important species in the forests of the tract, inhibits the growth of understory plants. The authors suggested that the litter inhibits seedling germination by blocking sunlight.

Quercus stellata was by far the most important canopy tree in the upland forests (Table 2). *Q. velutina* (black oak), *Carya texana* (black hickory), and *Q. marilandica* were next in abundance but all had importance percentages between 10 and 13, considerably lower values than that of *Q. stellata* (Table 2). In a study of 82 Cross Timbers stands, *Q. stellata* and *Q. marilandica* were codominant, *i.e.*, both had importance percentages greater than 25, in 79 stands (Rice and Penfound 1959). Thus, it seems that the upland forests at the Frank Tract exhibited a low abundance of *Q. marilandica* compared to other Cross Timbers sites.

I further subdivided the upland forests into five groups based on the dominant canopy trees. Classification was aided by a detrended correspondence analysis (DCA) which will be presented in a later section.

Quercus stellata-Q. marilandica Forests

These forests are most frequently found on ridgetops and exposed west-facing slopes (Table 3). I sampled 15 plots in this community. The *Quercus stellata-Q. marilandica* forests were more open, had more bare ground, and had less understory plant cover than any other upland forest community (Table 3). Slopes were gentle to moderate, with an average of 22 percent. *Q. stellata* was the dominant canopy tree, achieving its highest abundance in these stands (Table 4). *Q. marilandica* was codominant in most of these stands (Table 4). However, in three stands, *Q. marilandica* was unimportant and *Q. stellata* had an importance percentage of 79 or greater. *Carya texana* was next in importance, although its abundance was considerably less than that of *Q. marilandica* (Table 4). No other woody species achieved an importance greater than 4%.

The *Quercus stellata-Q. marilandica* community is the most common forest association in the Cross Timbers. In a study by Rice and Penfound (1959), one or both of these species was dominant, *i.e.*, had an importance percentage of 25 or greater in 74 of the 82 Cross Timbers stands sampled. Based on the definition of dominance used by these authors, 9 of the 15 *Q. stellata-Q. marilandica* plots in the current study were dominated by both species and 6 were dominated by only *Q. stellata*.

In plots codominated by *Quercus stellata* and *Q. marilandica*, the abundance of *Q. stellata* generally exceeded that of *Q. marilandica* by a factor of 1.5 to 2. However, in one plot on a ridgetop, *Q. marilandica* was almost twice as abundant as *Q. stellata*. The success of *Q. marilandica* on this site may be related to soil characteristics. The well-drained, fine sandy loam soils on the ridgetop were drier than those of the sideslopes

(Bourlier *et al.* 1979). *Q. marilandica* seems to be a better competitor on dry sites than other upland forest trees (Johnson and Risser 1971).

Quercus stellata-Vaccinium arboreum Forests

These forests are found on sites with a variety of aspects and exposures (Table 3). I sampled nine plots in this community type. Compared to the *Quercus stellata-Q. marilandica* stands, the *Q. stellata-Vaccinium arboreum* (farkleberry) stands had steeper slopes, rockier substrate, and higher moss cover (Table 3). These stands had more moss cover than any other upland forest community. As in the *Q. stellata-Q. marilandica* stands, herbaceous cover was sparse (Table 3). In all nine stands, *Q. stellata* and *V. arboreum*, an ericaceous understory shrub, were codominant (Table 4). In four stands, *Juniperus virginiana* was the second most important canopy tree (Table 4). However, in four other stands, *Q. velutina* was the second most important canopy tree and *J. virginiana* was relatively unimportant. In the remaining stand, *Q. marilandica* was the subdominant canopy tree.

Juniperus virginiana occupies a rather unique habitat in the forests of the Frank Tract. The typical habitat for this species in forests further east is a few specialized locations such as cliff edges, glades, and old fields in the early stages of succession (Bard 1952; Rochow 1972). At the Frank Tract, however, *J. virginiana* was not confined to such areas and sometimes achieved rather impressive sizes in the interior of sideslopes. In addition to size, the antiquity of many of these junipers is remarkable. Trees with ages in excess of 500 years have been documented on this site (Stahle

et al. 1996). This greatly exceeds the maximum age of 300 years alluded to by Fowells (1965).

The success of *Juniperus virginiana* in the mature forests of the Frank Tract is probably related to two factors. First, the open canopy of these forests (Table 3) allows more light to reach the forest floor, creating a suitable habitat for the shade-intolerant *J. virginiana*. Second, the location of these slopes on the eastern side of the Arkansas River may have provided more protection from fire than in surrounding areas, also favoring the fire-sensitive seedlings of *J. virginiana*. Forests on the eastern side of rivers are protected from fires being carried from west to east by the prevailing winds (Gleason 1913).

Quercus stellata-Carya texana-Quercus velutina Forests

This forest type occurs on a variety of aspects and topographic positions (Table 3). I sampled 21 plots in this community type. These stands had more herbaceous cover and less bare ground than the stands where *Quercus marilandica* and *Juniperus virginiana* were important (Table 3). Overall, *Q. stellata* was the most abundant tree species, with an average importance of 40 percent (Table 4). *Carya texana* and *Q. velutina* were next, with average importances of 21 and 20 percent, respectively. No other woody species achieved an importance greater than 5 percent.

Quercus stellata was the dominant canopy tree in most of the 21 stands in this group, but the subdominant canopy species varied. In six stands, *Carya texana* had an importance of 25 percent or greater. In eight stands, *Q. velutina* was subdominant, with an average importance of 20 percent or greater. In four stands, *Q. shumardii* (shumard

red oak) achieved an importance ranging from 10 to 32 percent. Finally, in three stands, *Q. stellata* had an importance of 61 percent or greater and other species were relatively unimportant.

Quercus velutina Forests

These stands had notably high importance percentages of *Quercus velutina* (Table 4). There were four stands in this forest type; one was on a north-facing slope, two were on east-facing slopes, and one was on a west-facing slope (Table 3). Other less important species were *Q. stellata*, *Q. shumardii*, *Carya texana*, *Vaccinium arboreum*, and *Juniperus virginiana* (Table 4).

The *Quercus velutina*-dominated stands in the forests of the Frank Tract may represent a rare association in the Cross Timbers. In a study of 82 stands throughout the Oklahoma Cross Timbers, Rice and Penfound (1959) found only five stands in which *Q. velutina* had an importance percentage greater than 25.

The high importance of *Quercus velutina* at this site is probably due to the unique topography. Although *Q. velutina* occupies dry sites in more mesic deciduous forests, in the Cross Timbers this species is confined to the most mesic sites and is not found in stands codominated by *Q. stellata* and *Q. marilandica* (Fowells 1965; Johnson and Risser 1971; Kennedy 1973). Its success at the Frank Tract may be due to the numerous dissected ridges on the site, many of which have a more or less northern aspect and are sheltered from direct solar radiation by shading from nearby land masses. The combination of these factors probably creates a more humid microhabitat, favoring species such as *Q. velutina*.

Quercus shumardii Forests

These forests are confined to north and east-facing slopes (Table 3). They were the steepest of the upland forest communities, with an average slope of 55 percent (Table 3). They also had a higher percent canopy cover than other upland forests. The ground cover was characterized by large sandstone boulders and outcrops, and the forests had a higher percent cover of rock than any other upland forest community (Table 3). *Quercus shumardii* was by far the most abundant species, and *Carya texana* and *Q. muehlenbergii* (chinquapin oak) were next in importance (Table 4).

The *Quercus shumardii* association on the north-facing slopes of the Frank Tract appears to be a rare community in the Cross Timbers. *Q. shumardii* had an importance percentage of 40 or greater in three of the four plots sampled in this association. In contrast, *Q. shumardii* did not achieve dominance, *i.e.*, an importance percentage greater than 25, in any of the 82 Cross Timbers stands sampled by Rice and Penfound (1959). *Q. shumardii* seems to be more important in the more mesic oak-hickory forests of eastern Oklahoma, where it reportedly formed distinctive associations with *Q. alba* (white oak) on north-facing slopes (Rice and Penfound 1959). In a reanalysis of the upland forest data collected by Rice and Penfound (1959), Risser and Rice (1971) found *Q. shumardii* to be the most mesic of the oaks in the Cross Timbers.

Miscellaneous Ridgetop Forests

Several forest plots on the ridgetops were not placed in one of the five categories previously defined because of unique species composition. One plot, located near a main road, was dominated by *Carya texana* but had a very high abundance of *Cercis*

canadensis (redbud; I.V.=33%). Another plot near the road was dominated by *Quercus stellata* but had an unusually high abundance of *Cocculus carolinus* (Carolina snailseed), a woody vine (I.V.=29%). In addition, the *Cocculus* was mainly seen growing on *Prunus mexicana* (big-tree plum; I.V.=7%), a tree that was relatively uncommon overall.

Another plot had a high abundance of *Ulmus rubra* (slippery elm; I.V.=69%), a tree that was scattered but relatively common on the ridgetops. Finally, a rather unusual plot was located in an area where a man-made pond once existed. This plot had contrasting species composition, with high abundances of *Quercus marilandica* and *Platanus occidentalis* (sycamore), species with very different moisture requirements. It is likely that the pond was constructed decades ago and provided enough moisture to allow species like *Platanus occidentalis* to become established in an otherwise dry environment where *Q. marilandica* was abundant.

Glades

The glades of the Frank Tract are prairie-like openings within the upland forests. These openings are small, the largest was approximately 10 m x 50 m, and are located on exposed, gently sloping, west to northwest-facing sideslopes within the *Quercus stellata*-*Q. marilandica* forests. As in the savannas, *Schizachyrium scoparium* and other tallgrass prairie species (especially those adapted to dry, harsh environments) covered most of the ground. However, unlike the savannas, the glades had substantial cover of rock and bare ground (Table 1). *Juniperus virginiana* and *Q. stellata* were the only woody species encountered in the glade plots, and *J. virginiana* had a slightly higher importance percentage than *Q. stellata* (Table 2).

Glades are widespread in the eastern deciduous forests. They occur in the forests of Tennessee, along the Mississippi River from Minnesota to Missouri, and along the prairie-forest transitional zone from Wisconsin to Oklahoma (Curtis 1959). *Juniperus virginiana* is common in all of these glades (Quarterman 1950; Bray 1955; Rochow 1972; Pallardy *et al.* 1988).

Narrow Forest Ravines

The ravines are narrow gulleys located between steep sideslopes near inlets of the lake. No woody species clearly dominated the community, but *Juniperus virginiana* had the highest importance percentage (Table 2). Slightly less important were *Cornus drummondii* (rough-leaved dogwood), *Platanus occidentalis*, and *Quercus stellata*. *Ilex decidua* (deciduous holly), a shrub, was encountered in one of the ravine plots. This species was not found in any of the other 84 plots sampled at the Frank Tract.

Floodplain Community

This community is in a valley between steep sideslopes. A permanent stream, Brush Creek, flows south through the valley to the Arkansas River just below Keystone Lake. Approximately 100 m wide at its widest point, the floodplain at the sample locations was probably plowed at one time, as evidenced by dense stands of *Verbascum thapsus* (common mullein), *Cirsium altissimum* (tall thistle), and *Lespedeza cuneata* (sericea lespedeza), herbaceous species that are exotic to North America. The most abundant woody species in the floodplain was *Quercus stellata*, followed by *Cornus drummondii* and *Juniperus virginiana* (Table 2). No other woody species achieved an

importance of more than 5 percent. Understory growth was much more vigorous here than in the upland forests (Table 1).

The floodplain of Brush Creek has a physiognomy and species composition notably different from the other lowland communities studied in this region. Several pieces of evidence indicate that the lower part of this valley was cleared at one time and is now in a state of succession. First, the overall appearance of the floodplain landscape is that of an open savanna punctuated by scattered trees and dense patches of woody vegetation. In addition, the basal area of woody vegetation was lower in the floodplain than in any of the upland forest communities. In contrast, studies in the Cross Timbers and the Ozarks have shown that basal area of woody vegetation is greater in floodplains than in adjacent upland forests (Rice 1965; Zimmerman and Wagner 1979). This would seem to indicate that a forest, not a savanna landscape, is the steady-state vegetation type for this site.

Quercus stellata was the most important tree in the floodplain of the Frank Tract. This contrasted with studies of floodplains in nearby Cross Timbers sites, where *Q. stellata* was unimportant and stands were dominated mostly by *Ulmus americana* (american elm) and occasionally by *Celtis occidentalis* (hackberry; Rice 1965). In the present study, *U. americana* was not encountered in any of the floodplain samples and *C. occidentalis* was rare.

Cornus drummondii had the second highest importance percentage of any species in the floodplain and it formed dense thickets in some places. This shade intolerant shrub is also indicative of a successional community, because it thrives in open habitats but diminishes in importance as the canopy becomes more closed.

Riparian Community

This community is located in and along Brush Creek. *Platanus occidentalis* was the most abundant woody species, followed by *Juniperus virginiana* and the vine *Smilax bona-nox* (greenbriar; Table 2). The riparian community was rather open, with an average canopy cover of just 24 percent (Table 1). The ground was largely covered by understory plants and water (Table 1). Compared to the narrow ravines near the lake, the community along Brush Creek had substantially less bare ground and rock and about five times as much herbaceous cover (Table 1).

The streamside forests along Brush Creek were dominated by *Platanus occidentalis*. *Juglans nigra* (black walnut), *Smilax bona-nox*, and *Cercis canadensis* were also important, although to a lesser degree. *P. occidentalis* also was reported to have a high importance in the bottomlands of the northern Ozarks in Missouri (Rochow 1972; Zimmerman and Wagner 1979), but, interestingly, was not reported as a dominant in the bottomland forests of north-central Oklahoma (Rice 1965).

Harrison (1974), traveling throughout the Cross Timbers in Texas and Oklahoma, qualitatively described the gallery forests as being dominated by *Salix nigra* (black willow), *Populus deltoides* (cottonwood), and *Celtis laevigata* (sugarberry). However, I rarely encountered these species at the Frank Tract. In fact, *S. nigra* and *P. deltoides* were completely absent from plots in the lowland communities of the Frank Tract, and *C. laevigata* was found in only one plot in the floodplain.

Lakeshore Community

This community is clearly a disturbed habitat, being heavily altered by the impoundment of Keystone Lake. Three woody species occurred in the plots sampled here: *Cephalanthus occidentalis* (buttonbush), *Diospyros virginiana* (persimmon), and *Platanus occidentalis*. *C. occidentalis* had the highest importance percentage (Table 2). The lakeshore community contained the largest amount of bare ground of any community at the Frank Tract (Table 1). It also contained a large amount of rock and little herbaceous cover.

Pond Community

I sampled one plot in a pond, probably designed for oil containment. The area immediately surrounding the pond was dominated by *Salix nigra* (I.V.=46%), an uncommon species overall. *Juniperus virginiana* (I.V.=31%) was also abundant on the periphery of the pond, probably due to shelter from fire.

GRADIENT ANALYSIS

All Communities

In a detrended correspondence analysis (DCA) of all plots, the first axis separated the upland communities on the left from the lowland communities on the right (Fig. 3). The first axis represented a strong gradient, as indicated by a length of 5.2 standard deviation units (SD) and by an eigenvalue of 0.596. The upland forests, savannas, and glades had the lowest scores along this axis, the floodplain had intermediate scores, and the riparian and lakeshore communities had the highest scores. Mesic species such as

Platanus occidentalis, *Cephalanthus occidentalis*, *Juglans nigra*, and *Smilax bona-nox* had the highest scores along DCA axis I, while more xeric species such as *Prunus angustifolia*, *Rhus copallina* (winged sumac), *Vaccinium arboreum*, *Amelanchier arborea* (juneberry), and *Quercus marilandica* had the lowest scores. Thus, I interpreted DCA axis I as a gradient in increasing soil moisture from the uplands down to the lowlands.

The second axis of the DCA of all plots highlighted differences among the upland communities (Fig. 3). This axis was 3.8 SD in length and had an eigenvalue of 0.289, indicating a weaker gradient relative to the first axis. The upland savannas had the highest scores along this axis, while forests dominated by *Quercus shumardii* on north-facing slopes had the lowest scores. I interpreted DCA axis II as a gradient in degree of site exposure (*i.e.*, the amount of solar radiation reaching the site), with the savannas being the most exposed upland communities and the forests on north slopes the least exposed. Based on this interpretation, species such as *Rhus glabra*, *Q. marilandica*, and *Prunus angustifolia* were associated with the most exposed habitats, while species such as *Q. muehlenbergii*, *Q. shumardii*, *Rhus copallina*, and *Fraxinus americana* (white ash) were found in the most sheltered habitats (Fig. 3).

A canonical correspondence analysis (CCA) of all plots and species is shown in Figs. 4a, 4b, and 4c. All three figures represent the results of one analysis; they are broken apart merely for convenience. The orientation of plots and species along the first axis of the CCA (Figs. 4a and 4c) was remarkably similar to that of the first DCA axis. In the CCA, surface water and pH were positively correlated with axis I (Fig. 4b), with the lowland communities having higher values for these variables than the upland

communities (Fig. 4a). This further supported the soil moisture gradient inferred from the DCA. It should be noted that the riparian communities were the only communities with surface water and that differences in pH among the communities were not significant ($p < 0.05$; Table 1). Aluminum was negatively correlated with CCA axis I (Fig. 4b), but differences in aluminum content among the communities were not significant (Table 1).

The orientation of plots and species along the second axis of the CCA was also similar to that along the second DCA axis (Figs. 4a and 4c). In the CCA, communities on north-facing slopes had low scores along the second axis, while communities on south and west-facing slopes and ridgetops had high scores (Fig. 4b). Plots with a northern aspect had higher amounts of nutrients and organic matter than those with a southwestern or ridgetop position. Several soil factors, including organic matter, potassium, manganese, zinc, and cation exchange capacity (CEC), were highly negatively correlated with the second CCA axis. In general, the savannas had low values for these variables relative to other communities (Fig. 4a), and some of these differences were significant (Table 1). Compared to other upland communities, the glades had higher values for several soil parameters, including organic matter, CEC, magnesium, and sulfur (Table 1). However, the glades were low in phosphorous and zinc relative to the other upland communities.

Another noteworthy gradient in the CCA was a strong gradient in soil sodium that separated the lakeshore plots from all other plots (Figs. 4a and 4b). The lakeshore and glade communities had significantly higher levels of sodium than several other communities (Table 1).

Upland Forests

In order to further understand the relationships among the upland forest communities, I performed a second series of ordinations on only these communities. A DCA of forest plots is shown in Figure 5. Plots are grouped according to the five forest types described earlier.

The first DCA axis represented a relatively weak gradient, with an eigenvalue of 0.345 and a gradient length of about 3 SD (Fig. 5). I interpreted this axis as a gradient from xeric to mesic communities. The most xeric stands had low scores along DCA axis I and high abundances of one or more of the following: *Quercus stellata*, *Q. marilandica*, *Juniperus virginiana*, and *Vaccinium arboreum* (Fig. 5). The most mesic stands had high scores along axis I and high abundances of *Q. muehlenbergii* and *Q. shumardii*. Stands dominated by *Carya texana* or *Q. velutina* were intermediate in their response to the presumed moisture gradient.

The gradient represented by the second DCA axis was considerably weaker than the first, with a length of 1.7 SD and an eigenvalue of 0.161 (Fig. 5). This axis separated the two xeric stands from each other: the *Quercus stellata-Vaccinium arboreum* stands had high scores along axis II relative to the *Q. stellata-Q. marilandica* stands. In addition, the more pure *Q. velutina* stands had high scores relative to the mixed stands of *Q. stellata*, *Carya texana*, and *Q. velutina*. Among the species, *V. arboreum* had an extremely high score along DCA axis II relative to other species.

A CCA of all forest plots supported the xeric-to-mesic gradient by showing a strong gradient in increasing soil fertility along the first axis (Fig. 6). As in the DCA, *Q. shumardii* stands were distinctly separated from all other stands along the first axis

(Fig. 6a). These stands were associated with high calcium, magnesium, cation exchange capacity (CEC), and organic matter, while other stands generally had lower values for these variables (Figs. 6a and 6b). This was further supported by statistical analysis which showed that the *Q. shumardii* forests had significantly higher calcium and organic matter than any other forest type, except the *Q. velutina* stands (Table 3). In addition, magnesium and CEC were higher in *Q. shumardii* stands relative to other forest types, but not all of these differences were significant. Of the important canopy species, *Q. muehlenbergii* was associated with the highest nutrient levels, while *Q. marilandica* was associated with the lowest nutrient levels (Fig. 6c).

CCA axis I also showed a distinct separation of plots on north slopes from those on all other exposures, as seen by the positions of the centroids for the topographic dummy variables (Fig. 6b). This also supported the interpretation of a gradient in increasing soil moisture, since northern exposures are known to have greater soil moisture than other exposures (Werling and Tajchman 1984).

The position of *Platanus occidentalis* (a mesic species) on the xeric end of the gradient (Figs. 5 and 6c) seems to violate the interpretation given above. However, there is an explanation. *Platanus* only occurred in a single forest plot where *Quercus marilandica* (a xeric species) was dominant. This site was described earlier in the subsection entitled "Miscellaneous Ridgetop Forests". The occurrence of *P. occidentalis* in a *Q. marilandica*-dominated plot caused the former to behave as a xeric species in the ordination.

Although I was unable to interpret DCA axis II, the second axis of the CCA provided some helpful insights into the important gradients influencing the orientation of

plots. As in the DCA, the *Quercus stellata-Vaccinium arboreum* plots were separated from most other forest plots along the second axis (Fig. 6a). These stands were associated with low levels of manganese and low pH (Figs. 6a and 6b). In fact, these stands had significantly lower manganese than any other forest type except the *Quercus velutina* stands (Table 3). In general, the *Q. stellata-V. arboreum* stands had lower levels of most soil nutrients relative to other stands, although these differences were not always significant (Table 3). These stands were also associated with high levels of aluminum and rock cover and steep slopes (Figs. 6a and 6b). They had higher values for aluminum than other stands, but the differences were not significant (Table 3).

LANDSCAPE PATTERNS

The savannas, as a group, were more heterogeneous in woody species composition than any other upland community. This was shown by the extreme range of scores for savannas along both axes in the DCA of upland plots (Fig. 3). The observed heterogeneity may be related to the manner in which woody species are recruited into the savanna landscape. The savannas of the Frank Tract contained extensive clonal colonies of *Rhus glabra* and *R. copallina*. In a prairie-forest mosaic similar to that of the Frank Tract, Petranka and McPherson (1979) concluded that colonies of *R. copallina* were essential for the establishment of woody plants in the prairie. They found that the density of shrub and tree seedlings growing in the center of *R. copallina* clones was significantly greater than that in the prairie adjacent to the clone. In addition, several of the woody species growing in the midst of the *Rhus* clones were not encountered in samples in the adjacent prairie. The *Rhus* clones encouraged woody recruitment by inhibiting

herbaceous growth through allelopathy and reducing light intensity. This formation of *R. copallina* clusters would tend to increase the heterogeneity of the landscape, especially if the clonal patches differed from each other in species composition.

At the Frank Tract, the foregoing picture of woody recruitment also is supported by the observation that the trees of the savannas generally occur in dense clumps, not as single, uniformly spaced individuals. This is particularly true of the most abundant savanna tree, *Quercus marilandica*. Although the clumped pattern of this species may initially be promoted by recruitment under clonal *Rhus* thickets, it is probably maintained by the tendency of oaks to reproduce by sprouting from the parent tree rather than from seeds when top-killed (Powell and Lowry 1980).

Interestingly, the savannas of the Frank Tract not only include species characteristic of xeric upland habitats, such as *Quercus marilandica*, but also include *Cercis canadensis*, a species characteristic of mesic lowland habitats (Fig. 3). It is surprising to find *C. canadensis* in the savannas because of the droughty conditions created by the sandy, well-drained soil. The answer to this mystery may again lie in microhabitat alterations by the clonal *Rhus* thickets. The soil moisture underneath *R. copallina* clones was significantly greater than that in adjacent open prairie (Petranka and McPherson 1979).

Another factor that may have contributed to the observed heterogeneity of savannas is related to the sampling method. Having noticed the heterogeneous nature of the savannas, I attempted to sample at least one example of each different vegetation component. Thus, the plots may have been more different from each other in this subjective sampling scheme than they would have been had I used a random sampling

design. The small number of samples (7) probably compounded the effects of the subjectivity in sampling.

PLANT COMMUNITY-ENVIRONMENT RELATIONSHIPS

The use of direct gradient analysis (*e.g.*, CCA) for exploratory ecological studies, such as the present one, has been questioned (Økland 1996). For exploratory studies, the author argues that indirect gradient analysis (*e.g.*, DCA) is a more appropriate tool. DCA orients plots according to their beta diversity, or species composition, relative to each other (Gauch 1982). On the other hand, CCA disregards beta diversity and instead constrains plots along the measured environmental gradients (terBraak and Prentice 1988). If important environmental variables are not input in CCA, the investigator may miss important gradients structuring the community in question and this may lead to faulty interpretations regarding community-environment relationships (Økland 1996).

In the present study, I concluded that the environmental variables I measured can confidently be used to interpret community patterns. I base this conclusion on two observations that apply to all analyses. First, the orientation of plots and species in the DCA was similar to that of the CCA (Figs. 3-6). Second, the eigenvalues for the first and second axis of the DCA were similar to those of the CCA, with the CCA eigenvalues being only slightly lower (Figs. 3-6). Both of these factors indicated that the variation in species composition was explained fairly well by the measured environmental variables (ter Braak 1986).

Topographic position was probably the most important variable influencing species composition in the plant communities of the Frank Tract. Among all communities, the strongest gradient was one that separated the uplands from the lowlands (Figs. 3 and 4). Likewise, among the upland communities, the ridgetop areas were distinguished from forests on northern exposures along a rather long gradient (Figs. 5 and 6).

Topography exerts its influence on community structure by determining the amount of solar radiation that reaches a site. Solar radiation, in turn, influences the moisture and nutrient regimes of a site. For example, southwestern slopes receive greater amounts of solar radiation than northeastern slopes (Hutchins *et al.* 1976). Increased solar radiation affects the moisture regime of a site by accelerating evaporative losses (Hutchins *et al.* 1976). Several studies have shown that north-facing slopes have greater soil moisture than south-facing slopes (Franzmeier *et al.* 1969; Hutchins *et al.* 1976; Werling and Tajchman 1984). Higher soil moisture facilitates faster rates of litter decomposition on north slopes by providing suitable conditions for microarthropods and other decomposers (Mudrick *et al.* 1994). Hence, the soils of north-facing slopes are richer in organic matter than those of south-facing slopes (Franzmeier *et al.* 1969; Hicks and Frank 1984). The decomposition of this organic matter increases the levels of certain nutrients such as exchangeable manganese (Christensen *et al.* 1950).

The results of the present study suggest that topographic position may influence the species composition of a site by affecting decomposition and nutrient cycling. At the Frank Tract, communities on north slopes had the highest levels of organic matter and soil nutrients (Figs. 4b and 6b). In contrast, exposed communities on ridgetops and

southwestern exposures had the lowest levels of organic matter and soil nutrients (Figs. 4b and 6b).

Other forest studies have also confirmed the importance of topographic factors such as aspect in shaping the environment and species composition of a community. In a gradient analysis of oak-hickory stands in Missouri, Ware *et al.* (1992) found that aspect was significantly correlated with a DCA axis that separated stands on south and west-facing slopes, dominated by *Quercus muehlenbergii* and *Juniperus virginiana*, from stands on north and east-facing slopes, where more mesic species such as *Q. rubra* (red oak), *Acer saccharum* (sugar maple), and *Tilia americana* (american basswood) were more abundant.

One unexpected result was that gradients related to soil fertility were relatively unimportant in separating the lowland communities from the upland communities (Figs. 4a and 4b). Of the lowland communities, the ravines had the highest levels of nutrients and organic matter, but few of the parameters were significantly different from the uplands (Table 1). Even so, the species composition was much different in the lowlands when compared to the uplands (Fig. 4c). Thus, one might conclude that soil moisture is providing the major influence on species composition in the lowlands. This is further supported by the CCA which showed that surface water and pH were highly correlated with an axis separating the lowlands from the uplands (Figs. 4a and 4b).

Other studies have confirmed the importance of moisture in determining forest composition. In a gradient analysis of the western Cross Timbers in Oklahoma, Dooley and Collins (1984) concluded that a moisture gradient separated *Quercus stellata* - *Q. marilandica* forests from more mesophytic forests characterized by moisture-loving

species such as *Acer saccharum*. In a gradient analysis of an oak-hickory forest in Missouri, Zimmerman and Wagner (1979) found three discrete communities: bottomlands, protected slopes, and exposed south-facing slopes. The authors attributed differences in species composition between the three types to a gradient in moisture.

Another unexpected result was that the glades had the highest levels of organic matter and most nutrients (Table 1). Similarly, glades in the Missouri Ozarks were characterized by high levels of soil organic matter, nitrogen, and potassium (Pallardy *et al.* 1988). This result is surprising because of the dry, rocky nature of glade soils, the low productivity, and the lack of woody growth. The relatively high nutrient content of glade soils is probably due to higher levels of clay and organic matter, essentially the only components of soil that bind ions for plant uptake (Foth and Turk 1972). Cation exchange capacity (CEC) measures the ability of a soil to retain cations and anions for plant uptake and, thus, indirectly is an indicator of clay and organic matter content. The soils of the glades had a significantly higher CEC than those of other communities, except the ravines and lakeshore (Table 1).

If soils in the glades had more nutrients available for plant uptake than those of adjacent forests, the question remains as to why woody growth was limited in these tiny islands of grasses. The answer to this question is not clear, but one possibility is that some other nutrient is limiting the growth of trees in these areas. For example, phosphorous and zinc were significantly lower in the glades than in the upland forests (Table 1). Also, the shallow bedrock underlying the glades may retard woody growth. In addition, low soil moisture may be inhibiting the establishment of seedlings.

High levels of sodium in the glades and lakeshore communities may be related to several factors. First, irrigation runoff may have contributed to the high sodium levels in soils near the lake. Keystone Lake receives agricultural runoff from contributing rivers and streams, and this is known to increase the salinity of bodies of water (Bresler *et al.* 1982). In addition, the Arkansas River drains the Great Salt Plains, and this natural source of salts contaminates the water. Second, high evaporation rates may have increased soil sodium content in open habitats such as the glades.

High levels of aluminum in the *Quercus stellata-Vaccinium arboreum* forests were probably related to soil pH. These forests had the lowest pH of any upland forest (Table 3 and Fig. 6), and acid soils are known to cause mobilization of aluminum (Foth and Turk 1972).

SPECIES-ENVIRONMENT RELATIONSHIPS

Quercus marilandica was the most xeric of the important tree species in the upland forests of the Frank Tract (Fig. 3). It reached its peak abundance on exposed southwest slopes (Table 3). An ordination of dominant tree species in upland forests across Oklahoma confirmed the preference of *Q. marilandica* for the most xeric conditions (Risser and Rice 1971). A similar response to a moisture gradient was reported for *Q. marilandica* in the oak-hickory forests of Wisconsin (Peet and Loucks 1977). The success of this species on xeric sites, however, may be more related to its ability to tolerate low nutrient levels than its resistance to drought: a severe drought on a site in western Oklahoma killed 81.5% of the *Q. marilandica* trees (Rice and Penfound 1959).

Quercus stellata had the greatest ecological amplitude of any of the dominant forest trees, as shown by its high importance percentages in four of the five forest types (Table 4). The reason for its success is probably related to its superior ability to tolerate frequent droughts and fires and its longevity. During a severe drought in western Oklahoma, only 8.5% of *Q. stellata* individuals died compared to 81.5% of *Q. marilandica* individuals (Rice and Penfound 1959). In addition, *Q. stellata* had a much greater survival rate after annual and periodic burning than did members of the red oak group, including *Q. marilandica* and *Q. velutina* (Huddle and Pallardy 1996). Annual burning reduced the survival of large red oaks but had little effect on the survival of large *Q. stellata*. In addition, it is not uncommon for individuals of this species to attain ages of 300-400 years (Harlow *et al.* 1991; Stahle and Chaney 1994), while other canopy dominants on this site are short-lived, *i.e.*, less than 200 years, in comparison (Fowells 1965).

Carya texana and *Quercus velutina* were intermediate in their response to a presumed moisture gradient (Fig. 3) and often occurred together as canopy subdominants with *Q. stellata* (Table 4). In general, *C. texana* preferred sites with higher soil pH and manganese than *Q. velutina* (Figs. 4b and 4c). These findings agree with those of Farrell and Ware (1991), who found that a high importance of *Carya* spp. in the upland forests of Virginia was associated with high calcium, magnesium, and pH, and the association was significant for calcium and magnesium ($p < 0.05$). In the same study, *Q. velutina* reached its peak abundance on sites with moderate to high values for calcium, magnesium, and pH, but, unlike *Carya* spp., its importance was not significantly correlated with any of these variables (Farrell and Ware 1991).

Quercus velutina has one of the greatest ecological amplitudes of any of the oaks of the eastern deciduous forests. It can be found in the mesophytic forests of the southern Appalachians, as well as in xeric habitats of the prairie-forest transitional zone. In most stands of the Frank Tract, *Q. stellata* was notably more important than *Q. velutina*. The greater abundance of *Q. stellata* in these forests is probably not related to soil nutrient levels. Stands dominated by *Q. velutina* did not differ significantly from *Q. stellata*-dominated stands for any of the soil nutrients measured (Table 3). This indicates that *Q. velutina* is well adapted to nutrient poor environments. This is further confirmed by forest studies in southern Wisconsin, where *Q. velutina* was abundant in nutrient-poor, sandy soils (Peet and Loucks 1977).

A more plausible explanation for the competitive advantage of *Quercus stellata* over *Q. velutina* is that the former is more tolerant of frequent droughts and fires that occur in this region. In a stand in the southern Appalachians, all individuals of *Q. velutina* were killed in a severe drought (Hursh and Haasis 1931).

Quercus muehlenbergii was the most mesic of the important forest trees at the Frank Tract (Fig. 3). This species occurred almost exclusively on a steep, north-facing slope in association with *Q. shumardii* and *Carya texana* (Table 4). Similarly, Rice and Penfound (1959) reported that a *Q. muehlenbergii* stand on a north-facing slope in the Wichita Mountains was the most mesic of the 208 upland forest stands they sampled across Oklahoma. This contrasts with other forest studies of oak forests, where *Q. muehlenbergii* was important in xeric conditions. In gallery forests of northeast Kansas, the abundance of *Q. muehlenbergii* was correlated with increasing slope and decreasing silt content of the soil, indicating a preference for xeric sites (Abrams 1986).

In Missouri, this species occurred on exposed, south-facing slopes where it was a codominant with *Juniperus virginiana* (Rochow 1972; Zimmerman and Wagner 1979). A similar habitat was reported for *Q. muehlenbergii* in the oak-hickory forests of Wisconsin, where this species was described as the most xeric of the white oaks (Curtis 1959). It also occurred on xeric, southwestern slopes in the Appalachians of West Virginia (Hicks and Frank 1984; Mudrick *et al.* 1994).

Because *Quercus muehlenbergii* appears to thrive in both xeric and mesic conditions, moisture is probably not the primary determinant of its distribution. However, nutrient availability may play a role. The soils underlying the forests of the Frank Tract were generally nutrient poor and had a low cation exchange capacity (CEC), but the *Q. shumardii* stands on north and east slopes had notably higher CEC, organic matter, and soil nutrients than other stands (Table 3). It was in these stands that *Q. muehlenbergii* reached its peak abundance. These mesic, "nutrient-rich" sites at the Frank Tract may have soil fertility comparable to that of xeric sites in deciduous forests further east. In a study on a north slope in the Ozarks, *Q. muehlenbergii* occurred almost exclusively on limestone-derived soils but was uncommon on sandy soils (Read 1952).

The forests of the Frank Tract were notably void of understory shrubs, but *Vaccinium arboreum* was quite successful in the xeric *Quercus stellata*-dominated forests on acid, nutrient-poor soils and relatively steep topography (Fig. 4). A similar habitat was reported for other members of this genus in the upland forests of Virginia (Smith 1995).

CONCLUSIONS

The Frank Tract contains a mosaic landscape typical of the Cross Timbers region. Important communities in this landscape include savannas, glades, upland forests, and lowland communities. The tract included a diversity of upland forest types. On the most xeric exposures, *Quercus stellata* and *Q. marilandica* were important canopy trees, with few other species being present. These species were unimportant on mesic, north-facing slopes where *Q. shumardii*, *Carya texana*, and *Q. muehlenbergii* had high importances.

The most important gradients influencing community composition were related to topographic position. Upland communities were very different in species composition from lowland communities, and these differences were correlated with a gradient in increasing surface water from uplands down to lowlands. Ridgetops were very different in species composition from mesic, north-facing slopes, and these differences were correlated with a gradient in increasing soil fertility from ridgetops to north-facing slopes.

LITERATURE CITED

- Abrams, M. D. 1986. Historical development of gallery forests in northeast Kansas. *Vegetatio*, **65**:29-37.
- Arend, J. L. 1950. Influence of fire and soil on distribution of eastern redcedar in the Ozarks. *J. For.*, **48**:129-130.
- Barclay, B. D. 1947. The woody vegetation of Bear's Glen, a Washington Irving stopover. *Proc. Okla. Acad. Sci.*, **28**:39-57.
- Bard, G. E. 1952. Secondary succession on the Piedmont of New Jersey. *Ecol. Monogr.*, **22**:195-215.
- Bell, E. L. and L. C. Hulbert. 1974. Effect of soil on occurrence of Cross Timbers and prairie in southern Kansas. *Trans. Kans. Acad. Sci.*, **77**:203-209.
- Bourlier, B. G., J. D. Nichols, W. J. Ringwald, P. J. Workman and S. Clemmons. 1979. Soil survey of Osage County, Oklahoma. USDA Soil Conservation Service and USDI Bureau of Indian Affairs, Washington, DC.
- Bragg, T. B. 1971. Post-settlement invasion of woody species in Kansas tall-grass prairie [thesis]. Kansas State University, Manhattan, KS.

- Bray, J. R. 1955. The savanna vegetation of Wisconsin and an application of the concepts order and complexity to the field of ecology [dissertation]. University of Wisconsin Press, Madison.
- Bresler, E., B. L. McNeal and D. L. Carter. 1982. Saline and sodic soils. Springer-Verlag, New York.
- Bruner, W. E. 1931. The vegetation of Oklahoma. *Ecol. Monogr.*, **1**:99-188.
- Christensen, P. D., S. J. Toth and F. E. Bear. 1950. The status of soil manganese as influenced by moisture, organic matter, and pH. *Soil Sci. Soc. Proc.*, **14**:279-282.
- Curtis, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison.
- Cutter, B. E. and R. P. Guyette. 1994. Fire frequency on an oak-hickory ridgetop in the Missouri Ozarks. *Am. Midl. Nat.*, **132**:393-398.
- Dooley, K. L. and S. L. Collins. 1984. Ordination and classification of western oak forests in Oklahoma. *Amer. J. Bot.*, **71**:1221-1227.
- Duck, L. B. and J. B. Fletcher. 1943. A game type map of Oklahoma. Oklahoma Game and Fish Department, Oklahoma City, OK.

- Dwyer, D. D. and P. W. Santelmann. 1964. A comparison of post oak-blackjack oak communities on two major soil types in north central Oklahoma. Oklahoma State University Agricultural Experimental Bulletin B-626, Stillwater, OK.
- Dyksterhuis, E. J. 1948. The vegetation of the western Cross Timbers. *Ecol. Monogr.*, **18**:325-376.
- Farrell, J. D. and S. Ware. 1991. Edaphic factors and forest vegetation in the Piedmont of Virginia. *Bull. Torrey Bot. Club*, **118**:161-169.
- Foreman, C. T. 1947. The Cross Timbers. The Star Printery, Inc., Muskogee, OK.
- Foth, H. D., and L. M. Turk. 1972. Fundamentals of soil science, fifth edition. John Wiley & Sons, Inc., New York.
- Fowells, H. A. 1965. Silvics of forest trees of the United States. Agriculture Handbook No. 271. U.S. Department of Agriculture, Washington D.C.
- Franzmeier, D. P., E. J. Pedersen, T. J. Longwell, J. G. Byrne and C. K. Losche. 1969. Properties of some soils in the Cumberland Plateau as related to slope aspect and position. *Soil Sci. Soc. Am. Proc.*, **33**:755-761.

- Gauch, H. G., Jr. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, England.
- Gleason, H. A. 1913. The relation of forest distribution and prairie fires in the Middle West. *Torrey*, 13:173-181.
- Harlow, W. M., E. S. Harrar, J. W. Hardin and F. M. White. 1991. Textbook of dendrology, seventh edition. McGraw-Hill, New York.
- Harrison, T. P. 1974. A floristic study of the woody vegetation of the North American Cross Timbers [dissertation]. North Texas State University, Denton, TX.
- Hicks, R. R., Jr. and P. S. Frank, Jr. 1984. Relationship of aspect to soil nutrients, species importance and biomass in a forested watershed in West Virginia. *For. Ecol. Man.*, 8:281-291.
- Hill, M. O. and H. G. Gauch, Jr. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio*, 42:47-58.
- Huddle, J. A. and S. G. Pallardy. 1996. Effects of long-term annual and periodic burning on tree survival and growth in a Missouri Ozark oak-hickory forest. *For. Ecol. Man.*, 82:1-9.

- Hursh, C. R. and F. W. Haasis. 1931. Effects of 1925 summer drought on southern Appalachian hardwoods. *Ecology*, **12**:380-386.
- Hutchins, R. B., R. L. Blevins, J. D. Hill and E. H. White. 1976. The influence of soils and microclimate on vegetation of forested slopes in eastern Kentucky. *Soil Sci.*, **121**:234-241.
- Johnson, F. L. and P. G. Risser. 1971. Some vegetation-environment relationships in the upland forests of Oklahoma. *Ecology*, **60**:655-663.
- Johnson, F. L., and P. G. Risser. 1975. A quantitative comparison between an oak forest and an oak savannah in central Oklahoma. *Southwest. Nat.*, **20**:75-84.
- Kartesz, J. T. 1994. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland, second edition. Timber Press, Portland, OR.
- Kennedy, W. 1841. The rise, progress, and prospects of the republic of Texas. Molyneaux Craftsmen, Inc., Fort Worth, TX.
- Kennedy, R. K. 1973. An analysis of selected Oklahoma upland forest stands including both overstory and understory components [dissertation]. University of Oklahoma, Norman, OK.

- Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Special Publication No. 36. American Geographical Society, Washington, D.C.
- Küchler, A. W. 1974. A new vegetation map of Kansas. *Ecology*, **55**:585-604.
- Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. *For. Sci.*, **2**:314-320.
- McPherson, J. K. and G. L. Thompson. 1972. Competitive and allelopathic suppression of understory by Oklahoma oak forests. *Bull. Torrey Bot. Club*, **99**:293-300.
- Mudrick, D. A., M. Hoosein, R. R. Hicks, Jr. and E. C. Townsend. 1994. Decomposition of leaf litter in an Appalachian forest: effects of leaf species, aspect, slope position and time. *For. Ecol. Man.*, **68**:231-250.
- Oklahoma Climatological Survey. 1996. Climatological information for Osage County [on-line]. Available World Wide Web: <http://radar.etr.ou.edu/ocs/climo/osage.html>
- Økland, R. H. 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? *J. Veg. Sci.*, **7**:289-292.

- Pallardy, S. G., T. A. Nigh and H. E. Garrett. 1988. Changes in forest composition in central Missouri: 1968-1982. *Am. Midl. Nat.*, **120**:380-390.
- Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology*, **74**:2215-2230.
- Peet, R. K. and O. L. Loucks. 1977. A gradient analysis of southern Wisconsin forests. *Ecology*, **58**:485-499.
- Petranka, J. W. and J. K. McPherson. 1979. The role of *Rhus copallina* in the dynamics of the forest-prairie ecotone in north-central Oklahoma. *Ecology*, **60**:956-965.
- Powell, J. and D. P. Lowry. 1980. Oak (*Quercus* spp.) sprouts growth rates on a central Oklahoma shallow savannah range site. *J. Range Man.*, **33**:312-313.
- Quarterman, E. 1950. Major plant communities of Tennessee cedar glades. *Ecology*, **31**:234-254.
- Read, R. A. 1952. Tree species occurrence as influenced by geology and soil on an Ozark north slope. *Ecology*, **33**:239-246.
- Rice, E. L. 1965. Bottomland forests of north-central Oklahoma. *Ecology*, **46**:708-714.

- Rice, E. L. and W. T. Penfound. 1959. The upland forests of Oklahoma. *Ecology*, 40:593-608.
- Risser, P. G. and E. L. Rice. 1971. Phytosociological analysis of Oklahoma upland forest species. *Ecology*, 52:940-945.
- Robertson, P. A. and A. L. Heikens. 1994. Fire frequency in oak-hickory forests of southern Illinois. *Castanea*, 59:286-291.
- Rochow, J. J. 1972. A vegetational description of a mid-Missouri forest using gradient analysis techniques. *Am. Midl. Nat.*, 87:377-396.
- Schwegman, J. E., and R. C. Anderson. 1984. Effect of eleven years of fire exclusion on the vegetation of a southern Illinois barren remnant. Pages 146-148 in G. K. Clambey and R. H. Pemble, editors. *The Prairie: Past, Present, and Future. Proceedings of the Ninth North American Prairie Conference.* Tri-College University Center for Environmental Studies, Fargo, North Dakota.
- Smith, M.-L. 1995. Community and edaphic analysis of upland northern hardwood communities, central Vermont, USA. *For. Ecol. Man.*, 72:235-249.
- Stahle, D. W. 1996. Tree rings and ancient forest history, p. 321-343. *In:* M. B. Davis (ed.). *Eastern old-growth forests.* Island Press, Washington, D.C.

- Stahle, D. W. and P. L. Chaney. 1994. A predictive model for the location of ancient forests. *Nat. Areas J.*, **14**:151-158.
- Stahle, D. W. and M. K. Cleaveland. 1993. Southern oscillation extremes reconstructed from tree rings of the Sierra Madre Occidental and Southern Great Plains. *J. Clim.*, **6**:129-140.
- Stahle, D. W., J. G. Hehr, G. G. Hawks, Jr., M. K. Cleaveland and J. R. Baldwin. 1985. Tree-ring chronologies for the southcentral United States. Tree-Ring Laboratory and Office of the State Climatologist, University of Arkansas, Fayetteville, AR.
- Stahle, D. W., M. D. Therrell, M. K. Cleaveland and S. A. Roe. 1996. The bioreserve potential of the ancient Cross Timbers on the Frank Tract, Osage County, Oklahoma. Tree-Ring Laboratory, University of Arkansas, Fayetteville, AR.
- Taylor, R. J. and C. E. S. Taylor. 1994. An annotated list of the ferns, fern allies, gymnosperms and flowering plants of Oklahoma. Southeastern Oklahoma State University, Durant, OK.
- ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**:1167-1179.

- ter Braak, C. J. F. and I. C. Prentice. 1988. A theory of gradient analysis. *Adv. Ecol. Res.*, **18**:271-317.
- ter Braak, C. J. F. 1997. CANOCO - a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis. Microcomputer Power, Ithaca, New York.
- Therrell, M. D. 1996. A predictive model for locating ancient forests in the Cross Timbers of Osage County, Oklahoma [thesis]. University of Arkansas, Fayetteville, AR.
- Ware, S., P. L. Redfearn, Jr., G. L. Pyrah and W. R. Weber. 1992. Soil pH, topography and forest vegetation in the central Ozarks. *Am. Midl. Nat.*, **128**:40-52.
- Weaver, J. E. and F. E. Clements. 1938. Plant ecology, second edition. McGraw-Hill Book Company, New York.
- Werling, J. A., Jr. and S. J. Tajchman. 1984. Soil thermal and moisture regimes on forested slopes of an Appalachian watershed. *For. Ecol. Man.*, **7**:297-310.

Zimmerman, M. and W. L. Wagner. 1979. A description of the woody vegetation of oak-hickory forest in the Northern Ozark Highlands. *Bull. Torr. Bot. Club.*, **106**:117-122.

TABLE 1.—Environmental characteristics (mean \pm standard deviation) for the woody plant communities of the Frank Tract. Means with the same letter are not significantly different ($p < 0.05$) by Scheffe's pairwise comparisons test. Site factors are reported as percentages but were arcsine transformed before statistical analysis. Cations and anions are reported in parts per million (ppm) but were log transformed before statistical analysis. CEC = cation exchange capacity.

Variable	Savannas (n = 7)	Upland forests (n = 57)	Glades (n = 3)	Ravines (n = 2)	Floodplain (n = 8)	Riparian (n = 2)	Lakeshore (n = 3)
Site Factors							
Slope	7.29 \pm 2.81 ^a	28.9 \pm 22.0 ^a	9.33 \pm 7.02 ^a	25.0 \pm 18.4 ^a	10.9 \pm 11.5 ^a	10.5 \pm 2.12 ^a	14.7 \pm 11.2 ^a
Canopy cover	22.3 \pm 13.5 ^c	66.7 \pm 11.6 ^a	18.1 \pm 3.01 ^{bc}	58.3 \pm 9.90 ^{ac}	63.0 \pm 20.8 ^{ac}	23.6 \pm 5.48 ^{bc}	1.75 \pm 1.64 ^b
Bare ground	1.57 \pm 1.24 ^b	11.9 \pm 12.7 ^{ab}	16.0 \pm 20.8 ^{ab}	35.0 \pm 7.07 ^{ab}	3.0 \pm 3.21 ^b	5.50 \pm 6.36 ^{ab}	40.3 \pm 34.5 ^a
Rock cover	0.00 \pm 0.00 ^a	19.8 \pm 23.5 ^a	13.3 \pm 5.77 ^a	25.0 \pm 7.07 ^a	1.25 \pm 2.05 ^a	5.50 \pm 6.36 ^a	27.0 \pm 12.1 ^a
Understory cover	87.1 \pm 11.1 ^a	14.9 \pm 19.8 ^b	66.7 \pm 15.3 ^a	12.5 \pm 10.6 ^{bc}	49.1 \pm 21.5 ^c	57.5 \pm 3.53 ^a	17.0 \pm 15.7 ^{bc}
Moss cover	0.14 \pm 0.24 ^a	2.45 \pm 4.26 ^a	0.17 \pm 0.29 ^a	0.25 \pm 0.35 ^a	0.56 \pm 0.68 ^a	0.00 \pm 0.00 ^a	0.00 \pm 0.00 ^a
Surface water	0.00 \pm 0.00 ^a	0.00 \pm 0.00 ^a	0.00 \pm 0.00 ^a	0.00 \pm 0.00 ^a	0.00 \pm 0.00 ^a	15.0 \pm 7.07 ^b	0.00 \pm 0.00 ^a
Soil Factors							
Organic (%)	1.20 \pm 0.27 ^b	2.82 \pm 1.35 ^{ab}	3.90 \pm 1.05 ^{ab}	5.20 \pm 1.13 ^a	2.45 \pm 1.06 ^{ab}	1.70 \pm 0.28 ^{ab}	1.53 \pm 1.10 ^{ab}
pH	6.26 \pm 0.58 ^a	5.71 \pm 0.63 ^a	6.10 \pm 0.69 ^a	5.60 \pm 0.42 ^a	6.43 \pm 0.40 ^a	6.60 \pm 0.42 ^a	6.23 \pm 0.95 ^a
CEC (M.E./100g)	7.67 \pm 1.98 ^b	11.2 \pm 4.97 ^b	26.8 \pm 5.01 ^a	16.4 \pm 4.48 ^{ab}	12.3 \pm 3.36 ^b	9.47 \pm 1.59 ^b	13.4 \pm 8.48 ^{ab}
Al (ppm)	347.3 \pm 70.6 ^a	411.5 \pm 114.4 ^a	547.7 \pm 206.4 ^a	429.5 \pm 60.1 ^a	297.5 \pm 64.1 ^a	254.5 \pm 27.6 ^a	433.0 \pm 212.0 ^a
B	0.55 \pm 0.15 ^a	0.54 \pm 0.17 ^a	0.52 \pm 0.15 ^a	0.64 \pm 0.04 ^a	0.72 \pm 0.16 ^a	0.64 \pm 0.04 ^a	0.68 \pm 0.12 ^a
Ca	1007.7 \pm 434.2 ^a	1173.1 \pm 657.9 ^a	2420.7 \pm 240.0 ^a	1643 \pm 140.0 ^a	1708.8 \pm 638.7 ^a	1254.0 \pm 244.7 ^a	1399.0 \pm 760.4 ^a
Cu	0.81 \pm 0.26 ^a	0.90 \pm 0.72 ^a	0.93 \pm 0.35 ^a	1.33 \pm 0.16 ^a	1.26 \pm 0.35 ^a	1.32 \pm 0.36 ^a	1.23 \pm 0.35 ^a
Fe	74.9 \pm 19.2 ^c	127.8 \pm 42.6 ^{ab}	77.0 \pm 10.1 ^{bc}	248.5 \pm 44.5 ^a	157.9 \pm 54.9 ^{ab}	167.0 \pm 11.3 ^{ab}	204.7 \pm 20.6 ^a
P	10.0 \pm 4.0 ^{ab}	19.1 \pm 9.0 ^b	6.33 \pm 1.53 ^a	14.5 \pm 6.36 ^{ab}	16.5 \pm 8.33 ^{ab}	9.50 \pm 2.12 ^{ab}	16.7 \pm 8.14 ^{ab}
K	84.1 \pm 17.2 ^a	96.4 \pm 37.0 ^a	174.7 \pm 25.7 ^a	97.0 \pm 11.3 ^a	91.9 \pm 34.6 ^a	92.0 \pm 1.41 ^a	104.7 \pm 80.4 ^a

TABLE 1.—Continued

Variable	Savannas (n = 7)	Upland forests (n = 57)	Glades (n = 3)	Ravines (n = 2)	Floodplain (n = 8)	Riparian (n = 2)	Lakeshore (n = 3)
Mg	125.7 ± 34.3 ^b	184.9 ± 135.5 ^b	869.3 ± 20.6 ^a	246.0 ± 2.83 ^{ab}	222.5 ± 84.0 ^b	226.0 ± 94.8 ^{ab}	308.0 ± 248.7 ^{ab}
Mn	64.0 ± 18.2 ^a	98.7 ± 50.8 ^a	72.7 ± 8.02 ^a	103.5 ± 54.4 ^a	99.9 ± 22.7 ^a	86.5 ± 26.2 ^a	57.3 ± 14.2 ^a
Na	26.4 ± 22.9 ^{bc}	23.2 ± 10.9 ^b	80.0 ± 1.0 ^a	24.5 ± 3.54 ^{ab}	23.8 ± 8.71 ^b	25.5 ± 10.6 ^{ab}	84.7 ± 51.2 ^a
S	17.4 ± 4.20 ^b	24.2 ± 5.65 ^{bc}	43.3 ± 16.2 ^a	28.5 ± 4.95 ^{ab}	25.4 ± 7.39 ^{ab}	24.5 ± 9.19 ^{ab}	37.3 ± 17.1 ^{ac}
Zn	4.36 ± 1.33 ^{ab}	7.51 ± 3.17 ^a	2.0 ± 0.1 ^b	5.65 ± 0.64 ^{ab}	6.60 ± 2.52 ^a	5.15 ± 2.47 ^{ab}	2.10 ± 0.56 ^b

TABLE 2.—Average importance of woody species in the plant communities of the Frank Tract. Importance values were calculated as the average of relative density and relative basal area. Species listed have an importance percentage ≥ 10 in at least one plot in one of the community types.

	Code	Savannas (n = 7)	Upland Forests (n = 57)	Glades (n = 3)	Ravines (n = 2)	Floodplain (n = 8)	Riparian (n = 2)	Lakeshore (n = 3)
Trees								
<i>Amelanchier arborea</i>	AMAR	-	1.1	-	-	-	-	-
<i>Carya texana</i>	CATE	5.5	12.8	-	10.6	10.1	-	-
<i>Cercis canadensis</i>	CECA	8.3	1.2	-	-	2.6	10.2	-
<i>Diospyros virginiana</i>	DIVI	4.6	0.1	-	6.7	2.8	6.3	31.3
<i>Fraxinus americana</i>	FRAM	4.8	1.0	-	0.2	0.9	-	-
<i>Juglans nigra</i>	JUNI	-	-	-	-	1.7	16.0	-
<i>Juniperus virginiana</i>	JUVI	2.8	6.2	57.1	20.6	9.0	-	-
<i>Platanus occidentalis</i>	PLOC	-	0.2	-	14.9	1.7	44.2	-
<i>Quercus marilandica</i>	QUMA	24.9	11.2	-	-	0.1	-	-
<i>Q. muehlenbergii</i>	QUMU	-	1.2	-	-	1.2	-	-
<i>Q. shumardii</i>	QUSH	-	5.8	-	-	2.6	-	-
<i>Q. stellata</i>	QUST	5.6	37.0	42.9	14.6	25.4	-	-
<i>Q. velutina</i>	QUVE	0.5	13.2	-	-	4.0	-	-
<i>Sideroxylon</i>								
<i>lanuginosum</i>	SILA	-	0.3	-	0.7	2.7	3.7	-
<i>Ulmus rubra</i>	ULRU	5.6	1.7	-	-	5.9	-	-

TABLE 2.—Continued

Species	Code	Savannas (n = 7)	Upland forests (n = 57)	Glades (n = 3)	Ravines (n = 2)	Floodplain (n = 8)	Riparian (n = 2)	Lakeshore (n = 3)
Shrubs								
<i>Cephalanthus</i>								
<i>occidentalis</i>	CEOC	-	-	-	0.5	2.6	-	57.8
<i>Cornus drummondii</i>	CODR	-	0.1	-	15.0	14.5	0.5	-
<i>Prunus angustifolia</i>	PRAN	14.1	-	-	-	-	-	-
<i>Rhus copallina</i>	RHCO	6.8	0.3	-	-	-	-	-
<i>R. glabra</i>	RHGL	16.4	-	-	-	0.2	-	-
<i>Vaccinium arboreum</i>	VAAR	-	5.3	-	-	-	-	-
Vines								
<i>Cocculus carolinus</i>	COCA	-	0.5	-	-	-	0.2	-
<i>Parthenocissus</i>								
<i>quinquefolia</i>	PAQU	-	0.1	-	-	2.2	0.3	-
<i>Smilax bona-nox</i>	SMBO	-	-	-	9.3	5.1	15.3	-

TABLE 3.—Environmental characteristics (mean ± standard deviation) for the upland forest communities of the Frank Tract. Means with the same letter are not significantly different ($p < 0.05$) by Scheffe's pairwise comparisons test. Slope and cover values are reported as percentages but were arcsine transformed before statistical analysis. All cations and anions are reported in parts per million (ppm) but were log transformed before statistical analysis. CEC = cation exchange capacity.

Variable	<i>Q. stellata</i> – <i>Q. marilandica</i> stands (QUST-QUA) (n = 15)	<i>Q. stellata</i> – <i>V. arboreum</i> stands (QUST-VAAR) (n = 9)	<i>Q. stellata</i> – <i>C. texana</i> – <i>Q. velutina</i> stands (QUST-CATE) (n = 21)	<i>Q. velutina</i> stands (QUVE) (n = 4)	<i>Q. shumardii</i> stands (QUSH) (n = 4)
Site Factors					
Topographic position:					
North slope (no. plots)	1	2	4	1	3
East slope	3	4	8	2	1
South slope	1	3	1	0	0
West slope	8	0	4	1	0
Ridgetop	2	0	4	0	0
Slope	22.4 ± 13.5 ^a	37.8 ± 28.0 ^a	28.0 ± 22.6 ^a	37.0 ± 15.5 ^a	54.5 ± 14.2 ^a
Canopy cover	61.1 ± 8.82 ^a	67.5 ± 7.60 ^a	66.1 ± 13.5 ^a	74.2 ± 4.84 ^a	74.9 ± 2.92 ^a
Bare ground	24.1 ± 15.0 ^a	6.44 ± 6.11 ^{bc}	8.36 ± 8.21 ^{bc}	18.8 ± 10.3 ^{ab}	0.88 ± 0.85 ^c
Rock cover	16.9 ± 20.8 ^a	33.6 ± 30.6 ^a	15.6 ± 23.4 ^a	18.8 ± 10.3 ^a	42.5 ± 9.57 ^a
Understory cover	9.93 ± 10.2 ^a	3.78 ± 1.56 ^a	18.9 ± 25.5 ^a	12.5 ± 8.66 ^a	16.5 ± 7.0 ^a
Moss cover	0.92 ± 1.12 ^b	8.06 ± 7.97 ^a	1.42 ± 1.64 ^b	3.38 ± 4.46 ^{ab}	1.63 ± 2.29 ^{ab}
Soil Factors					
Organic (%)	2.63 ± 1.25 ^b	2.70 ± 1.12 ^b	2.47 ± 1.11 ^b	3.35 ± 0.93 ^{ab}	5.28 ± 1.89 ^a
pH	5.81 ± 0.71 ^a	5.19 ± 0.39 ^a	5.69 ± 0.65 ^a	5.73 ± 0.39 ^a	6.13 ± 0.46 ^a
CEC (M.E./100g)	10.9 ± 6.02 ^{ab}	9.28 ± 2.40 ^b	11.0 ± 4.91 ^{ab}	10.1 ± 2.14 ^{ab}	18.9 ± 1.99 ^a

TABLE 3.—Continued

Variable	<i>Q. stellata</i> – <i>Q. marilandica</i> stands (QUST-QUMA) (n = 15)	<i>Q. stellata</i> – <i>V. arboreum</i> stands (QUST-VAAR) (n = 9)	<i>Q. stellata</i> – <i>C. texana</i> – <i>Q. velutina</i> stands (QUST-CATE) (n = 21)	<i>Q. velutina</i> stands (QUVE) (n = 4)	<i>Q. shumardii</i> stands (QUSH) (n = 4)
Al (ppm)	430.6 ± 141.1 ^a	439.7 ± 64.9 ^a	411.9 ± 124.5 ^a	388.0 ± 33.0 ^a	409.0 ± 108.3 ^a
B	0.51 ± 0.13 ^a	0.48 ± 0.09 ^a	0.52 ± 0.17 ^a	0.61 ± 0.13 ^a	0.83 ± 0.19 ^a
Ca	1108.7 ± 559.1 ^b	764.2 ± 416.8 ^b	1150.0 ± 663.0 ^b	1086.3 ± 405.8 ^{ab}	2358.5 ± 583.9 ^a
Cu	0.77 ± 0.25 ^a	0.71 ± 0.12 ^a	1.03 ± 1.15 ^a	0.86 ± 0.11 ^a	1.26 ± 0.17 ^a
Fe	124.1 ± 58.2 ^a	135.8 ± 29.9 ^a	128.0 ± 43.8 ^a	129.8 ± 29.5 ^a	118.8 ± 21.6 ^a
Mg	199.9 ± 201.5 ^{ab}	126.6 ± 53.2 ^b	169.4 ± 111.8 ^b	165.0 ± 44.5 ^{ab}	347.5 ± 54.8 ^a
Mn	106.0 ± 50.9 ^a	52.7 ± 33.0 ^c	98.9 ± 41.6 ^{ab}	96.0 ± 38.9 ^{ac}	164.8 ± 79.2 ^a
P	15.9 ± 9.33 ^a	15.0 ± 6.08 ^a	21.7 ± 8.98 ^a	22.8 ± 7.46 ^a	28.5 ± 8.89 ^a
K	91.1 ± 36.3 ^a	76.8 ± 26.9 ^a	97.1 ± 39.7 ^a	93.8 ± 17.1 ^a	135.5 ± 15.8 ^a
Na	22.3 ± 8.59 ^a	26.0 ± 19.7 ^a	22.3 ± 9.10 ^a	21.0 ± 2.31 ^a	22.3 ± 4.92 ^a
S	24.5 ± 7.41 ^a	22.3 ± 3.64 ^a	23.4 ± 4.72 ^a	25.3 ± 3.95 ^a	32.8 ± 1.71 ^a
Zn	6.83 ± 3.08 ^a	5.47 ± 1.86 ^a	7.38 ± 2.83 ^a	9.50 ± 2.29 ^a	11.2 ± 4.58 ^a

TABLE 4.—Average importance of woody species in the upland forest communities of the Frank Tract. Importance values were calculated as the average of relative density and relative basal area. Species listed have an importance value ≥ 10 in at least one plot in one of the community types.

	Code	<i>Q. stellata</i> - <i>Q. marilandica</i> stands (QUST-QUMA) (n = 15)	<i>Q. stellata</i> - <i>V. arboreum</i> stands (QUST-VAAR) (n = 9)	<i>Q. stellata</i> - <i>C. texana</i> - <i>Q. velutina</i> stands (QUST-CATE) (n = 21)	<i>Q. velutina</i> stands (QUVE) (n = 4)	<i>Q. shumardii</i> stands (QUSH) (n = 4)
Trees						
<i>Amelanchier arborea</i>	AMAR	-	0.6	1.7	4.2	0.7
<i>Carya texana</i>	CATE	7.1	2.3	21.4	7.5	18.0
<i>Cercis canadensis</i>	CECA	-	-	0.5	-	4.3
<i>Fraxinus americana</i>	FRAM	0.2	-	0.9	1.2	8.2
<i>Juniperus virginiana</i>	JUVI	4.0	15.8	4.0	6.4	0.9
<i>Quercus marilandica</i>	QUMA	26.2	9.1	4.8	1.0	0.3
<i>Q. muehlenbergii</i>	QUMU	-	-	-	1.0	16.7
<i>Q. shumardii</i>	QUSH	0.3	2.0	4.7	9.7	42.7
<i>Q. stellata</i>	QUST	57.8	32.5	39.9	14.2	3.3
<i>Q. velutina</i>	QUVE	1.5	10.4	19.9	48.0	4.4
Shrubs						
<i>Vaccinium arboreum</i>	VAAR	2.0	26.6	0.3	6.5	-

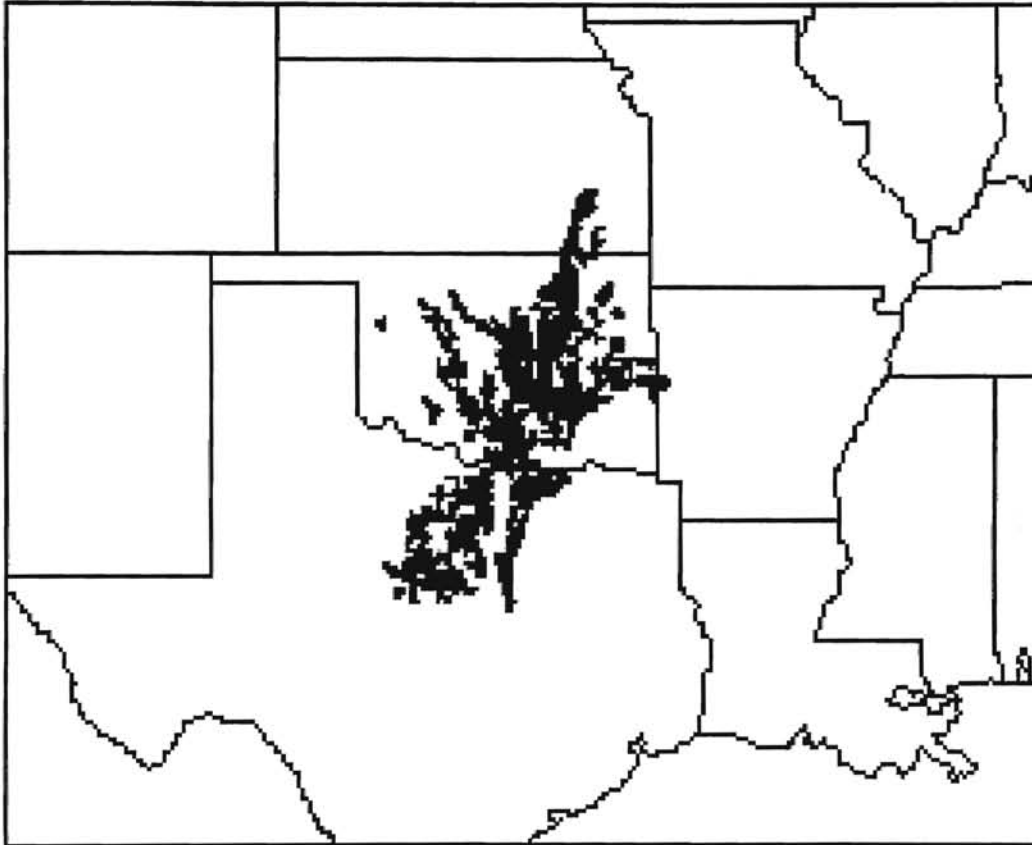


Fig. 1. --The potential distribution of the Cross Timbers prior to settlement (adapted from Küchler 1964).

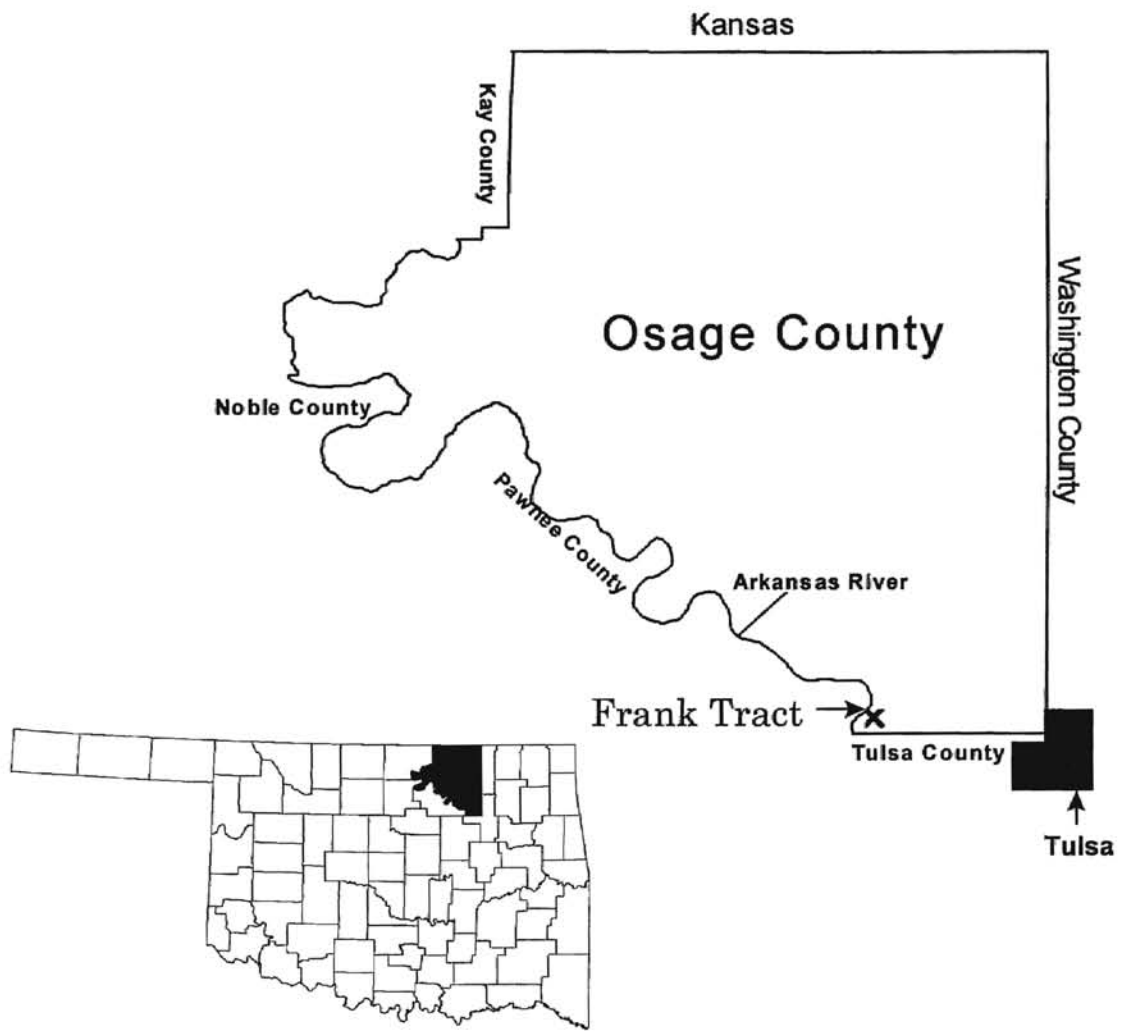


Fig. 2.--Location of the Frank Tract, Osage County, Oklahoma.

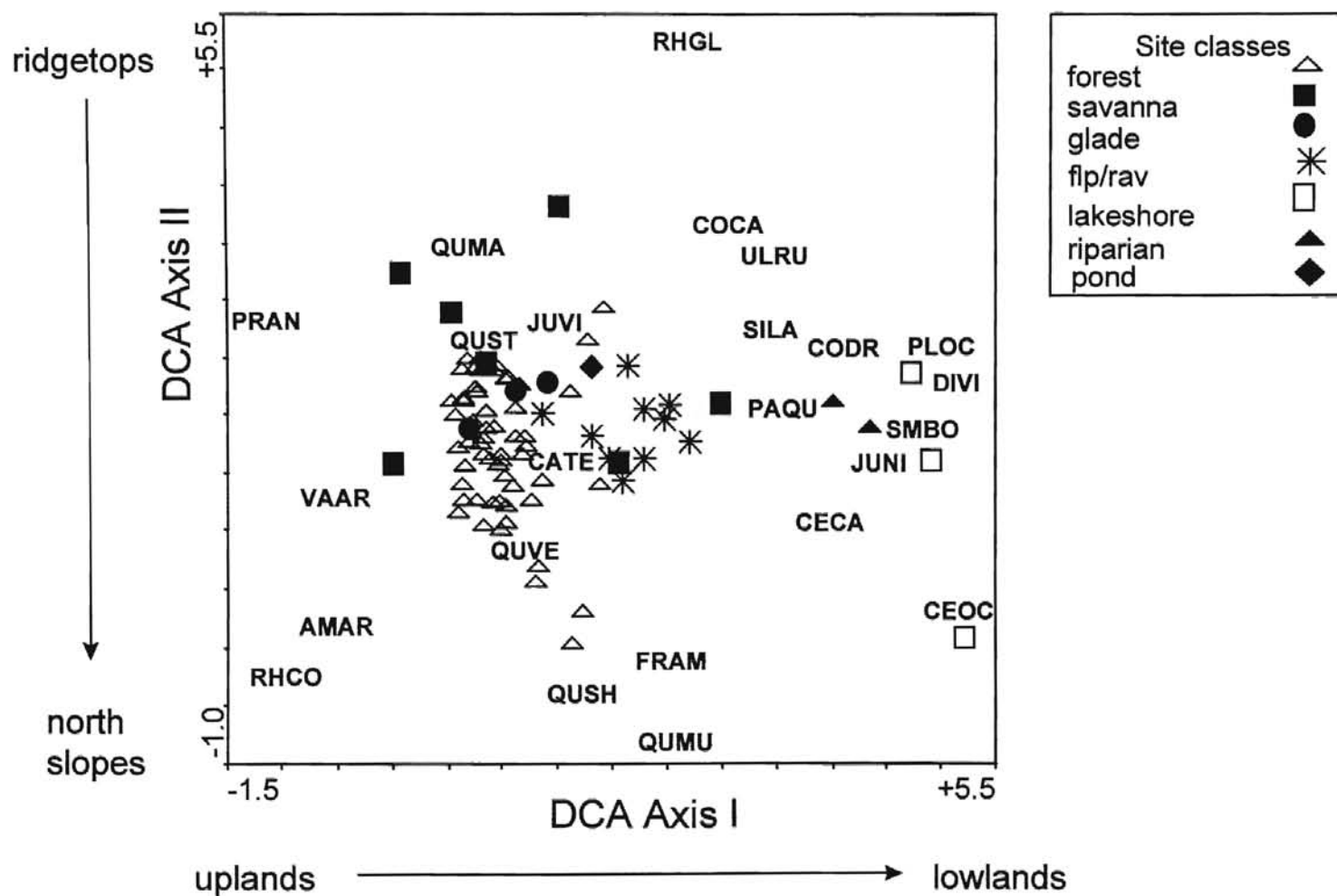


Fig. 3.—Detrended correspondence analysis of the woody plant communities of the Frank Tract. Eigenvalues were 0.596 for the first axis and 0.289 for the second axis. Four-letter species codes are defined in Table 2. Species listed have an importance percentage greater than or equal to 10 in at least one plot in one site class.

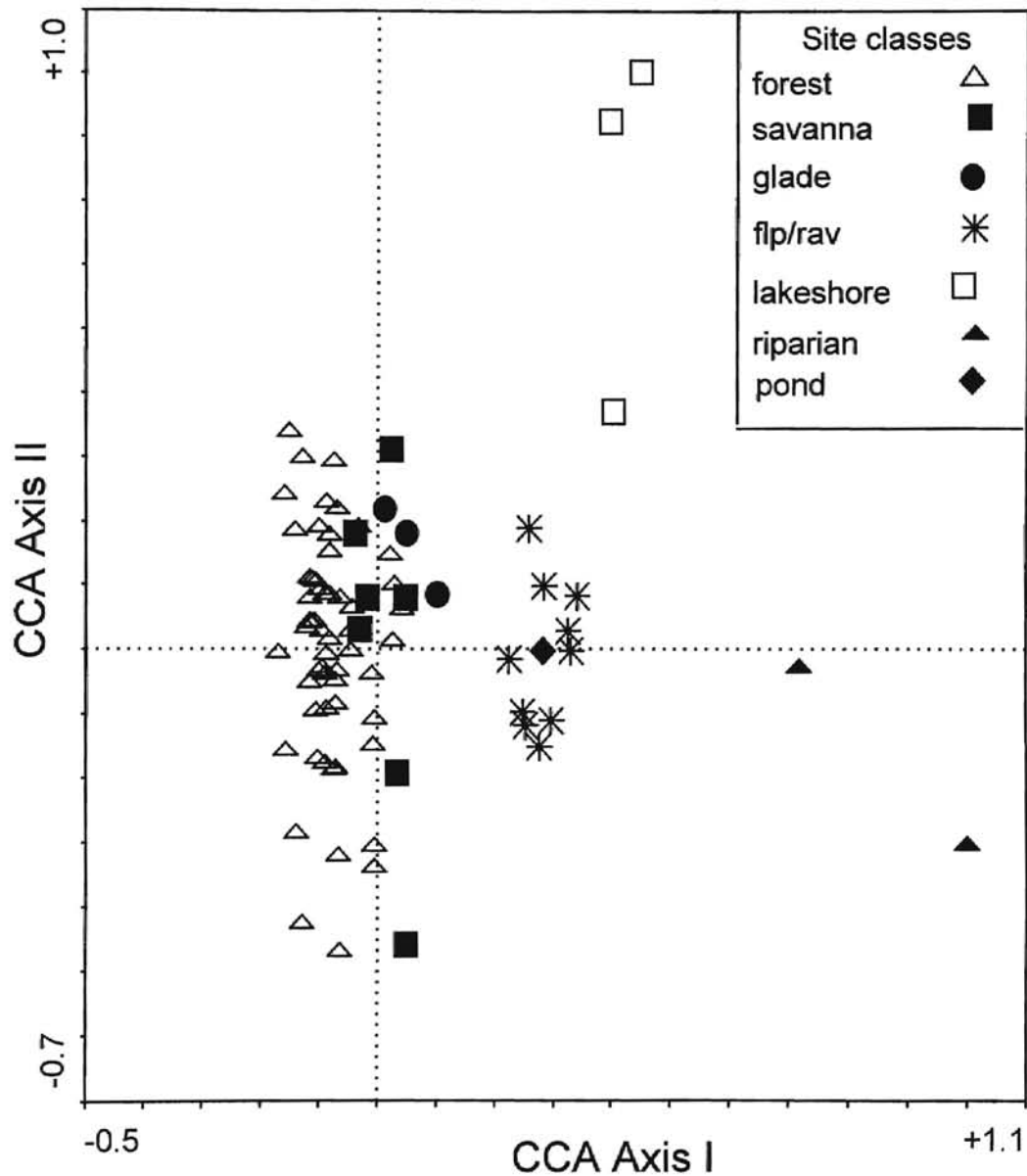


Fig. 4a

Fig. 4.--Canonical correspondence analysis of the woody plant communities of the Frank Tract. Eigenvalues were 0.402 for the first axis and 0.225 for the second axis. (a) Scatterplot of samples. (b) Scatterplot of environmental variables. Topographic position variables are plotted as centroids; all other variables are represented as biplot arrows. (c) Scatterplot of species; four-letter codes are defined in Table 2. Species listed have an importance percentage greater than or equal to 10 in at least one of the site classes.

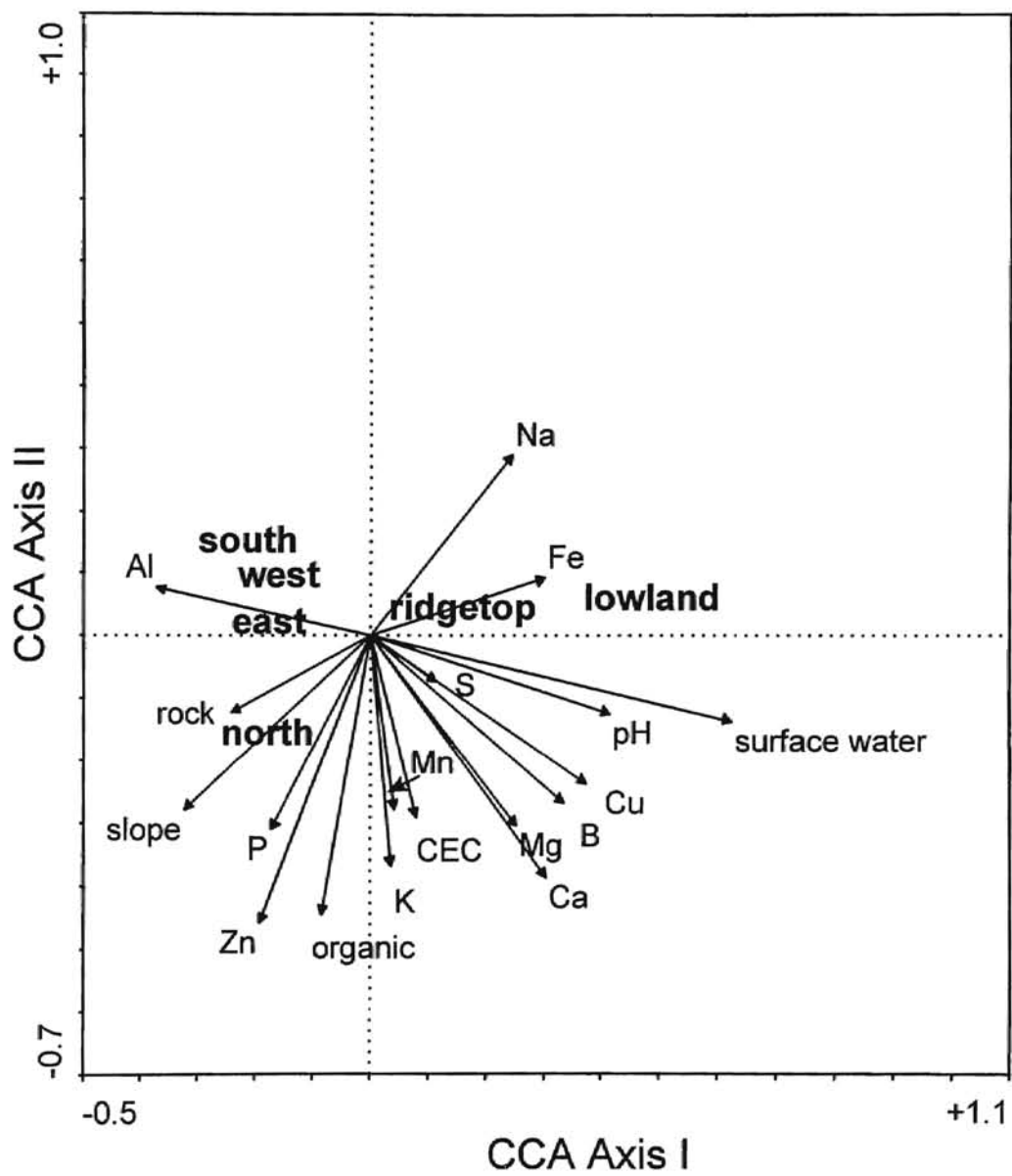


Fig. 4b

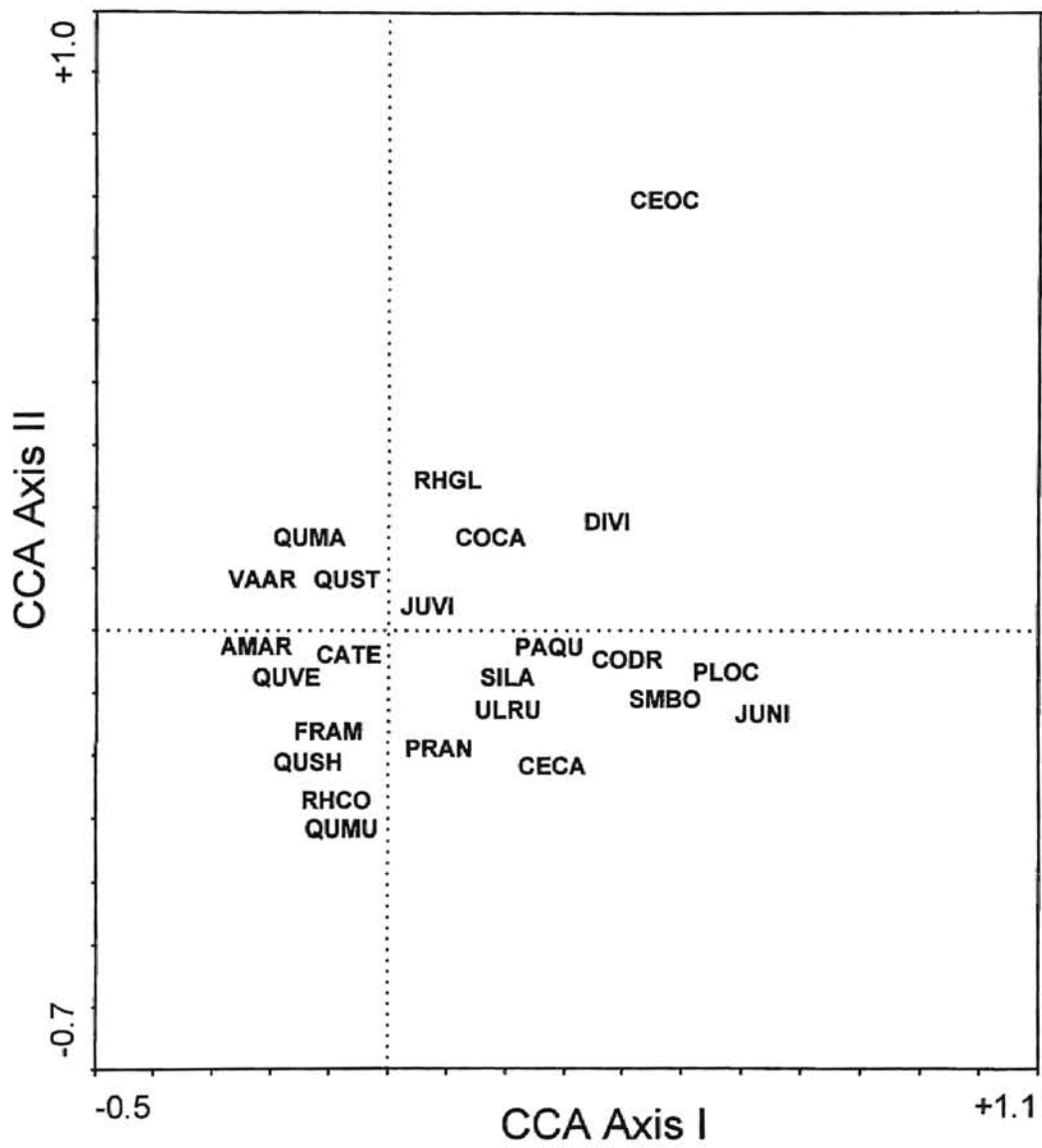


Fig. 4c

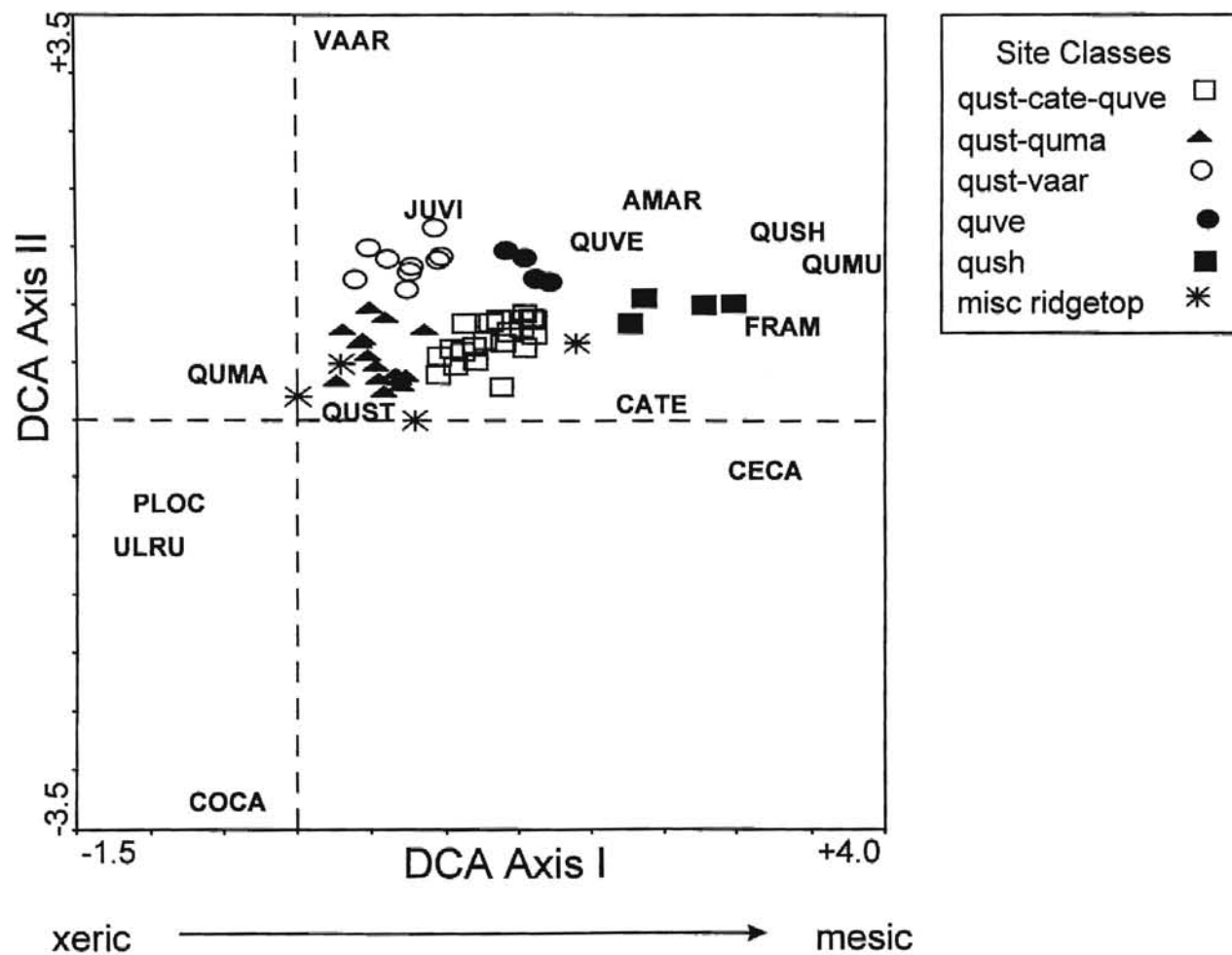


Fig. 5.—Detrended correspondence analysis of the upland forest communities of the Frank Tract. Eigenvalues were 0.345 for the first axis and 0.161 for the second axis. Site classes are defined in Table 3, except for “misc ridgetop” which is described in the text. Four-letter species codes are defined in Tables 2 and 4. Species listed have an importance percentage greater than or equal to 10 in at least one plot in one site class.

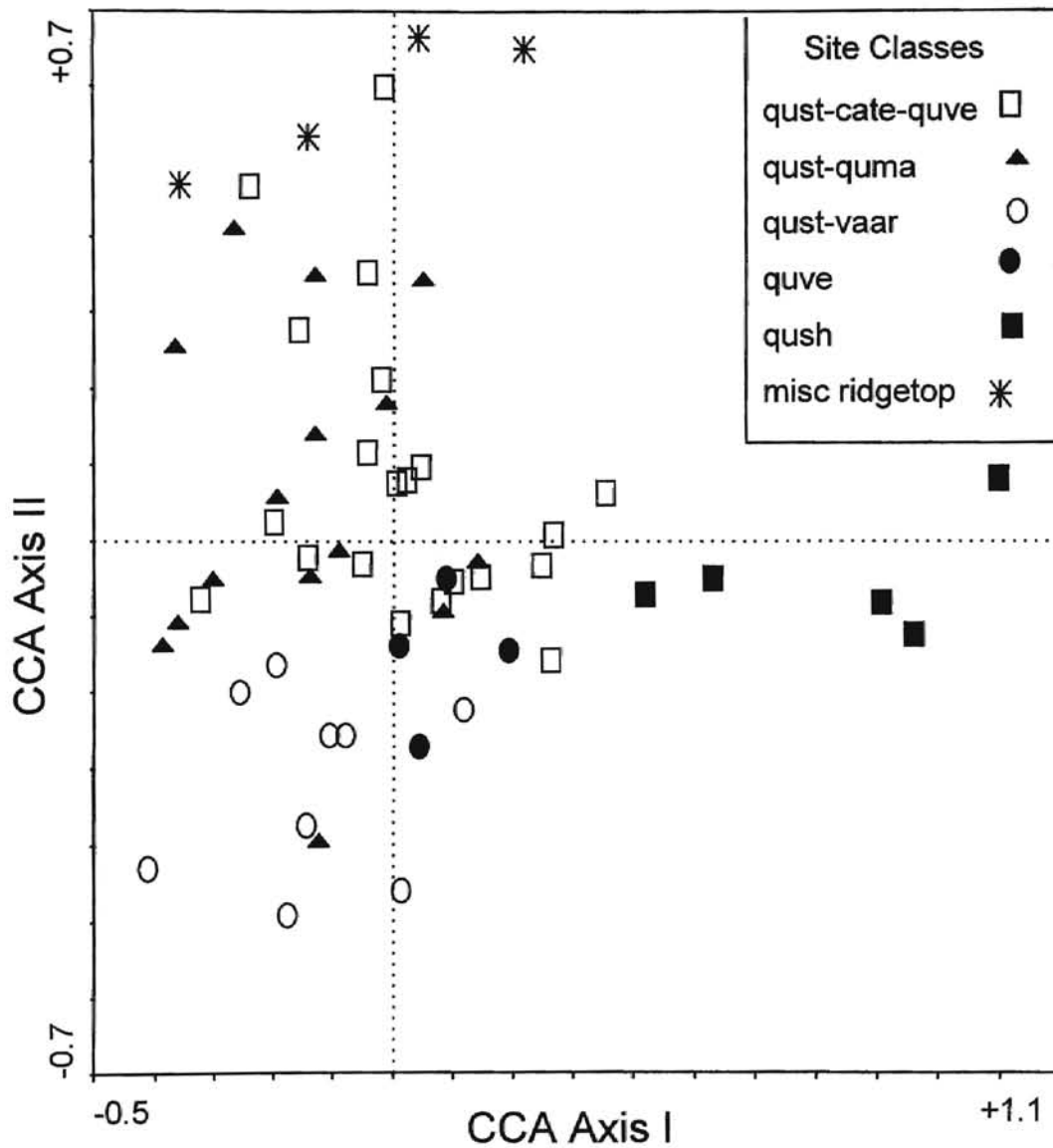


Fig. 6a

Fig. 6.—Canonical correspondence analysis of the upland forest communities of the Frank Tract. Eigenvalues were 0.253 for the first axis and 0.145 for the second axis. (a) Scatterplot of samples. Site classes are defined in Table 3, except for "misc ridgetop" which is described in the text. (b) Scatterplot of environmental variables. Topographic position variables are plotted as centroids in boldface type; all other variables are represented as biplot arrows. (c) Scatterplot of species; four-letter codes are defined in Tables 2 and 4. Species listed have an importance percentage greater than or equal to 10 in at least one plot in one site class.

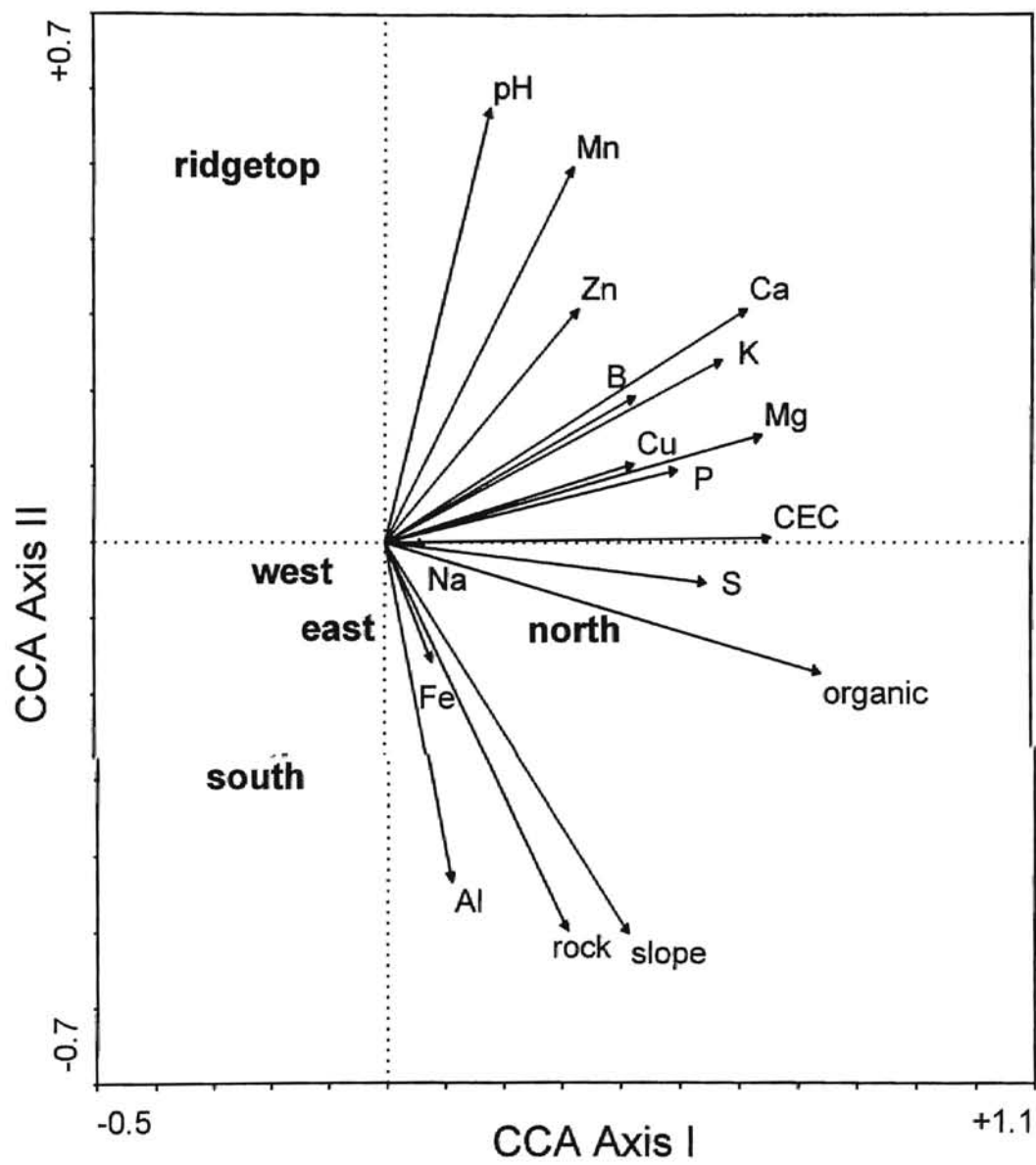


Fig. 6b

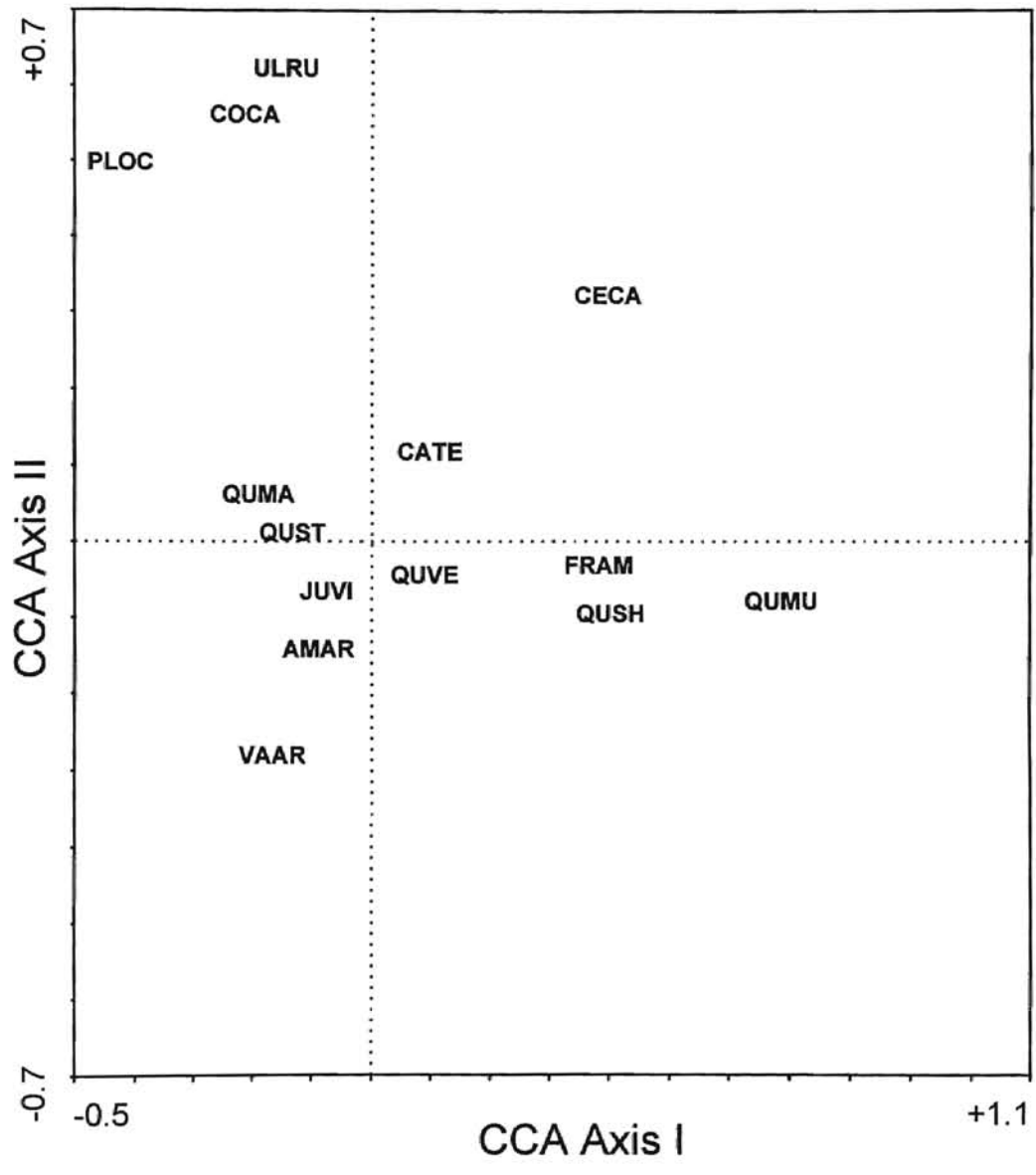


Fig. 6c

CHAPTER II

VASCULAR FLORA OF A TRACT OF ANCIENT CROSS TIMBERS IN OSAGE COUNTY, OK

ABSTRACT

During 1996 and 1997, I surveyed the vascular plants on a tract of ancient Cross Timbers in southern Osage County, Oklahoma. I found 268 species in 187 genera and 72 families. The flora was typical of tallgrass prairie and xeric eastern deciduous forests. The largest families were Poaceae (42 species), Fabaceae (32 species), and Asteraceae (31 species). These three families composed almost 40% of the vascular flora. Twenty species (7% of the vascular flora) were exotic to North America and 248 were native.

INTRODUCTION

The Cross Timbers are a mosaic of forests, glades, and savannas that mark the transition from the eastern deciduous forests to the central grasslands. They extend from southeastern Kansas, through eastern and central Oklahoma, and into north-central Texas, forming a north-south oriented band of vegetation that dissects the tallgrass prairie vegetation type (Duck and Fletcher 1943; Küchler 1964). The forests of the Cross Timbers represent the westernmost extent of the eastern deciduous forests.

The Cross Timbers are particularly unique because of the old-growth forests they preserve. These forests largely escaped logging during the post-settlement era and therefore may contain more extant old-growth than any other eastern deciduous forest type (Stahle 1996). Dendrochronologists have recently discovered hundreds of uncut Cross Timbers forests, particularly in Oklahoma (Stahle *et al.* 1985; Stahle and

Cleaveland 1993; Therrell 1996). One such site, generally known as "The Frank Tract", is located in southern Osage County, Oklahoma. This tract is outstanding because its rugged slopes are highlighted by extensive stands of 150-300-year-old *Quercus stellata* and 150-500-year-old *Juniperus virginiana* (Therrell 1996). The purpose of the present study was to compile a checklist of the vascular flora of the Frank Tract. It is hoped that this information will aid future ecological studies and assessments of the area for possible conservation.

DESCRIPTION OF STUDY SITE

GEOGRAPHY

The Frank Tract is located in southern Osage County, Oklahoma, approximately 10 miles west of downtown Tulsa (36°10'29.8"N; 96°14'34.4"W). The site is bounded on the north and west by Keystone Reservoir, an impoundment of the Arkansas River, and borders U.S. Highway 412 at its southwestern corner. The tract is continuous, comprising portions of section 27, 28, 29, 32, and 33 in Township 20 N, Range 10 E, with a total area of 445 ha. Most of the tract (340 ha) is located in sections 28 and 33. The principal landowner is Irvin Frank of Tulsa, Oklahoma; the U.S. Army Corp of Engineers owns a small buffer zone along the lakeshore.

The topography of the area is quite variable. A level ridgetop runs from east to west, toward the lake, in the northern half of the tract and then turns abruptly to the south, running parallel to the lake through the remainder of the tract. The ridgetop is bounded by steep, rugged sideslopes, dissected by numerous inlets of the lake on the northern and western edges, and by a small north-south tributary (Brush Creek) in the

interior southeastern portion. Relief is approximately 100 m, ranging from 323 m on the ridgetops to 229 m in the floodplain of Brush Creek and at the lakeshore.

GEOLOGY AND SOILS

The site is located in the unglaciated Osage Plains of the Central Lowland Physiographic Province (Hunt 1974). The bedrock is sandstone (Johnson *et al.* 1972; Hunt 1974). The soils on the ridgetops are Dougherty fine sandy loam, first deposited by water and then added to by wind-blown sand from the river bed. The sideslopes are underlain by Niotaze-Darnell soils which are thin, nutrient-poor, rapidly drained and covered with numerous outcroppings of the underlying sandstone (Gray and Galloway 1959; Bourlier *et al.* 1979).

CLIMATE

The climate is subtropical, with hot summers and mild winters (Trewartha 1968). The growing season lasts for approximately 220 days (U.S. Department of Agriculture 1941). The average annual precipitation is 93 cm, with maximum precipitation in late spring and early fall and the least in the winter months (Oklahoma Climatological Survey 1996). Mean annual temperature is 14.9° C, with the highest temperature in July at 27.5° C and the lowest temperature in January at 0.7° C (Oklahoma Climatological Survey 1996).

DESCRIPTION OF PLANT COMMUNITIES

SAVANNAS

The savannas are tallgrass prairies interspersed with scattered trees and clonal shrubs. This is the predominant community type on the ridgetops. The dominant woody species are *Quercus marilandica*, *Rhus glabra*, and *Prunus angustifolia* (Chapter 1). Other common woody species are *Rhus copallina*, *Juniperus virginiana*, and *Ulmus rubra*. In the herbaceous layer, *Schizachyrium scoparium*, *Lespedeza* spp., *Achillea millefolium*, *Erigeron strigosus*, *Chamaecrista fasciculata*, and *Dichanthelium* spp. are abundant. Less abundant but still common are *Andropogon gerardii*, *Andropogon ternarius*, *Sorghastrum nutans*, *Tridens flavus*, *Tradescantia ohiensis*, *Asclepias viridis*, and *Cnidoscolus texanus*. Uncommon species include *Asclepias tuberosa*, *Commelina erecta*, and *Solanum dimidiatum*. In moist depressions, *Carex* spp. and *Juncus* spp. are abundant.

UPLAND FORESTS

The sideslopes of the Frank Tract are covered with a *Quercus-Carya* forest. Because of the open nature of these forests, grasses such as *Andropogon gerardii* are intermingled throughout. The canopy layer is dominated by *Quercus stellata*, *Quercus velutina*, *Carya texana*, and *Quercus marilandica*. On dry southwestern exposures, *Quercus stellata* and *Quercus marilandica* are canopy codominants, and few other woody species are present. These xeric forests are quite barren and have little understory plant cover. *Rhus aromatica* and *Vaccinium arboreum* are typical understory shrubs. Herbaceous species include *Antennaria plantaginifolia* and *Danthonia spicata*.

On mesic slopes with a northern aspect, *Quercus shumardii* dominates the forest canopy. Other common trees are *Carya texana*, *Quercus muehlenbergii*, *Fraxinus americana*, and *Amelanchier arborea*. Here, the understory is slightly more developed than on the drier slopes. *Chasmanthium latifolium* often forms dense clones. Other less common species include *Arisaema triphyllum*, *Tradescantia ohiensis*, *Ribes aureum*, and *Spiranthes lacera*.

GLADES

The glades are small prairie openings within the forest on dry slopes. As in the savannas, *Schizachyrium scoparium* dominates the herbaceous layer, but the glades are considerably more barren and rocky than the savannas. Common species include *Andropogon gerardii*, *Lespedeza virginica*, and *Echinacea pallida*. Less common species include *Opuntia humifusa*, *Mimosa quadrivalvis* var. *angustata*, *Amorpha canescens*, and *Baptisia bracteata* var. *leucophaea*. Several species in the glades were not noted in other habitats: *Dalea purpurea* var. *purpurea*, *Liatris squarrosa*, and *Psoralidium tenuiflorum*.

LOWLAND COMMUNITIES

These areas were present in the narrow ravines and the wider floodplain of Brush Creek. Important woody species in the lowlands include *Quercus stellata*, *Cornus drummondii*, *Platanus occidentalis*, *Juglans nigra*, and *Cercis canadensis*. The latter three species are particularly abundant along the banks of Brush Creek.

The floodplain of Brush Creek supports a diversity of herbaceous species, including a number of species not observed elsewhere in the tract. The plain adjacent to Brush Creek was probably plowed at one time, as evidenced by its open, savanna-like physiognomy and by the presence of exotic species such as *Lespedeza cuneata*, *Cirsium altissimum*, and *Verbascum thapsus*. Other common herbaceous species include *Coreopsis grandiflora* var. *grandiflora*, *Valerianella radiata*, *Krigia cespitosa*, *Asplenium platyneuron*, *Chasmanthium latifolium*, *Achillea millefolium*, *Eupatorium serotinum*, and *Panicum virgatum*. Several herbaceous species prefer the moist banks and stream bed of Brush Creek: *Scirpus lineatus*, *Amorpha fruticosa*, *Carex vulpinoidea*, *Polygonum punctatum*, and *Penthorum sedoides*.

LAKESHORE

Lake Keystone is a flood-control impoundment which has substantial changes in water levels during the year. Its shores are periodically inundated for varying lengths of time. Common woody species present along them are *Cephalanthus occidentalis* and *Diospyros virginiana*. Common herbaceous species include *Dichanthelium acuminatum* var. *fasciculatum* and *Diodia virginiana*, both of which form dense colonies. Other species include *Amaranthus rudis*, *Lechea tenuifolia*, *Juncus tenuis*, *Teucrium canadense* var. *virginicum*, and *Gaura parviflora*.

DISTURBED-SITE COMMUNITIES

The Frank Tract contains several active oil wells, containment ponds, and access roads to them. These disturbed areas have a species composition very different from

other communities. In addition, most of the exotic species encountered on the site occur in these areas. Along the roadsides, *Melilotus officinalis*, *Bromus japonicus*, *Verbena stricta*, *Sorghum halepense*, and *Cirsium altissimum* are abundant. *Typha angustifolia* forms thick stands in the ponds. Along the pond edge, *Cyperus* spp. and *Juncus* spp. compose much of the flora.

A unique community is located where a man-made pond once existed as indicated by the remains of a dam. In this area, *Quercus marilandica* and *Platanus occidentalis* are growing side-by-side, an unusual situation given the very different moisture requirements of these species. Also noteworthy is the thick growth of *Passiflora incarnata* (not observed elsewhere on the site) that covers the trees. It is likely that the pond was constructed decades ago and provided enough moisture to allow species like *Platanus occidentalis* to become established in an otherwise dry environment where *Quercus marilandica* was abundant.

METHODS

I surveyed the vascular flora during the growing seasons of 1996 and 1997. In 1996, I visited the site monthly from March through July and in September. In 1997, I visited the site monthly from March through October. All of the major plant communities were visited at least once during each phase of the growing season: spring, summer, and fall. Voucher specimens were prepared using standard herbarium techniques and deposited in the Oklahoma State University Herbarium (OKLA). Duplicate vouchers will be temporarily housed at OKLA and then donated to a Cross Timbers Preserve, should one be established. Taxa were identified using one or more of the following manuals:

Waterfall (1969), Steyermark (1981), Great Plains Flora Association (1986), Smith (1994), and Tyrl *et al.* 1994. Nomenclature follows Kartesz (1994) for scientific names and Taylor and Taylor (1994) for common names. Exotic status was determined using Taylor and Taylor (1994). This flora follows the standards listed in Palmer *et al.* (1995).

SUMMARY OF FLORISTIC SURVEY RESULTS

I found 268 species of vascular plants at the Frank Tract (Appendix A). These represent 187 genera in 72 families. The flora was typical of what one would expect in a mosaic landscape and included species indicative of tallgrass prairie and xeric eastern deciduous forests. The largest families were Poaceae (42 species), Fabaceae (32 species), and Asteraceae (31 species). These three families composed almost 40% of the vascular flora. Twenty species (7% of the vascular flora) were exotic to North America and 248 were native. None of the species were listed as federally threatened or endangered (Oklahoma Natural Heritage Inventory 1997). Twenty-one species (8% of the vascular flora) were not vouchered due to rarity of individuals, logistical constraints, or time limitations.

Because of their extensive old-growth cover, the upland forests are thought to be the least disturbed of the habitats at the Frank Tract. The results of the floristic survey supported this conclusion. Of the nineteen exotic species, only one species was identified in the upland forest, and this was a small population of *Taraxacum officinale* located along a drainage gully. The majority of the exotic species were confined to a relatively small area bordering oil wells and connecting roads.

LITERATURE CITED

Bourlier, B. G., J. D. Nichols, W. J. Ringwald, P. J. Workman and S. Clemmons. 1979. Soil survey of Osage County, Oklahoma. USDA Soil Conservation Service and USDI Bureau of Indian Affairs, Washington, DC.

Duck, L.B. and J.B. Fletcher. 1943. A game type map of Oklahoma. Oklahoma Game and Fish Department, Oklahoma City, OK.

Gray, F. and H.M. Galloway. 1959. Soils of Oklahoma. MP-56, Oklahoma State University Experiment Station, Stillwater.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Hunt, C.B. 1974. Natural regions of the United States and Canada. W.H. Freeman and Company, San Francisco.

Johnson, K.S., C.C. Branson, M.C. Neville, Jr., W.E. Ham, M.V. Marcher, and J.F. Roberts. 1972. Geology and earth resources of Oklahoma. Educational Publication 1, Oklahoma Geological Survey, University of Oklahoma, Norman.

Kartesz, J.T. 1994. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland, second edition. Timber Press, Portland.

Küchler, A.W. 1964. Potential natural vegetation of the conterminous United States. Special Publication No. 36. American Geographical Society, Washington, D.C.

Oklahoma Climatological Survey. 1996. Climatological information for Osage County [on-line]. Available World Wide Web: <http://radar.etr.ou.edu/ocs/climo/osage.html>

Oklahoma Natural Heritage Inventory. 1997. Federal & state endangered species in Oklahoma (list) [on-line]. Available World Wide Web: <http://www.biosurvey.ou.edu/fedspp.html>

Palmer, M.W., G.L. Wade, and P. Neal. 1995. Standards for the writing of floras. *BioScience* 45:339-345.

Smith, E.B. 1994. Keys to the flora of Arkansas. The University of Arkansas Press, Fayetteville.

Stahle, D.W. 1996. Tree rings and ancient forest history, p. 321-343. *In*: M. B. Davis (ed.). Eastern old-growth forests. Island Press, Washington, D.C.

- Stahle, D.W. and M.K. Cleaveland. 1993. Southern oscillation extremes reconstructed from tree rings of the Sierra Madre Occidental and Southern Great Plains. *J. Clim.*, 6:129-140.
- Stahle, D.W., J.G. Hehr, G.G. Hawks, Jr., M.K. Cleaveland and J.R. Baldwin. 1985. Tree-ring chronologies for the southcentral United States. Tree-Ring Laboratory and Office of the State Climatologist, University of Arkansas, Fayetteville, AR.
- Steyermark, J.A. 1981. Flora of Missouri. Iowa State University Press, Ames.
- Taylor, R.J. and C.E.S. Taylor. 1994. An annotated list of the ferns, fern allies, gymnosperms and flowering plants of Oklahoma. Southeastern Oklahoma State University, Durant.
- Therrell, M.D. 1996. A predictive model for locating ancient forests in the Cross Timbers of Osage County, Oklahoma [thesis]. University of Arkansas, Fayetteville, AR.
- Trewartha, G.T. 1968. An introduction to climate, 4th edition. McGraw-Hill Book Co., New York.

Tyrl, R.J., S.C. Barber, P. Buck, J.R. Estes, P. Folley, L.K. McGrath, C.E.S. Taylor, and R.A. Thompson. 1994. Identification of Oklahoma plants. Flora Oklahoma Incorporated, Stillwater.

U.S. Department of Agriculture (USDA). 1941. Yearbook of agriculture. Soils and men. Government Printing Office, Washington, DC.

Waterfall, U.T. 1969. Keys to the flora of Oklahoma, 4th edition. Privately published. Reprinted 1994 by Flora Oklahoma Incorporated, Stillwater, Oklahoma.

APPENDIX A

ANNOTATED CHECKLIST OF VASCULAR FLORA

Species listed below were collected on the Frank Tract during the growing season of 1996 and 1997. Families appear in alphabetical order within major groups.

Nomenclature follows Kartesz (1994) for scientific names and Taylor and Taylor (1994) for common names. Taxa marked with an asterisk (*) are exotic to North America. The community types the taxon most commonly occurs in are designated by the following symbols: SV = savanna, UF = upland forest, GL = glade, LC = lowland communities, LK = lakeshore community, and DS = disturbed area. Collection numbers are those of S.A. Roe.

FERNS AND FERN ALLIES

Adiantaceae

Cheilanthes lanosa (Michx.) D.C. Eat.—
Hairy Lipfern—UF (rock outcrops);
101.

Cheilanthes tomentosa Link.—Woolly
Lipfern—UF (rock outcrops); 243.

Aspleniaceae

Asplenium platyneuron (L.) B.S.P.—
Ebony Spleenwort—UF (rock
outcrops), LC; 102, 172, 228.

Asplenium trichomanes L.—Maidenhair
Spleenwort—UF (rock outcrops);
173.

Dryopteridaceae

Woodsia obtusa (Spreng.) Torr.—Blunt-
lobed Cliff Fern—UF (moist ledges);
91, 163, 171.

Equisetaceae

Equisetum hyemale L.—Winter Scouring
Rush—DS (moist seep on roadside);
379, specimen in sterile condition.

GYMNOSPERMS

Cupressaceae

Juniperus virginiana L.—Eastern Red
Cedar—UF, GL, LC; 235.

ANGIOSPERMS

Aquifoliaceae

Ilex decidua Walt.—Deciduous Holly—
LC (moist ravines); *not collected*.

Acanthaceae

Ruellia humilis Nutt.—Wild Petunia—
GL; 311.

Aceraceae

Acer negundo L. var. *texanum* Pax—Box
Elder—UF (noted only in one
location on ridgetop); 137.

Amaranthaceae

**Amaranthus rudis* Sauer—Water Hemp
—LK; 127.

Froelichia gracilis (Hook.) Moq.—
Cottonweed—SV (noted only in one
location); 77, 322.

Anacardiaceae

Rhus aromatica Ait.—Fragrant Sumac—
UF; 3, 41, 144.

Rhus copallina L. var. *latifolia* Engl.—
Winged Sumac—SV, UF; 256.

Rhus glabra L.—Smooth Sumac—SV;
216.

Toxicodendron radicans (L.) Kuntze ssp.
radicans—Poison Ivy—UF, LC; 50,
240.

Apiaceae

Spermolepis inermis (Nutt. ex DC.)
Mathias & Constance—Spreading
Scaleseed—SV; 193.

Apocynaceae

Apocynum cannabinum L.—Indianhemp
—DS (roadside; noted only in one
location); 378.

Araceae

Arisaema dracontium (L.) Schott—
Dragonroot—LC; 372.

Arisaema triphyllum (L.) Schott—Jack-
in-the-Pulpit—UF (moist slopes); 17.

Asclepiadaceae

Asclepias tuberosa L. ssp. *interior*
Woods.—Butterfly Milkweed—SV
(noted only in one location); *not*
collected.

Asclepias viridis Walt.—Green Milkweed
—SV, DS (roadsides); 49.

Asteraceae

Achillea millefolium L. var. *occidentalis*
DC.—Yarrow—DS (roadsides); 46.

Ambrosia psilostachya DC.—Western
Ragweed—DS (old road); 321.

Antennaria plantaginifolia (L.) Richards.
—Ladies' Tobacco—UF; 16.

Aster oolentangiensis Riddell—Blue
Aster—SV; 361.

Brickellia eupatorioides (L.) Shinnars
var. *corymbulosa* (Torr. & Gray)
Shinnars—False Boneset—DS
(middle of road); 341.

Chrysopsis pilosa Nutt.—Soft-hair Golden
Aster—SV, DS (roadsides); 60, 195.

Cirsium altissimum (L.) Hill—Tall Thistle
—DS (roadside); 330.

Conyza canadensis (L.) Cronq.—
Horseweed—UF; 355, 375.

Coreopsis grandiflora Hogg ex Sweet
var. *grandiflora*—Bigflower
Coreopsis—LC, UF; 218.

Echinacea pallida (Nutt.) Nutt.—Pale Coneflower—GL, DS; 215.

Elephantopus carolinianus Raeusch.—Elephant's Foot—UF; 338.

Erechtites hieraciifolia (L.) Raf. ex DC. var. *hieraciifolia*—Fireweed—UF; 139.

Erigeron strigosus Muhl. ex Willd.—Daisy Fleabane—SV, DS (roadsides); 47, 71, 192.

Eupatorium coelestinum L.—Mist Flower—SV; 358.

Eupatorium serotinum Michx.—Late Boneset—SV, LC, DS (oil well pad); 326, 333, 357, 370.

Gamochaeta purpurea (L.) Cabrera—Purple Cudweed—UF, SV; 33.

Gnaphalium obtusifolium L.—Sweet Everlasting—SV; 360, 371.

Helenium amarum (Raf.) H. Rock var. *amarum*—Sneezeweed—DS (roadsides); 65.

Helianthus annuus L.—Common Sunflower—DS (roadsides); 315.

Helianthus pauciflorus Nutt. ssp. *pauciflorus*—UF; 294.

Hieracium gronovii L.—Hawkweed—UF; 136, 257, 293.

Hieracium longipilum Torr.—Longbeard Hawkweed—DS (middle of road); 290.

Krigia cespitosa (Raf.) Chambers—Common Dwarf Dandelion—LC, LK; 13, 232.

Liatris squarrosa (L.) Michx. var. *hirsuta* (Rydb.) Gaiser—Gayfeather—GL; 124, 262, 308.

Prionopsis ciliata (Nutt.) Nutt.—Wax Goldenweed—DS (oil well pad); 314.

Pyrrhopappus carolinianus (Walt.) DC.—False Dandelion—DS (old road bed, edge of pond), LK; 84, 252, 273.

Rudbeckia hirta L. var. *pulcherrima* Farw.—Blackeyed Susan—DS (roadsides) 59, 246.

Solidago nemoralis Ait.—Old Field Goldenrod—GL; 356.

Solidago ulmifolia Muhl. ex Willd. var. *microphylla* Gray—Elmleaf Goldenrod—UF, DS (roadside); 296, 335, 342.

**Taraxacum officinale* G.H. Weber ex Wiggers—Common Dandelion—UF (noted in one location along drainage gully); 9.

Vernonia baldwinii Torr. ssp. *baldwinii*—Western Ironweed—UF, DS (middle of road); 122, 309.

Boraginaceae

Myosotis verna Nutt.—Early Scorpiongrass—UF; 169, 176, 206.

Brassicaceae

Arabis canadensis L.—Sicklepod—UF; 179, 180.

Cardamine parviflora L. var. *arenicola* (Britt.) O.E. Schulz—Smallflower Bitter Cress—UF (rock outcrops); 164.

**Lepidium densiflorum* Scrad.—Peppergrass—DS (oil well pad); 108, 181.

Cactaceae

Opuntia humifusa (Raf.) Raf. var. *humifusa*—SV, GL, UF; not collected.

Campanulaceae

Triodanis perfoliata (L.) Nieuwl.—Clasping Venus Looking-glass—SV; 194.

Caprifoliaceae

- Symphoricarpos orbiculatus* Moench—
Coralberry—UF; 313, 363.
Viburnum prunifolium L.—Rusty
Blackhaw—UF, LC; 18, 368.

Chenopodiaceae

- Chenopodium standleyanum* Aellen—
Standley's Goosefoot—UF; 129.
Chenopodium simplex (Torr.) Raf.—
Bigseed Goosefoot—UF; 130.

Cistaceae

- Lechea tenuifolia* Michx.—Narrowleaf
Pinweed—LK, UF; 247, 261.
Lechea mucronata Raf.—Pinweed—
DS (edge of pond); 281, 288.

Clusiaceae

- Hypericum drummondii* (Grev. & Hook.)
Torr. & Gray—Nits-and-lice—SV,
UF; 282, 354.
Hypericum hypericoides (L.) Crantz ssp.
multicaule (Michx. ex Willd.) Robson
—St. Andrews Cross—UF; 297.

Commelinaceae

- Commelina erecta* var. *deamiana*
Fern.—Erect Day-flower—SV; 70.
Tradescantia ohiensis Raf.—Spiderwort
—UF, SV; 28.

Cornaceae

- Cornus drummondii* C.A. Mey.—Rough-
leaved Dogwood—LC, UF; 222,
227, 237.

Crassulaceae

- Penthorum sedoides* L.—Ditch Stonecrop
—LC (middle of creek); 374.

Cyperaceae

- Carex brevior* (Dewey) MacKenzie ex
Lunell—Fescue Sedge—UF, LC; 39,
230.
Carex bushii MacKenzie—Carolina
Sedge—UF; 168, 200.
Carex festucacea Schkuhr ex Willd.—
Fescue Sedge—UF; 204.
Carex gravida Bailey var. *gravida*—
Heavy Sedge—UF; 175, 223.
Carex muehlenbergii Schkuhr ex Willd.
var. *enervis* Boott—Muhlenberg's
Sedge—UF; 167, 205, 208.
Carex muehlenbergii Schkuhr ex Willd.
var. *muehlenbergii*—Muhlenberg's
Sedge—UF; 36.
Carex nigromarginata Schwein.—UF
(moist slopes); 6.
Carex vulpinoidea Michx.—Fox Sedge—
LC; 225.
Cyperus echinatus (L.) Wood—Globe
Flatsedge—SV, UF, DS (roadside);
69, 260.
Cyperus lupulinus (Spreng.) Marcks ssp.
lupulinus—Houghton Flatsedge—
SV; 73.
Cyperus pseudovegetus Steud.—DS (old
road bed, edge of pond); 82, 272.
Cyperus strigosus L.—False Nutgrass—
LK; 128.
Eleocharis tenuis (Willd.) J.A. Schultes
var. *verrucosa* (Svens.) Svens.—
Slender Spikesedge—SV, UF (moist
seeps); 55, 158.
Fimbristylis autumnalis (L.) Roemer &
J.A. Schultes—Slender Fimbristylis—
SV; 83.
Rhynchospora globularis (Chapman)
Small—Globe Beakrush—DS (edge
of pond); 270.

Rhynchospora harveyi W. Boott—
Harvey's Beakrush—SV, UF, DS
(old road bed); 29, 52, 86, 211.
Scirpus lineatus Michx.—LC; 220.
Scleria ciliata Michx. var. *ciliata*—
Fringed Nutrush—SV; 32, 51.

Ebenaceae

Diospyros virginiana L.—Persimmon—
SV, LC, LK; 58, 226.

Ericaceae

Vaccinium arboreum Marsh.—
Farkleberry—UF (dry slopes); 188.

Euphorbiaceae

Acalypha gracilens Gray—Three-seeded
Mercury—DS (oil well pad); 105.
Chamaesyce maculata (L.) Small—DS
(middle of road); 114.
Cnidioscolus texanus (Muell.-Arg.) Small
—Bull Nettle—SV; DS (roadsides);
74.
Croton glandulosus L. var.
septentrionalis Muell.-Arg.—Croton
—DS (old road bed); 79.
Croton willdenowii Webster—
Crotonopsis—UF; 310.
Euphorbia corollata L.—Flowering
Spurge—DS (old road bed); 135.

Fabaceae

**Albizia julibrissin* Durz.—Mimosa—
UF (noted only in one location);
not collected.
Amorpha canescens Pursh—Leadplant—
GL; 233.
Amorpha fruticosa L.—False Indigo—
LC; 221.

Baptisia bracteata Muhl. ex Ell. var.
leucophaea (Nutt.) Kartesz &
Gandhi—Long-Bracted Wild
Indigo—GL, SV; 14, 38.

Cercis canadensis L.—Redbud—UF
(ridgetops) and LC (along Brush
Creek); 1, 150, 236.

Chamaecrista fasciculata (Michx.)
Greene—Partridge Pea—DS
(roadsides); 63.

Clitoria mariana L.—Butterfly Pea—
UF; 96, 103, 244, 258.

Crotalaria sagittalis L.—Rattlebox—
SV; 283.

Dalea purpurea Vent. var. *purpurea*—
Purple Prairie Clover—GL; 238.

Desmanthus illinoensis (Michx.) MacM.
ex B.L. Robins. & Fern.—
Bundleflower—DS (roadside); 115.

Desmodium canescens (L.) DC.—Hoary
Tickclover—DS (oil well pad); 327.

Desmodium ciliare (Muhl. ex Willd.) DC.
—Tick Trefoil—UF; 112, 259, 332.

Desmodium marilandicum (L.) DC.—
Tick Trefoil—UF; 347.

Desmodium paniculatum (L.) DC.—
Panicked Tickclover—UF; 346.

Desmodium perplexum Schub.—Panicked
Tickclover—UF; 133.

Desmodium sessilifolium (Torr.) Torr. &
Gray—Sessile Tickclover—SV, DS
(roadside); 287, 323.

Galactia volubilis (L.) Britt.—Downey
Milkpea—SV; 87.

Gleditsia triacanthos L.—Honey Locust
—LC; *not collected*.

Lespedeza capitata Michx.—Bush Clover
—SV, DS (old road bed); 31, 143.

**Lespedeza cuneata* (Dum.-Cours.) G.
Don—Sericea Lespedeza—LC (old
field); 376.

Lespedeza hirta (L.) Hornem.—Hairy
Lespedeza—UF; 352.

Lespedeza intermedia (S. Wats.) Britt.
—SV; 318.

- Lespedeza procumbens* Michx.—Trailing
Lespedeza—LC; 303.
- Lespedeza violacea* (L.) Pers.—Violet
Lespedeza—GL; 343.
- Lespedeza virginica* (L.) Britt.—Slender
Lespedeza—GL, UF, DS (old road
bed); 142, 214, 348.
- **Melilotus officinalis* (L.) Lam.—Yellow
Sweet Clover—DS (roadsides); 48,
68.
- Mimosa quadrivalvis* L. var. *angustata*
(Torr. & Gray) Barneby—Sensitive
Briar—GL; 234.
- Psoralidium tenuiflorum* (Pursh)
Rydb.—Wild Alfalfa—GL; 40, 307.
- Strophostyles helvula* (L.) Ell.—Wild
Bean—SV, DS (oil well pad); 104,
320.
- Strophostyles leiosperma* (Torr. & Gray)
Piper—Smoothseed Wild Bean—
DS (oil well pad); 94.
- Stylosanthes biflora* (L.) B.S.P.—Pencil
Flower—SV; 90.
- Tephrosia virginiana* (L.) Pers.—
Tephrosia—UF; 97.

Fagaceae

- Quercus marilandica* Muenchh.—
Blackjack Oak—UF, SV; 149.
- Quercus muehlenbergii* Engelm.—
Chinquapin Oak—UF (moist slopes);
364, 365.
- Quercus shumardii* Buckl.—Shumard
Red Oak—UF (moist slopes); 362,
366.
- Quercus stellata* Wangenh.—Post Oak—
UF, GL, LC; 151, 152, 156, 344.
- Quercus velutina* Lam.—Black Oak—
UF; not collected.

Gentianaceae

- Sabatia campestris* Nutt.—Prairie Rose—
GL; 245.

Grossulariaceae

- Ribes aureum* Pursh var. *villosum*
DC.—Buffalo Currant—UF (moist
slopes); 7.

Juglandaceae

- Carya cordiformis* (Wangenh.) K. Koch
—Bitternut Hickory—LC; not
collected.
- Carya illinoensis* (Wangenh.) K. Koch
—Pecan—LC; not collected.
- Carya texana* Buckl.—Black Hickory—
UF; 153, 154, 157, 161, 345.
- Juglans nigra* L.—Black Walnut—LC;
not collected.

Juncaceae

- Juncus brachycarpus* Engelm.—
Whiteroot Rush—DS (roadside); 89,
278.
- Juncus diffusissimus* Buckl.—Slimpod
Rush—DS (edge of pond); 275.
- Juncus dudleyi* Wieg.—Slender Rush—
LC; 229.
- Juncus interior* Wieg.—Inland Rush—
SV (moist depressions), DS (edge of
pond), UF; 53, 203, 268.
- Juncus marginatus* Rostk. var.
marginatus—Grassleaf Rush—DS
(old road bed, edge of pond); 80,
269.
- Juncus tenuis* Willd.—Slender Rush—
DS (middle of road), LK; 119, 253.
- Juncus validus* Coville var. *validus*—
Roundhead Rush—DS (old road bed,
edge of pond); 81, 271.
- Luzula bulbosa* (Wood) Smyth & Smyth
—Bulb Woodrush—UF; 159, 162.

Lamiaceae

- Monarda fistulosa* L.—Wild Bergamot—
UF; 121.

- Monarda punctata* L.—Horsemint—
DS (middle of road); 329.
- Prunella vulgaris* L. ssp. *lanceolata* (W.
Bart) Hulte'n—Common Self-Heal—
LC (moist stream banks); 299.
- Pycnanthemum tenuifolium* Schrad.—
Narrowleaf Mountainmint—LC
(moist stream banks), DS (dry pond);
286, 298.
- Salvia azurea* Michx. ex Lam.—Azure
Blue Sage—UF; 353.
- Scutellaria ovata* Hill—Eggleaf Skullcap
—GL, UF; not collected.
- Teucrium canadense* L. var. *virginicum*
(L.) Eat.—American Germander—
UF (moist areas), LK; 92, 255.

Liliaceae

- Allium canadense* L. var. *mobile*
(Regel) Ownbey—Wild Onion —UF;
207.
- Hypoxis hirsuta* (L.) Coville—Yellow
Stargrass—UF (rock outcrops); 165.

Linaceae

- **Linum medium* (Planch.) Britt. var.
texanum (Planch.) Fern.—Sucker
Flax—DS (edge of pond); 277.

Menispermaceae

- Cocculus carolinus* (L.) DC.—Carolina
Snailseed—UF, LC; not collected.

Molluginaceae

- **Mollugo verticillata* L.—Carpetweed—
DS (old road bed); 85.

Moraceae

- Morus rubra* L.—Red Mulberry—UF,
LC; not collected.

Oleaceae

- Fraxinus americana* L.—White Ash—
UF; 263.

Onagraceae

- Gaura parviflora* Dougl. ex Lehm.—
Velvety Gaura—LK; 126.
- Ludwigia alternifolia* L.—Bushy Seedbox
—DS (edge of pond); 280.
- Oenothera biennis* L.—Common Evening
Primrose—DS (roadside; noted in
only one location); 336.
- Oenothera laciniata* Hill—Cutleaf
Evening Primrose—DS (roadsides);
61.

Orchidaceae

- Spiranthes lacera* (Raf.) Raf.—Slender
Ladies'-tresses—UF (moist slopes);
349.

Oxalidaceae

- Oxalis dillenii* Jacq.—Yellow Wood
Sorrel—LK; 12.
- Oxalis violacea* L.—Violet Wood Sorrel
—UF, SV; 37, 155, 189, 334.

Passifloraceae

- Passiflora incarnata* L.—May-pop
Passionflower—DS (dry pond); 93.

Phytolaccaceae

- Phytolacca americana* L.—Pokeweed—
UF; 264.

Plantaginaceae

- Plantago aristata* Michx.—Bottlebrush
Plantain—DS (roadsides); 64.

- Plantago patagonica* Jacq.—Woolly
Plantain—DS (roadsides); 43.
Plantago virginica L.—Paleseed
Plantain—DS (roadsides); 45; 184.

Plantanaceae

- Platanus occidentalis* L.—Sycamore—
LC (moist ravines); not collected.

Poaceae

- Agrostis hyemalis* (Walt.) B.S.P.—
Ticklegrass—DS (bank of manmade
pond); 54.
Andropogon gerardii Vitman—Big
Bluestem—SV, UF; 331.
Andropogon ternarius Michx.—
Splitbeard Bluestem—SV; 317.
**Bromus japonicus* Thunb. ex Murr.—
Japanese Brome—DS (roadside);
120, 224.
**Bromus secalinus* L.—Cheat—DS; 217.
**Bromus tectorum* L.—Downy Brome—
DS; 183.
Cenchrus carolinianus Walt.—Sandbur—
DS (roadsides); 76.
Chasmanthium latifolium (Michx.) Yates
—Inland Seaoats—UF (moist slopes,
ravines); 99, 266.
**Cynodon dactylon* (L.) Pers.—Bermuda
Grass—DS (oil well pad); 109.
Danthonia spicata (L.) Beauv. ex Roemer
& J.A. Schultes—Poverty Grass—
UF; 110, 210.
Dichanthelium acuminatum (Sw.) Gould
& C.A. Clark var. *fasciculatum*
(Torr.) Freckmann—Woolly Panicum
—LK; 251.
Dichanthelium depauperatum (Muhl.)
Gould—Starved Panicum—UF; 187.
Dichanthelium linearifolium (Scribn. ex
Nash) Gould—Slimleaf Panicum—
GL, SV, UF; 42, 166, 177, 209.
Dichanthelium malacophyllum (Nash)
Gould—Softleaf Panicum—UF, DS;
35, 185.
Dichanthelium oligosanthos (J.A.
Schultes) Gould var. *scribnerianum*
(Nash) Gould—Small Panicgrass—
SV; 30, 199.
Dichanthelium scoparium (Lam.) Gould
—Velvet Panicgrass—LC; 98, 239.
Dichanthelium sphaerocarpon (Ell.) Gould
var. *sphaerocarpon*—Leafy Panicum
—SV, UF, LK, DS (oil well pad);
197, 202, 250, 291.
Dichanthelium villosissimum var.
praecocius (A.S. Hitchc. & Chase)
Freckman—Early Panicum—SV, UF;
198, 201.
Digitaria cognata (J.A. Schultes) var.
cognata—Fall Witchgrass—UF; 132.
**Digitaria sanguinalis* (L.) Scop.—Hairy
Crabgrass—DS (oil well pad); 95.
**Echinochloa crus-galli* (L.) Beauv.—
Barnyard Grass—DS (oil well pad);
325, 377.
Elymus virginicus L. var. *virginicus*—
Virginia Wild Rye—DS (roadsides);
66, 123, 241.
Eragrostis secundiflora J. Presl.—Red
Lovegrass—DS (roadsides); 62, 328.
**Festuca arundinacea* Schreb.—DS
(roadsides); 116.
**Festuca pratensis* Huds.—Meadow
Fescue—DS (roadsides); 117.
Festuca versuta Beal—Texas Fescue—
UF; 213.
Hordeum pusillum Nutt.—Little Barley—
DS (road bed); 44, 182.
Muhlenbergia capillaris (Lam.) Trin.—
Hairgrass—UF; 351.
Muhlenbergia racemosa (Michx.)
B.S.P.—Marsh Muhly—UF (moist
slopes); 312.
Muhlenbergia sobolifera (Muhl. ex
Willd.) Trin.—Rocky Muhly—UF;
138.

- Panicum anceps* Michx.—Beaked
Panicum—LC, UF (moist areas);
140, 305.
- Panicum virgatum* L.—Fall Switchgrass
—LC, DS (edge of pond); 279.
- Paspalum setaceum* Michx.—Thin
Paspalum—SV, DS; 78, 324.
- Schizachyrium scoparium* (Michx.) Nash
—Little Bluestem—SV, GL; 367.
- Setaria parviflora* (Poir.) Kerguelen—
Knotroot Bristlegrass—SV (low wet
areas); 72.
- Sorghastrum nutans* (L.) Nash—
Indiangrass—SV; 316.
- **Sorghum halepense* (L.) Pers.—Johnson
Grass; DS (roadsides); 67.
- Sphenopholis obtusata* (Michx.) Scribn.—
Prairie Wedgescale—UF; 34.
- Steinchisma hians* (Ell.) Nash—Gaping
Panicum—UF (moist ravines), DS
(edge of pond); 100, 274.
- Tridens flavus* (L.) A.S. Hitchc.—
Purpletop—UF, SV, DS (roadside);
141, 285, 319.
- Triplasis purpurea* (Walt.) Chapman—
Purple Sandgrass—DS (oil well pad);
106.
- Vulpia octoflora* (Walt.) Rydb.—
Sixweeks Fescue—UF; 191.

Polygonaceae

- Polygonum hydropiperoides* Michx.—
Mild Water Pepper—DS (edge of
pond); 276.
- Polygonum punctatum* Ell. var.
punctatum—Water Smartweed—
LC (middle of creek); 373.
- Rumex hastatulus* Baldw.—Heartwing
Sorrel—SV, DS (roadside); 88, 196,
292.

Portulacaceae

- Claytonia virginica* L.—Virginia
Springbeauty—UF; 8, 15, 145, 170.

Primulaceae

- Dodecatheon meadia* L.—Shooting
Star—UF; *not collected*.

Ranunculaceae

- Myosurus minimus* L. ssp. *minimus*—
Mousetail—LK; 10.

Rosaceae

- Amelanchier arborea* (Michx. f.) Fern.—
Juneberry—UF; 2, 147.
- Prunus angustifolia* Marsh.—Chickasaw
Plum—SV; 4, 148, 306.
- Prunus mexicana* S. Wats.—Big-tree
Plum—UF; 340.
- Rubus flagellaris* Willd.—Northern
Dewberry—UF; 174.
- Rubus oklahomus* Bailey—Highbush
Blackberry—SV; 267.

Rubiaceae

- Cephalanthus occidentalis* L.—
Buttonbush—LK; 125, 242.
- Diodia teres* Walt. var. *teres*—Rough
Buttonweed; DS (roadsides); 75,
289.
- Diodia virginiana* L.—Virginia
Buttonweed—LK; 249.
- Galium aparine* L.—Catchweed
Bedstraw—UF; 178.
- Galium pilosum* Ait. var. *pilosum*—Hairy
Bedstraw—LK, UF; 248, 295.
- Hedyotis nigricans* (Lam.) Fosberg—
Prairie Bluet—LK; 254.
- Houstonia pusilla* Schoepf—Tiny Bluet—
UF; 146, 190.

Salicaceae

- Populus deltoides* Bartr. ex Marsh.—
Cottonwood—DS; *not collected*.

Salix nigra Marsh.—Black Willow—
DS (edge of pond); *not collected*.

Sapindaceae

Sapindus saponaria L. var. *drummondii*
(Hook. & Arn.) L. Benson—
Soapberry—UF (noted in only one
location); *not collected*.

Sapotaceae

Sideroxylon lanuginosum Michx. ssp.
lanuginosum—Chittamwood—
UF; *not collected*.

Scrophulariaceae

Agalinis tenuifolia (Vahl) Raf. var.
macrophylla (Benth.) Blake—
Slenderleaf Agalinis—UF (moist
slopes); 350.

Buchnera americana L.—American
Bluehearts—SV; 359.

Nuttallanthus canadensis (L.) D.A.
Sutton—Oldfield Toadflax—DS;
186.

Nuttallanthus texanus (Scheele) D.A.
Sutton—Oldfield Toadflax—DS (oil
well pad); 107.

Penstemon tubiflorus Nutt.—Tubeflower
Penstemon—UF, SV; 212.

**Verbascum thapsus* L.—Common
Mullein—LC; 302.

**Veronica peregrina* L. ssp. *xalapensis*
(Kunth) Pennell—Purslane
Speedwell—LK; 11.

Simaroubaceae

**Ailanthus altissima* (P. Mill.) Swingle—
DS (oil well pad; noted only in one
location); *not collected*.

Smilacaceae

Smilax bona-nox L.—Greenbriar—UF,
LC; *not collected*.

Solanaceae

Datura stramonium L.—Jimsonweed—
UF; 131.

Physalis pubescens var. *integrifolia*
(Dunal) Waterfall—Downy Ground
Cherry—UF; 265.

Solanum carolinense L.—Carolina
Horsenettle—LC; 304.

Solanum dimidiatum Raf.—DS
(roadsides); 57.

Typhaceae

Typha angustifolia L.—Narrow-leaved
Cattail—DS (pond); 284.

Ulmaceae

Celtis laevigata Willd.—Sugarberry—
LC; *not collected*.

Celtis occidentalis L.—Hackberry—
LC; *not collected*.

Ulmus americana L.—American Elm—
LC; *not collected*.

Ulmus rubra Muhl.—Slippery Elm—
SV, UF; 380.

Urticaceae

Boehmeria cylindrica (L.) Sw.—False
Nettle—LC; 300.

Parietaria pensylvanica Muhl. ex Willd.
—Pennsylvania Pellitory—UF; 111.

Valerianaceae

Valerianella radiata (L.) Dufur.—
Common Beaked Cornsalad—LC;
219, 231.

Verbenaceae

- Glandularia canadensis* (L.) Nutt.—Rose
Vervain—DS (roadside); 5, 56.
Verbena bracteata Lag. & Rodr.—
Bracted Vervain—DS (middle of
road); 113.
Verbena stricta Vent.—Woolly Vervain
—DS (roadside); 118.
Verbena urticifolia L.—White Vervain—
LC (moist stream banks); 301.

Violaceae

- Viola sagittata* Ait.—Arrow-leaved
Violet—UF; 160.

Viscaceae

- Phoradendron leucarpum* (Raf.) Reveal
& M.C. Johnston—Mistletoe—UF,
LC; 369.

Vitaceae

- Cissus incisa* Des Moulins—Possum
Grape—UF (rock outcrops); 134.
Parthenocissus quinquefolia (L.) Planch.
—Virginia Creeper—UF, LC; 337.
Vitis vulpina L.—Winter Grape—UF,
LC; 339.

VITA

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