OLD-GROWTH FORESTS IN THE WESTERN CROSS TIMBERS OF TEXAS

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By

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Chapter 1

Introduction

The Cross Timbers span the ecotone between eastern deciduous forests and grasslands of the southern Great Plains. Within the Cross Timbers, savannahs, tallgrass prairies, and post oak (*Quercus stellata*)-dominated forests intermingle in a complex mosaic that may have sprawled across nearly 8 million ha of southeastern Kansas, Oklahoma, and northcentral Texas before European settlement (Küchler 1964; Figure 1.1). Approximately half the total area occupied by the Cross Timbers occurs in Oklahoma (2.4 million ha; Harrison 1974; Hoagland 1999). The Cross Timbers account for 400,000 ha in Kansas and slightly more than 1.6 million ha in Texas (Dyksterhuis 1948). Just south of the Red River, the Fort Worth Prairie divides the Texas Cross Timbers into the eastern and western Cross Timbers. Bounded on the east by the Blackland Prairie, the eastern Cross Timbers (404,700 ha) extend into parts of Cooke, Dallas, Denton, Hill, Johnson, McLennan, Sherman, and Tarrant counties. The western Cross Timbers—the focus of this dissertation—occupy 1.5 million ha in portions of Archer, Brown, Callahan, Clay, Comanche, Eastland, Erath, Hood, Jack, Montague, Palo Pinto, Parker, Shackelford, Somervell, Stephens, Throckmorton, Wise, and Young counties (Diggs et al. 1999). The western Cross Timbers vary in width from 50 km near the Red River to 160 km farther south (McCluskey 1972), and contain parts of two watersheds—the Trinity in the north and the Brazos in the south (McCluskey 1972).

Nearly level to gently rolling areas along the eastern and southern edges of the Cross Timbers contrast with high bluffs and steep hillsides, which characterize the central and western portions (McCluskey 1972; Harrison 1974). Cretaceous, sandy Woodbine and Trinity strata underlie much of the eastern and western Cross Timbers, but rocky Pennsylvanian strata occur near the westernmost edge (Diggs et al. 1999). Dyksterhuis (1948) used the term *fringe* to describe the western zone of high relief, rocky soils, and boulders, whereas the eastern zone of relatively level terrain was termed the *main belt* (Figure 1.2).

The low-fertility alfisols that characterize the western Cross Timbers have a sandy to sandy-loam texture, reddish clay subsoil, and relatively low pH (Harrison 1974). The loose, deep, light-colored sands of the main belt are classified in four soil associations: Windthorst-Duffau-Bunyan, Chaney-Demona-Pedernales, Patilo-Demona-Nimrod, and Pedernales-Cisco-Menard. Soils underlying the fringe are in the Bonti-Exray-Truce association. The occurrence of trees in this otherwise-prairie region of Texas is due primarily to well-drained soils, which allow infiltration of water and penetration of tree roots (Hoagland et al. 1999). In contrast, woody vegetation fares poorly on the clay soils (derived from limestone) that characterize neighboring prairies, even though annual precipitation is greater in the Blackland Prairie than in the Cross Timbers (Diggs et al. 1999). As a result of alternating deposition of sand and clay by the Cretaceous sea in the area now occupied by the Cross Timbers, limestone- and sandstone-derived soils are interwoven, and pockets of clay historically supported prairie vegetation (Costello 1969; Harrison 1974; Smeins & Diamond 1986).

Nineteenth-century explorers' accounts of the vegetation of the Cross Timbers differed dramatically (Diggs et al. 1999). One early traveler through the Cross Timbers described "an open growth of upland oaks interspersed with prairies," whereas a contemporary reported traveling through "very dense forest" (Foreman 1947). Others encountered either "an impervious underbrush of small bushy oak" or, alternately, "no undergrowth but a coarse grass" (Foreman 1947). These written records, though seemingly conflicting, corroborate the existence of a mosaic of vegetation types throughout the Cross Timbers.

Although differing in the details of their experiences, early explorers agreed upon the difficulty of traversing the Cross Timbers. For example, Washington Irving wrote, "I shall not easily forget the mortal toil, and the vexations of flesh and spirit, that we underwent occasionally, in our wanderings through the Cross Timber. It was like struggling through forests of cast iron" (Foreman 1947). One of Irving's companions expressed similar complaints about "that hilly stony region, with its almost impenetrable forest of the closest and harshest growth" (Foreman 1947). In 1832, a traveler through the Cross Timbers reported, "sometimes we have to go down deep ravines, which are always fortified by a triple rampart of scrub oaks tangled with vines and twenty other kinds of climbing plants. At other times we have to climb rocky slopes covered with little oaks" (Foreman 1947).

Undeterred by explorers' accounts of the Cross Timbers, pioneers arrived in the early 1850s and settled in areas that had both grassland and forest, and where soils could be tilled with rudimentary tools (Grubbs 1953; May 1962). Before European settlement, Caddo tribes had inhabited the Cross Timbers, and Comanches occupied prairies farther west (May 1962; Stroud 1968). Settlers rapidly cleared creek bottoms and small, level tracts of post oak, but large areas were not farmed until the 1880s (Grubbs 1953; May 1962). Corn and cotton were the first crops grown in the western Cross Timbers, and by 1900, cotton farming had become residents' primary source of income (Grubbs 1953). After only a decade of cultivation, however, the deep, sandy Windthorst soils eroded; as early as 1913, farms were retired from cotton cultivation and consolidated into livestock ranches (Dyksterhuis 1948; Grubbs 1953). A 1953 assessment of agricultural development in the western Cross Timbers concluded that the region's soils and topography were not suitable for cultivation and that "such land must be reverted to range grazing" (Grubbs 1953). Nearly twenty years later, Harrison (1972) found evidence of recent grazing at 48% of 200 randomly selected sites in the western Cross Timbers. Cattle ranching remains the region's primary economic activity; however, livestock production in the western Cross Timbers is low, compared with that of other rangelands (Bernardo et al. 1992).

Relatively little of the rough, rocky fringe was grazed or farmed, and commercial logging was not economically viable in the region (Bernardo et al. 1992), although some post oaks were cut for coal-mine props, fuel, fence posts, railroad ties, and rough lumber (Dyksterhuis 1948; McCluskey 1972; Therrell & Stahle 1998). Because they were not commercially useful or easily accessible, old-growth forests remain on rough terrain in the western Cross Timbers (Stahle 1996; Diggs et al. 1999). Remaining old-growth forests are threatened by expansion of cattle range, invasive species, suburban encroachment, and fire suppression (Fitzgerald et al. 2000). In addition, more than 99% of the western Cross Timbers is privately owned, and old-growth forests are sometimes mistaken for second-growth because of the relatively small size of drought-stressed, slow-growing, old post oak trees (5-15 m tall, 30-60 cm DBH) (Stahle & Chaney 1994). The few public, managed areas in the western Cross Timbers include the Lyndon B. Johnson National Grassland in Wise County (200 ha), Lake Mineral Wells State Park in Parker County (1090 ha), and two state recreation areas (679 ha).

Although old-growth forests in the western Cross Timbers span a continuum of human alteration, they may be one of the least disturbed natural communities left in Texas. Old-growth, post-oak dominated forests are valuable because they provide (1) habitat for native species, (2) benchmarks against which future landscape changes can be assessed, (3) core areas for ecological restoration, (4) opportunities for researchers and educators to understand and communicate the history and ecology of Texas, and (5) data for assessing historical and ongoing climate change through analysis of tree rings.

Prior to the start of this dissertation project, the University of Arkansas Tree-Ring Laboratory had documented old post oak trees in the western Cross Timbers during 25 years of extensive field research, but questions remained about the extent, distribution, and composition of remaining old-growth forests. In light of those uncertainties, as well as the ecological importance of remaining old-growth forests and ongoing threats to their persistence, this research project was designed to achieve four primary objectives:

1) develop and field test a comprehensive, cartographic model that incorporates remotely sensed imagery, digital soils and elevation data, and historical data to predict the area and distribution of remaining old-growth forests in the western Cross Timbers;

2) characterize the structure and composition of relatively undisturbed old-growth forests in the western Cross Timbers;

3) characterize the understory of old-growth forests in the western Cross Timbers, and assess the degree of anthropogenic modification, with reference to historical data; and

4) assess overstory and understory dynamics at high-quality old-growth forest sites.

Accurate mapping of the locations of old-growth forests is essential for increasing awareness of their existence and importance, as well as for restoration and conservation of ecological processes and native species in the region. But scientifically informed restoration and management of Cross Timbers tracts will require more than an accurate map of old-growth forest locations. Also essential is an understanding of the structure and composition of remaining old-growth forests, processes important in the dynamics of old-growth stands, and the degree of anthropogenic modification of native plant communities.

The results of this research are reported and discussed in Chapters 2-4. Chapter 2, "Predictive Modeling of Old-Growth Forests in the Western Cross Timbers," describes the development and field testing of a cartographic model to identify remaining old-growth forests in the region. My model predicted that old-growth forests occupied 19,166 ha in the western Cross Timbers, and field technicians surveyed 50 randomly selected transects (500,000 m^2 in all) within the predicted old-growth area. Approximately one-third of the area surveyed was old-growth, and more than 50% was second-growth. For old-growth sites, I constructed an overall post oak age structure, based on dating of increment cores from randomly selected trees $\geq$10 cm DBH. Although I found that Landsat ETM+ imagery was insufficient for distinguishing old- and second-growth post oak forests in the western Cross Timbers, my model successfully identified many large, undisturbed tracts of old-growth forest in the region.

Chapter 3, "Structure and Composition of Old-Growth Forests in the Western Cross Timbers of Texas," is the first quantitative, ecological characterization of old-growth forests in the western Cross Timbers. This chapter reports the results of point-quarter sampling (Cottam & Curtis 1956) at the 16 old-growth sites identified during field testing of the predictive model. I found that, although post oak was characteristic of old-growth sites, post oak dominance varied from 0.46 to 0.99. Approximately one-third of 648 randomly selected post oaks were ≥150 years old, and 7.2% were ≥200 years old. I used post oak age structures to propose quantitative methods of distinguishing old-growth forests from second-growth and cull forests in the region. I found that forest composition differed between the tree and sapling layers, and that aspect was an important determinant of tree density and post oak age structure. My findings, with regard to post oak recruitment and Ashe juniper (*Juniperus ashei*) invasion, may have implications for forest succession.

Chapter 4 is titled, "Canopy and Understory Dynamics in Old-Growth Forests of the Western Cross Timbers: Succession, Invasion, and Recruitment." In it, I address questions—several of which were raised by the results reported in Chapter 3—about the overstory and understory dynamics of old-growth forests in the western Cross Timbers. Chapter 4 focuses on two outstanding old-growth sites that occurred within the area of the old-growth model. For those two sites, I documented age structures for five tree species that occurred with post oak in old-growth overstories. I considered old-growth forest succession and invasion, in light of age structures and the results of point-quarter sampling. I also developed tree-ring chronologies for each site and compared them with post oak recruitment and climate data. Finally, I quantitatively characterized the understory of one old-growth site, which had both old-growth forest and savannah communities on steep slopes and ridgetops, respectively. I made qualitative comparisons with historical vegetation data from "relict" sites in the western Cross Timbers (Dyksterhuis 1948), and discussed invasion of the understory.

Chapter 5, "Conclusions," establishes research priorities for the western Cross Timbers, and synthesizes the results presented in Chapters 2-4. In this chapter, I also discuss limitations of my research approach, and highlight the major findings.

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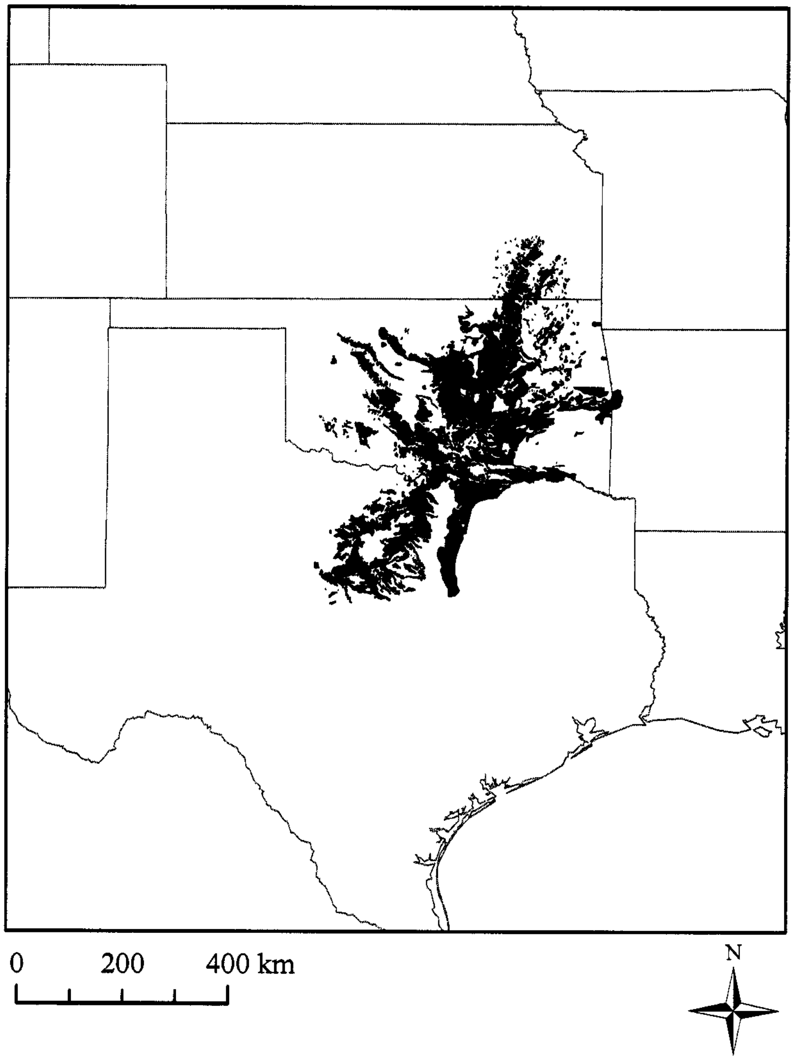

Figure 1.1. Historical extent of the Cross Timbers (approximately 8 million ha; Küchler 1964), which included savannahs, tallgrass prairies, and post oak-dominated forests at the time of European settlement.

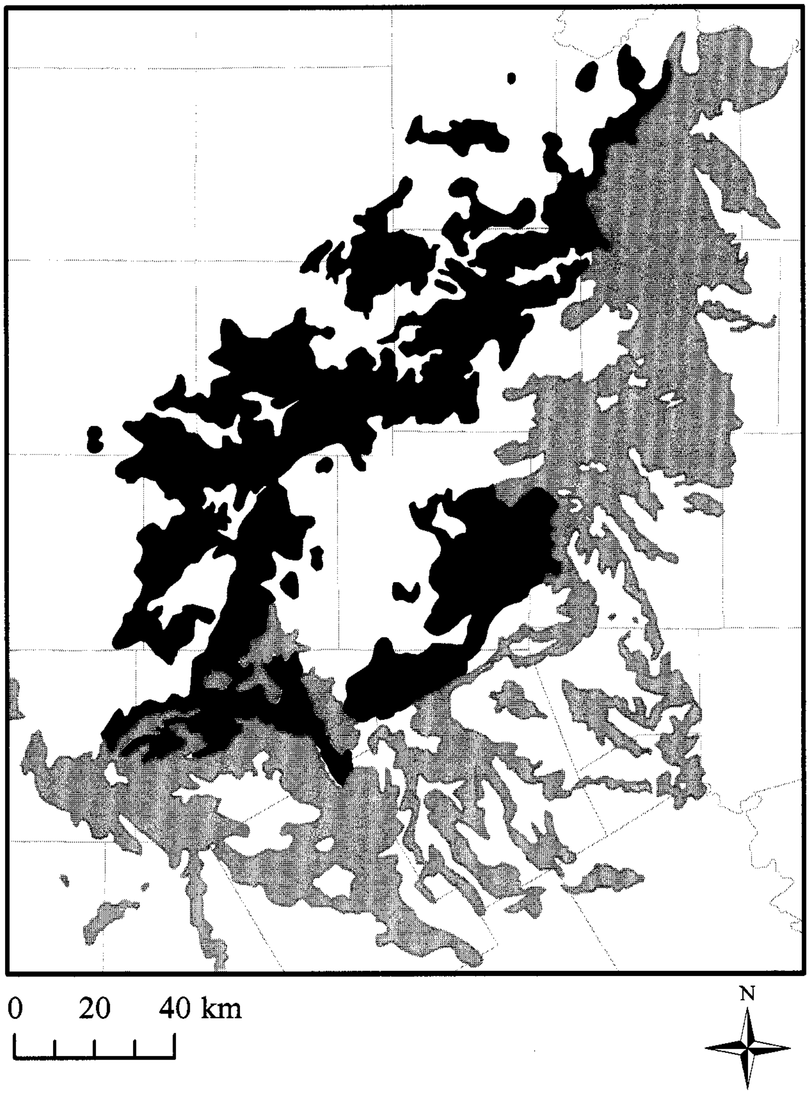

Figure 1.2. Main belt (gray; relatively level terrain) and fringe (black; high relief) regions of the western Cross Timbers of Texas, as mapped by Dyksterhuis (1948).

Chapter 2

Predictive Modeling of Old-Growth Forests in the Western Cross Timbers

ABSTRACT

We developed a predictive environmental model to locate old-growth forests in the western Cross Timbers of Texas. Because of infertile soils and rugged terrain, large-scale commercial logging did not occur in the western Cross Timbers, and old-growth forests—dominated by 150- to 250-year-old post oak (*Quercus stellata*) trees—remain in the region. We addressed the following questions: (1) Can predictive modeling based on land cover, soil, and topographic variables be used to produce an accurate map of old-growth forests in the western Cross Timbers? (2) How much old-growth remains in the western Cross Timbers, and how is it distributed across the region? (3) Can Landsat ETM+ imagery be used to distinguish old- and second-growth post oak forests? Our model was constrained to infertile, sandy or rocky soils on steep ($\geq$8%) slopes, where historical clearing had not occurred and where satellite imagery indicated presence of upland deciduous forest. We tested the model at 50 random sample points, and we used tree-ring dating to determine minimum ages for randomly selected post oak trees at old-growth sites. Our model predicted that 19,166 ha of old-growth forest remain in the western Cross Timbers. Of the 500,000 m^2 we surveyed (10,000 m^2 along each of 50 transects) within the area predicted to retain old-growth forest, 32.4% was old-growth, 7.9% was cut-over forest including defective old trees ("cull"), 53.6% was second-growth, and 6.1% was cleared land. Post oaks $\geq$100 years old made up 74.5% of the canopy at old-growth sites; 32.6% of post oaks were $\geq$150 years old; and 8.0% were $\geq$200 years old. Heart rot was common in old trees, so we used linear regression to estimate the ages of hollow post oaks. Our model successfully identified many large, undisturbed tracts of old-growth forest in the western Cross Timbers, but was not as accurate as a

similar model developed for the Cross Timbers of eastern Oklahoma. Landsat ETM+ imagery was not sufficient to distinguish old- and second-growth post oak forests in the western Cross Timbers. Future modeling efforts in the Cross Timbers could incorporate a more restrictive slope constraint. The modeling protocol we employed could be used to map noncommercial old-growth forests in other regions.

INTRODUCTION

About half the land area in the continental United States was forested at the time of European settlement (Yahner 1995). Commercially valuable timber accounted for 90% of the 445 million ha of virgin forest (Clawson 1979), and large-scale logging of those commercial forests has dramatically changed the U.S. landscape. Noncommercial forests, which made up 44 million ha of the original forest cover, were not suitable for commercial logging because they were inaccessible, occupied steep slopes in rugged terrain, or occurred on poor soils that resulted in slow tree growth (Stahle & Chaney 1994; Therrell & Stahle 1998). Many noncommercial forests survive in relatively unaltered condition, as evidenced by the development of tree-ring chronologies, dating back centuries, from hundreds of sites throughout the contiguous United States (Stahle & Chaney 1994).

An accurate map of surviving, noncommercial old-growth forests would be valuable for designing conservation strategies, and one approach to the development of such a map is predictive modeling of environmental variables that limit forests' commercial value. To assess the effectiveness of this approach, the Tree-Ring Laboratory at the University of Arkansas has developed models to locate noncommercial old-growth forests in the Cross Timbers, which span the ecotone between eastern deciduous forests and grasslands of the southern Great Plains. The Cross Timbers are dominated by relatively small, slow-growing post oak (*Quercus stellata*), but patches of savanna and tallgrass prairie intermingle with forests in a complex mosaic that once spanned nearly 8 million ha of southeastern Kansas, eastern Oklahoma, and northcentral Texas (Küchler 1964; Figure 2.1a). Cross Timbers forests occur on well-drained, sandstone-derived soils, whereas clay soils derived from limestone and shale support prairie vegetation (Diggs et al. 1999; Hoagland et al. 1999).

Therrell (1996) and Therrell and Stahle (1998) incorporated digital soil and elevation data into an environmental model to predict the locations of old-growth Cross Timbers forests in southern Osage County, Oklahoma. Included within the model were 11,308 ha of steep (15-45%) slopes with infertile soils. Field-testing showed that undisturbed old-growth forests occupied 74% of the modeled area. Old-growth canopies were dominated by post oak trees that were hundreds of years old, but ≤15 m tall and ≤60 cm in diameter (Therrell & Stahle 1998).

Bayard (2003) used Landsat TM imagery, a digital elevation model (DEM), and Küchler's (1964) potential natural vegetation map to predict the locations of old-growth Cross Timbers forests in eastern Oklahoma. The model, which was 77% accurate in the field, estimated that more than 1,000 km^2 of old-growth forest remained in eastern Oklahoma.

Although most ecological research on the Cross Timbers has focused on Oklahoma (Risser & Rice 1971; Johnson & Risser 1972; Roe 1998; Clark 2003), Therrell and Stahle (1998) proposed that the Texas Cross Timbers might also retain old-growth forests. Dendrochronological field research by the Tree-Ring Laboratory had provided limited evidence of forest tracts in northcentral Texas dominated by presettlement post oak, and we sought to estimate the extent and distribution of old-growth forests in the western Cross Timbers of Texas (historical distribution mapped by Dyksterhuis [1948]; Figure 2.1b).

We hypothesized that old-growth forests in the western Cross Timbers would survive where commercial logging and clearing for pasture had not been economically viable enterprises. Based on that hypothesis, we developed a comprehensive cartographic model that integrated (1) environmental data on soils and terrain, (2) historical data on forest cover, and (3) a land-cover classification derived from recent satellite imagery. Specifically, we predicted that old-growth forests would survive on steep ($\geq$8%) slopes covered by sandy or rocky, infertile soils, in areas where historical clearing was not known to have occurred and where satellite imagery indicated the landscape was still wooded.

METHODS

Predictive Model Development

Working within a geographic information system (ArcGis version 8.3), we used digital soils data to identify and isolate the sandy and rocky, infertile soils that support the post oak-dominated forests of the Cross Timbers. For 17 counties in our study area, we downloaded SSURGO (Soil Survey Geographic) data, the most detailed level of county-wide soil mapping (National Resources Conservation Service [NRCS]; http://www.nrcs.usda.gov). SSURGO data, which were digitized from the original county soil surveys, have a scale of 1:24,000. For two counties in our study area, SSURGO data were not yet available, so we downloaded the more generalized STATSGO (State Soil Geographic) data (scale 1:250,000) from the NRCS. To identify Cross Timbers soils, we used Dyksterhuis' (1948) soil-based delineation of the western Cross Timbers boundary, as well as the county soil surveys, which describe potential ("climax") vegetation for soil series and associations. For all counties in the study area, we generated a shapefile that included only series or associations that historically supported post oak woodland or forest. We exported the shapefile to raster format for integration into the model.

To identify relatively steep slopes in the study area, we used a seamless, 1:24,000 scale DEM from the U.S. Geological Survey (USGS; National Elevation Dataset [http://edcnts12.cr.usgs.gov/ned/default.asp]). Using the Spatial Analyst extension of ArcGIS, we extracted slopes from the DEM and reclassed the slope grid to produce a map of slopes $\geq$8%.

To obtain historical data on potential old-growth forests, we downloaded digital raster graphics (DRGs) from the Texas Natural Resources Information Service (www.tnris.org) for all quadrangles in our study area. DRGs are digitized versions of USGS 7.5-minute topographic maps (1:24,000 scale), and areas that were forested at the time of a map's production are shown in solid green (clearings are mapped in white). We used the DRGs to identify areas that had been cleared by the date of the map and, therefore, could not retain old-growth forests. For each quadrangle, we digitized historically cleared areas from the DRGs and created a shapefile of areas to exclude from the old-growth predictive model.

Satellite imagery was an important component of the old-growth predictive model because it allowed us to distinguish areas currently covered by deciduous forest from other land-cover types in the study area. We obtained recent (1999-2002) winter and summer Landsat ETM+ imagery (30-m resolution) of the study area, and we used PCI Geomatica to georeference, orthorectify, mosaic, and subset the images. Using a GPS unit (Trimble GeoExplorer II) in the field, we collected training data for the following categories: old-growth post oak, second-growth post oak, juniper (*Juniperus* spp.), mesquite (*Prosopis glandulosa*), crop, pasture/prairie, urban, and water. We used the CSIG algorithm in XPACE to create spectral signatures for each land-cover type and the CHNSEL algorithm to select the six best image bands for use in distinguishing land-cover types (three bands each from summer and winter). After calculating signature separabilities, we combined old-growth and second-growth training sites into a general "post oak forest" category (with the exception of 10 sites, which we withheld for use in post hoc testing of the classification).

We conducted a supervised classification of each scene in PCI, using the "maximum likelihood without null class" algorithm, which assigns pixels to a class if they are inside a predetermined threshold (defined as a number of standard deviations) of the class signature. Pixels outside the threshold for all classes are classified based on the minimum distance to a class mean. After classifying the imagery, we applied a 3 X 3 mode filter to reduce "noise" (isolated pixels) in the output, and then exported the classification to a shapefile. In ArcMap, we exported post oak forest cover to a separate shapefile.

We used the raster calculator in the Spatial Analyst extension of ArcGIS to multiply the slope and soils grids, producing a Boolean map in which only areas with

Cross Timbers soils *and* slopes $\geq 8\%$ had a value of 1 (other areas had a value of 0). That grid was multiplied by the post oak forest grid to further constrain the map to areas covered by old-growth forest. We exported this preliminary model (which met the soil, slope, and land-cover criteria) to a shapefile. In ArcMap, we performed a union between the combined soil/slope/land-cover shapefile and the cleared-land shapefile (derived from DRGs). We used a definition query to eliminate historically cleared lands from the model, and then used another definition query to select only parcels ≥ 16.2 ha (40 acres) for the final old-growth predictive model.

Field-Testing the Model

With an ArcView simple random sample script, we generated 50 random points within the area predicted by our model to retain old-growth forest. Between 3 April and 12 June 2003, we visited all 50 sites to test the model's accuracy (points were located in the field using USGS 7.5-minute topographic maps and DRGs enlarged to a scale of 1:6,000). At each site, we established a 200 x 50 m transect (10,000 m^2) along a randomly determined azimuth and surveyed the transect to assess proportions occupied by four land-cover types: 1) old-growth forest, 2) cull forest, 3) second-growth forest, and 4) cleared land. Old-growth forests were dominated by 150- to 300-year-old post oak in the canopy, and all other post oak age classes were also represented. (In the Cross Timbers, old post oak can be identified by a number of field characters: longitudinally twisted trunks, canopies consisting of only a few, heavy limbs, and broken tops.) Standing dead trees and fallen logs were present in old-growth stands, and signs of human disturbance were absent (Stahle & Chaney 1994). Cull forests—the products of selective logging or heavy fire damage—were young stands dotted with old, commercially undesirable trees. Second-growth forests had few trees older than 100 years, and stumps, roads, and fences provided evidence of human disturbance. Cleared lands were woodlands that had been converted to pasture.

At 10 points along each old-growth transect (points spaced 20 m apart), we located the closest post oak ≥10 cm in diameter at breast height (DBH) in each of four quadrants and used a Swedish increment borer to obtain a 5-mm, nondestructive core sample. At least 40 post oak trees were cored at each site identified as old-growth with this random sampling design. With the Douglass (1941) method of crossdating, we assigned exact dates to all annual rings on each core and determined minimum tree ages. When core samples were obtained in the field, increment borers sometimes missed the pith (which was not always in the center of the tree); for those post oaks, we documented the date of the earliest ring that was present, but the trees were even older. Similarly, coring a relatively large post oak with heart rot (a common condition) produced only a short core sample and a conservative age for the tree (Stahle & Chaney 1994). For cores that reached (or approached) pith, we regressed tree age against diameter, and used the linear regression model to estimate the ages of hollow trees (Clark 2003). Because the cores were obtained from randomly selected post oak, we used the dating results to construct post oak age structures for old-growth forests in the western Cross Timbers.

We used bootstrapping (Davison & Hinkley 1997; Manly 1997) to construct 95% confidence intervals around the mean percent transect area identified as relatively undisturbed old-growth, cull forest, second-growth, and cleared land in the western Cross Timbers. For a given cover type, we took a random sample of size 50 (with replacement) from the data, and then calculated the mean percent cover. After 1,000 iterations, we used the 2.5 and 97.5 percentiles from these means as the lower and upper bounds of the 95% confidence interval. We used Mann-Whitney U-tests to determine whether significant differences existed between model "successes" and "failures" in mean slope, elevation, or distance from an urban area.

RESULTS

Image Classification

Classification of the Landsat images revealed that, for this portion of the Cross Timbers, old-growth and second-growth post oak forests were spectrally indistinguishable. Signature separability measures the degree to which two land-cover categories can be statistically discriminated with spectral information; separability (calculated as Bhattacharya Distance) ranges from 0-2, and values below 1.9 are considered poor (Richards 1986). Separability for old-growth and second-growth post oak was only 1.3, and did not increase when signatures were created with different individual bands, band ratios, or indices such as the Tasseled Cap components. The effects of poor separability were evident when we attempted to distinguish old- and second-growth with a maximum likelihood classification (withholding six old-growth and six second-growth training sites for model testing): although all six old-growth sites were correctly classified, only two second-growth sites were correctly classified (the other four were misclassified as old-growth).

When we merged old-growth and second-growth into a general "post oak forest" category and performed a maximum likelihood classification, all 10 of the known post oak sites that we withheld from the training data were correctly classified. Average separability among all pairs of classes was 1.99, and the minimum separability (1.92) was between mesquite and post oak forest. The Kappa coefficient, which ranges from 0-1, is used to determine whether a classification is significantly better than randomly assigning pixels to classes (Congalton 1996). For our classification, Kappa was high (0.98, SD=0.00116). At least 99% of training pixels were correctly classified for water, pasture/prairie, juniper, urban, and crop (Table 2.1). For post oak forest, 98.27% of training pixels were correctly classified. Average accuracy (the average of all class accuracies) was 98.95%, and overall accuracy (a weighted average) was 99.21%.

Model Accuracy

Our final old-growth predictive model included 19,166 ha (74 mi^2) in the western Cross Timbers (Figure 2.2). The two largest contiguous tracts in the predictive model were approximately 800 ha, and 16 other tracts were larger than 150 ha. Old-growth forests were predicted to occur in 11 counties, but two of those (Jack and Palo Pinto counties) contained 68% of the total model area.

When we tested the model in the field, we found undisturbed old-growth forests along 20 of the 50 random sample transects within the area predicted to retain old-growth (Table 2.2; Figures 2.3 & 2.4). At 14 sample sites, old-growth covered the entire 10,000 m^2 transect; at other sites with at least some old-growth, the proportion ranged from 15%-99%. Overall, old-growth forests made up 161,875 m^2 (32.4%) of the 500,000 m^2 (10,000 m^2 at each of 50 sites) we surveyed. The 95% confidence interval for the mean percent old-growth ranged from 29.6% to 40.7%. Cull forests occurred on portions of 12 transects (7.9%; 95% CI [2.9, 14.3]), and two transects were entirely cull. Second-growth forests occurred along 32 sample transects (19 transects were entirely second-growth), and accounted for 53.6% (95% CI [40.7, 65.3]) of the total transect length surveyed. Cleared land accounted for 6.1% (95% CI [2.0, 11.8]) of the total transect length surveyed, occurring along parts of 9 transects and the full length of one transect.

Crossdating of the 714 cores we obtained from randomly selected post oaks at old-growth sites indicated that 74.5% of canopy post oak trees were $\geq$100 years old (adjusted ages; Figure 2.5). Trees older than 150 years made up 32.6%, and 8.0% were older than 200 years. The oldest post oak cored at an old-growth site was at least 278 years old. Other tree species we observed at old-growth sites were blackjack oak (*Quercus marilandica*), cedar elm (*Ulmus crassifolia*), Texas ash (*Fraxinus texensis*), Ashe juniper (*Juniperus ashei*), mesquite, chittamwood (*Sideroxylon lanuginosum*), sugar hackberry (*Celtis laevigata*), Mexican plum (*Prunus mexicana*), and Texas red oak (*Quercus buckleyi*).

Comparing model "successes" (old-growth sample points) and "failures" (second-growth, cull, or cleared) with Mann-Whitney U-tests, we found that mean slope was significantly steeper (p=0.02) at old-growth sites (mean=24.3%, SD=9.5) than at sites incorrectly predicted to retain old-growth (mean=18.2%, SD=6.9). There was no significant difference in mean elevation or distance from an urban area between the two types of sites.

DISCUSSION

At the 50 random sample sites, our old-growth model was 32.4% accurate. Applying this accuracy to the total predictive model area of 19,166 ha suggests that approximately 6,210 ha (24 mi^2) of old-growth forest survive in the western Cross Timbers. Although this area of old-growth represents only 1.2% of the 1.5 million ha (6,000 mi^2) originally mapped by Dyksterhuis (1948), old-growth forests still dominate the landscape in portions of the western Cross Timbers (e.g., parts of Palo Pinto and Jack counties). From some vantage points on steep slopes, we could see only unbroken old-growth forest, blanketing the rough terrain in every direction (Figure 2.6).

The relatively undisturbed old-growth forests that survive in the western Cross Timbers are authentic representatives of the presettlement landscape. If they are preserved, these remnants can provide (1) habitat for native species; (2) data on historical climate change, through analysis of tree rings (Stahle & Cleaveland 1995); (3) benchmarks against which to assess landscape changes in Texas; (4) core areas for ecological restoration; and (5) tools for educators and researchers to use in exploring the history, ecology, and biodiversity of the region.

Our model proved less accurate in the field than did recent old-growth modeling efforts in the Oklahoma Cross Timbers (Therrell 1996; Therrell & Stahle 1998; Bayard 2003), which relied on fewer data sources. This discrepancy was not particularly surprising, given the earlier settlement of Texas and the longer time frame over which human modification of the landscape has occurred. In addition, the proximity of the Texas Cross Timbers to the Dallas-Fort Worth metropolitan area has led to development pressure on Cross Timbers forests. Furthermore, the widespread occurrence of second-growth forests poses a greater challenge to modeling efforts in Texas, where relatively steep slopes seem to have been less of a deterrent to wood cutting (we found second-growth forests on slopes as steep as 26%).

On average, old-growth forests occupied steeper slopes (up to 41.9%) than did sites that were historically logged or cleared for pasture; thus, future modeling efforts might use a more restrictive slope constraint than the 8% we employed. Although such a restrictive model might achieve a higher accuracy in the field, it would do so at the cost of excluding some outstanding old-growth areas (one of our old-growth sites had a slope of only 9.4%). The ideal model would map *all* the old-growth that remains in the western Cross Timbers, and *only* the old-growth; in reality, a trade-off exists, and our model is an attempt to reconcile these two goals to identify large areas of old-growth throughout the varied terrain of the region. We incorporated a 16.2-ha (40-acre) minimum parcel size to limit the final old-growth map to areas most suitable for conservation and restoration. Smaller tracts of old-growth undoubtedly remain, but they are more likely to have experienced indirect human alteration through edge effects (Van Dyke 2003).

Identification and exclusion of currently wooded, but historically cleared areas enabled us to eliminate approximately 7,770 ha (30 mi^2) of second-growth forest from the potential model area. Despite our incorporation of historical land-cover data into the predictive model, second-growth forest still covered 53.6% of the total transect length we surveyed in the field. With multispectral Landsat ETM+ imagery, we identified and excluded areas suitable for old-growth that are currently in pasture or cultivation, but we could not distinguish second-growth forests with individual image bands or band combinations.

In coniferous forests of the U.S. Pacific Northwest, multispectral imagery has been used to distinguish old- and second-growth forests (Cohen & Spies 1992; Fiorella & Ripple 1993; Jakubauskas 1996; Lefsky et al. 2001). Canopy height differences seem to be a key factor in determining stand age with multispectral imagery in coniferous forests, but old- and second-growth forests in the western Cross Timbers are similar in stature. And even in coniferous forests, researchers are challenged by the small observable scale of old-growth characteristics (such as fallen logs, standing snags, and small, but old trees) and, especially, by the fact that forest age classes distinguishable on the ground often overlap widely (or entirely) in terms of their reflectance values (Nel et al. 1994; Sabol et al. 2002). Working in the Rocky Mountains, Nel et al. (1994) achieved an accuracy of 73% in classifying old-growth with Landsat TM imagery, but second-growth was misclassified as old-growth 66% of the time. For these reasons, although multispectral imagery played an important role in our model, imagery was insufficient as a model in itself.

In our model, we integrated winter and summer imagery to discriminate vegetation types in leaf-on conditions and identify areas dominated by evergreen *Juniperus* species. Future modeling efforts in the western Cross Timbers might benefit from repeated field observations to determine if there are times of year when visible differences between old- and second-growth forests occur (such as when leaves emerge in spring or when chlorophyll begins to break down in fall). Incorporation of imagery from those times of year might allow for more thorough exclusion of second-growth from the model area and consequently provide the basis for more accurate mapping of old-growth post oak forests.

Smeins and Diamond (1986) estimate that <1% of the western Cross Timbers is contained in managed areas, and many privately owned old-growth forest tracts in the western Cross Timbers are threatened by clearing for expanded cattle range and by suburban encroachment (Fitzgerald et al. 2000). Our field-tested predictive model will serve an important role in identifying potential areas for conservation and restoration of old-growth forests in the western Cross Timbers. In addition, the modeling protocol we employed may be useful in mapping noncommercial old-growth forests throughout the United States and around the world.

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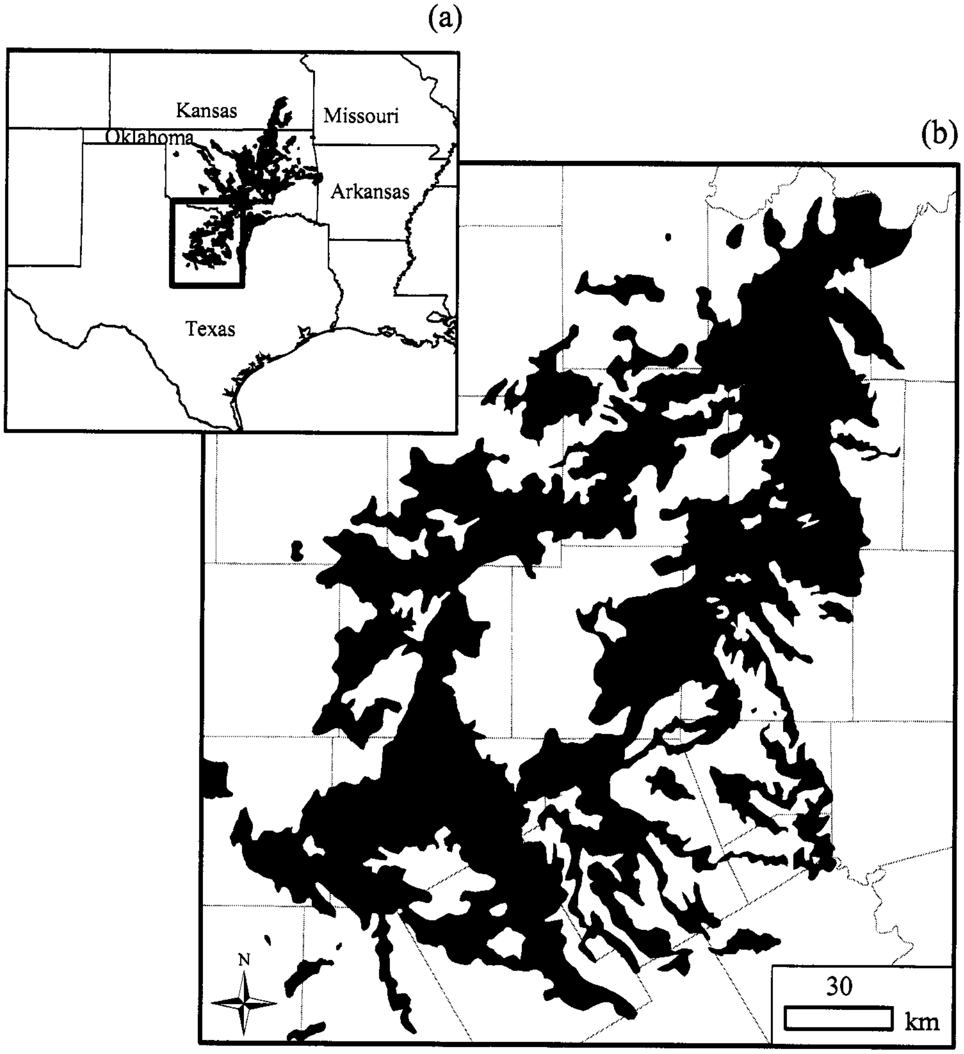

Figure 2.1. Historical extent of (a) the Cross Timbers, as mapped by Küchler (1964; 8 million ha); and (b) the western Cross Timbers of Texas, as mapped by Dyksterhuis (1948; 1.5 million ha).

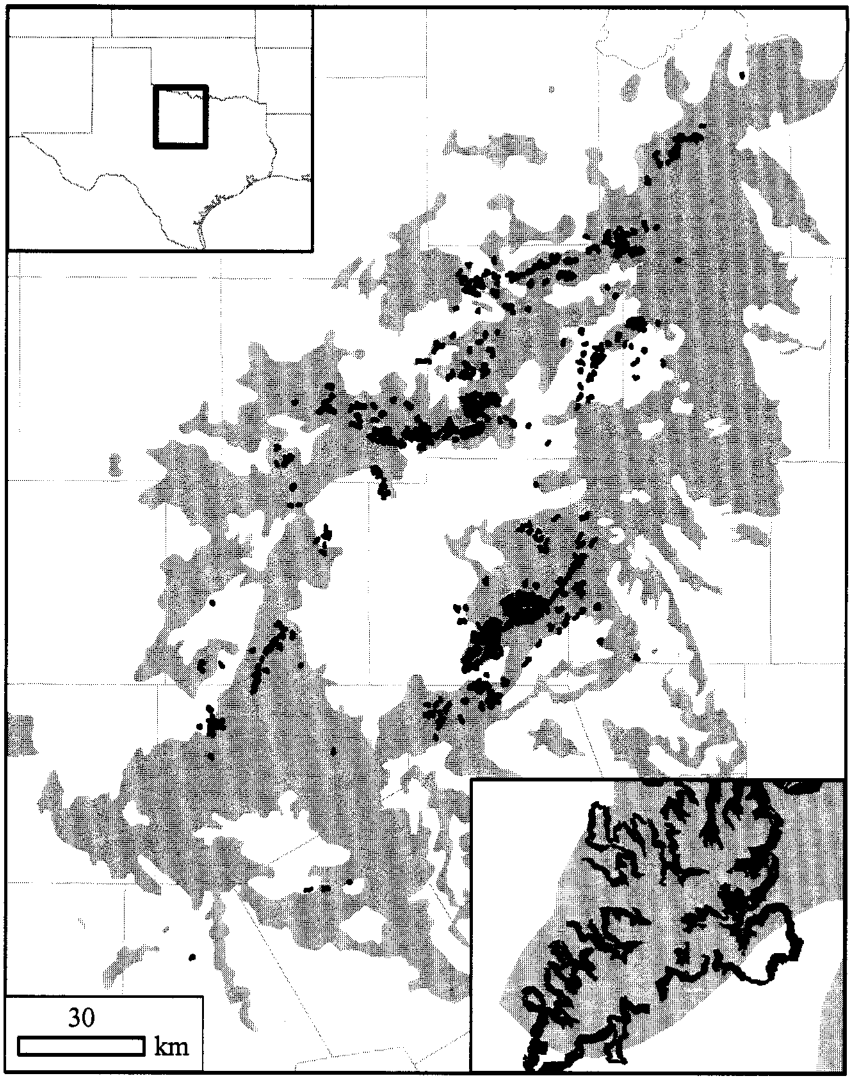

Figure 2.2. Old-growth predictive model (in black) identifies 19,166 ha (74 square miles) of potential old-growth forest in the western Cross Timbers of Texas. Approximate historical extent of the western Cross Timbers (Dyksterhuis 1948) is in gray. The model includes steep (≥8%) slopes with infertile, rocky or sandy soils, where clearing has not occurred, and where recent satellite imagery indicates coverage by deciduous forest. Lower right inset shows a portion of the model in detail at 1:250,000 scale.

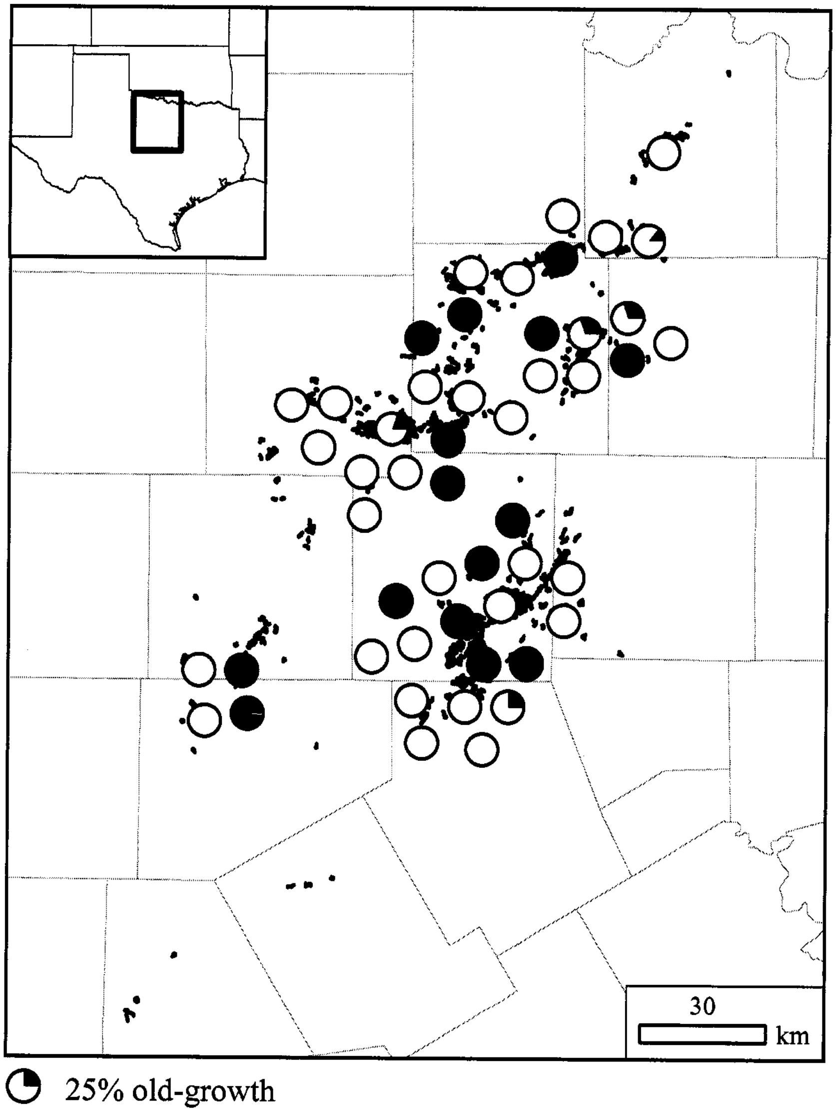

Figure 2.3. Random sample sites (50) surveyed to test the old-growth predictive model. At each site, percent coverage by old-growth forest, cull forest, second-growth forest, and cleared land was assessed along a 200 x 50 m, randomly oriented transect. Pie charts display the percentage of old-growth along each transect. The old-growth predictive model is in black.

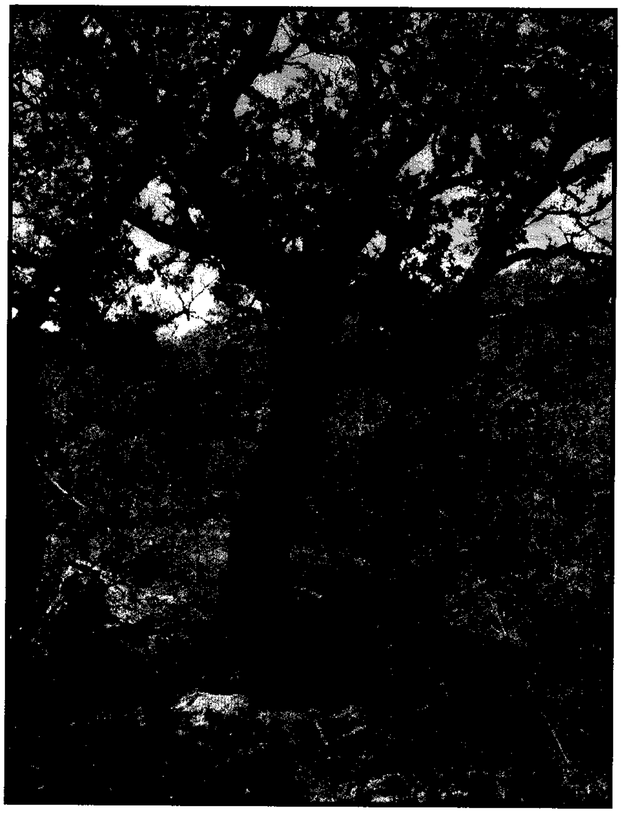

Figure 2.4. Post oak trees from 150-250 years old dominate steep, rocky slopes in the western Cross Timbers. This old post oak was found during field testing of the predictive model at a sample transect in southern Stephens County, Texas.

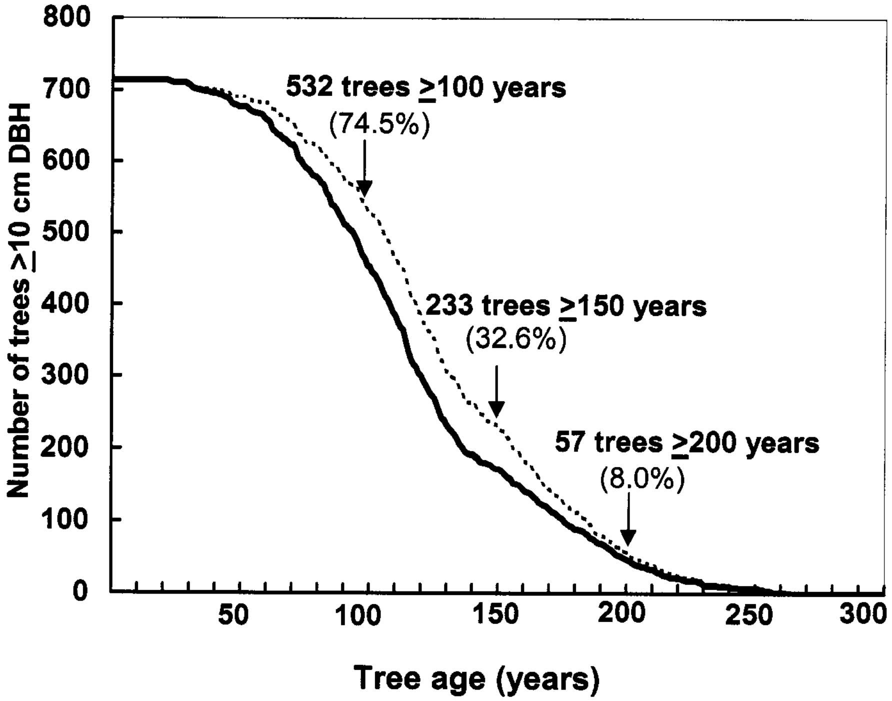

Figure 2.5. Minimum ages, as determined by tree-ring dating of increment cores, of 714 randomly selected post oak ≥10 cm DBH from 20 old-growth forest sites in the western Cross Timbers. Solid line represents tree ages without adjustment for hollow trees or missing rings; dashed line represents adjusted ages.

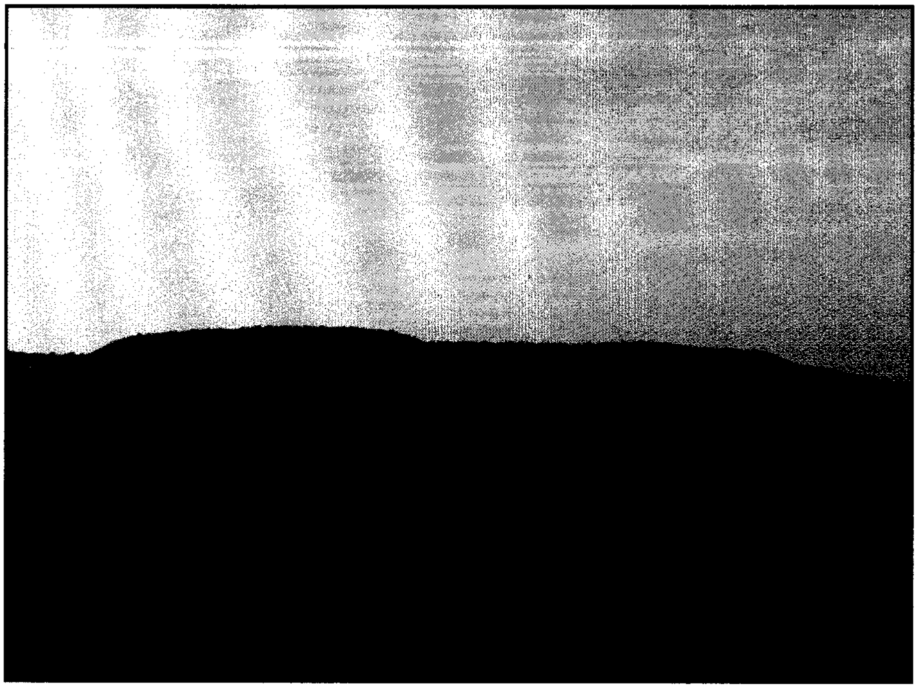

Figure 2.6. Unbroken expanse of old-growth forest in the western Cross Timbers, as seen from a random sample transect in Palo Pinto County, Texas. Approximately one-third of the area predicted to retain old-growth forest is in this county.

Table 2.1. Confusion matrix for the image classification, indicating the percent of training pixels classified in each category.

Land-Cover Category	Code	Pixels	1	2	3	4	5	6	7	8
Water	1	19839	99.10	0.00	0.00	0.00	0.00	0.90	0.00	0.00
Pasture/prairie-bright	2	1391	0.00	99.28	0.00	0.29	0.00	0.07	0.36	0.00
Post oak forest	3	1101	0.00	0.00	98.27	0.09	1.45	0.18	0.00	0.00
Juniper	4	1147	0.00	0.17	0.17	99.39	0.00	0.26	0.00	0.00
Mesquite	5	68	0.00	0.00	4.41	0.00	95.59	0.00	0.00	0.00
Urban	6	1533	0.00	0.00	0.00	0.00	0.00	100.00	0.00	0.00
Crop	7	1513	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00
Pasture/prairie-dark	8	1016	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00

Table 2.2. Area (m^2) and percent of four land-cover types along 50, 200 x 50 m (10,000 m^2) sample transects in the western Cross Timbers of Texas. Within the area predicted to retain old-growth forest, transects were randomly located, and all transects were visited between 3 April and 12 June 2003.

Transect	UTM coordinates (zone 14)		Old-growth[a] forest		Cull[b] forest		Second-growth[c] forest		Cleared[d] land	
number	North	East	m^2	%	m^2	%	m^2	%	m^2	%
01	3611508	568740	10,000	100.0						
02	3599739	513456	10,000	100.0						
03	3597967	512463	9,875	98.8					125	1.3
04	3618967	578413	10,000	100.0						
04	3587741	504642					10,000	100.0		
06	3680021	556027	10,000	100.0						
07	3657442	562491	10,000	100.0						
08	3606262	571326	10,000	100.0						
09	3704085	601130	1,500	15.0	3,750	37.5	2,250	22.5	2,500	25.0
10	3704953	599905					8,500	85.0	1,500	15.0
11	3606353	565165	2,500	25.0			7,500	75.0		
12	3611178	571050	10,000	100.0						
13	3596386	566885					10,000	100.0		
14	3593586	570999					10,000	100.0		
15	3601653	565349					10,000	100.0		
16	3606294	568189					10,000	100.0		
17	3681455	599324	3,000	30.0			7,000	70.0		
18	3699711	589148	10,000	100.0						
19	3658926	558965			10,000	100.0				
20	3696115	567591			10,000	100.0				
21	3694688	582425					10,000	100.0		

Transect	UTM coordinates (zone 14)		Old-growth[a] forest		Cull[b] forest		Second-growth[c] forest		Cleared[d] land	
number	North	East	m^2	%	m^2	%	m^2	%	m^2	%
22	3618460	575346					10,000	100.0		
23	3665403	567159					10,000	100.0		
24	3613749	569274					10,000	100.0		
25	3678152	595852	10,000	100.0						
26	3636033	578189	10,000	100.0						
27	3675462	594768					10,000	100.0		
28	3603193	562665					10,000	100.0		
29	3659304	558108							10,000	100.0
30	3592691	554090					10,000	100.0		
31	3629964	581103					10,000	100.0		
32	3622246	590849					10,000	100.0		
33	3599908	512400			2,000	20.0	8,000	80.0		
34	3622029	590451					10,000	100.0		
35	3684914	604388	10,000	100.0						
36	3657730	548964	2,000	20.0	1,000	10.0	6,250	62.5	750	7.5
37	3725351	613593					10,000	100.0		
38	3679088	602488			2,250	22.5	2,250	22.5	5,500	55.0
39	3702148	601041					10,000	100.0		
40	3658343	541096			2,750	27.5	4,750	47.5	2,500	25.0
41	3648879	541830					10,000	100.0		
42	3664051	535370			3,250	32.5	5,500	55.0	1,250	12.5
43	3663474	527712			1,000	10.0	9,000	90.0		
44	3645543	542519			2,625	26.2	3,250	32.5	4,125	41.3
45	3693987	565689	10,000	100.0						
46	3665337	570066			500	5.0	7,250	72.5	2,250	22.5

Transect	UTM coordinates (zone 14)		Old-growth[a] forest		Cull[b] forest		Second-growth[c] forest		Cleared[d] land	
number	North	East	m^2	%	m^2	%	m^2	%	m^2	%
47	3656924	560305	10,000	100.0						
48	3671260	592516			500	5.0	9,500	95.0		
49	3611818	569856	10,000	100.0						
50	3684878	605333	3,000	30.0			7,000	70.0		
Total			161,875	32.4	39,625	7.9	268,000	53.6	30,500	6.1
95% CI				(29.6, 40.7)		(2.9, 14.3)		(40.7, 65.3)		(2.0, 11.8)

[a] Old-growth forest showed evidence of human disturbance and was dominated by post oak (*Quercus stellata*) from 150-300 years old.

[b] Cull forest had been selectively logged, and scattered old trees were found within a younger forest.

[c] Second-growth forest contained few post oak ≥100 years old and had evidence of human disturbance.

[d] Cleared land had been converted to pasture.

Chapter 3

Structure and Composition of Old-Growth Forests in the Western Cross Timbers of Texas

ABSTRACT

We characterized the structure and composition of 16 relatively undisturbed old-growth forest sites on dry, steep slopes with infertile soils in the western Cross Timbers of Texas. Between 3 April and 12 June 2003, we conducted point-quarter vegetation sampling at each site (along a randomly oriented, 200 x 50 m transect) for trees (≥10 cm diameter at breast height [DBH]) and saplings (<10 cm DBH). In stature, composition, and site conditions, old-growth forests in the western Cross Timbers differed dramatically from the classic image of North American old-growth forests. On average, old-growth sites were dominated in the tree layer by post oaks (*Quercus stellata*), many of which were old (150-300 years), but relatively small (<40 cm DBH). Post oak dominance varied widely among sites (0.46-0.99). Using standard tree-ring dating methods, we dated 648 randomly selected post oak trees ≥10 cm DBH; nearly 75% were ≥100 years old, 30.5% were ≥150 years old, and 7.2% were ≥200 years old. Forest composition was dependent upon canopy layer (i.e., tree vs. sapling) and aspect. Total tree density and post oak age structure differed significantly between north- and south-facing slopes. Overall, post oak regeneration appeared low, and was significantly lower at steeper sites and sites with higher tree species richness. Post oak age-structure data provided evidence of episodic recruitment, but also indicated a steady decline in recruitment after the late 1800s. Ashe juniper (*Juniperus ashei*)—a problematic invasive species elsewhere in Texas—may emerge as a management problem in old-growth forests in this region.

INTRODUCTION

Historically, attempts to identify, define, and assess the status and condition of old-growth forests in North America have been biased toward one particular type of old-growth—the mesic, cathedral-like forest in which very large, very old trees are dominant and the understory is lush (e.g., forests dominated by eastern hemlock [*Tsuga canadensis*] or Douglas-fir [*Pseudotsuga menziesii*]; Franklin & Spies 1991; Frelich & Graumlich 1994; Orwig et al. 2001). Research in montane, coniferous forests has informed this classic image of the old-growth ecosystem (Foster et al. 1996).

The bias toward mesic old-growth has been persistent in ecology and forestry. For example, Parker (1989) explicitly excluded dry, upland old-growth forests from estimates of remaining old-growth in the central hardwoods region (Arkansas, Illinois, Indiana, Iowa, Kentucky, Missouri, Ohio, and parts of Michigan, Minnesota, and Tennessee). In some cases, this bias has resulted in serious underestimates of the extent of old-growth forests. Parker (1989) estimated that 275 ha of mesic old-growth forest remain in northern Arkansas, but Stahle and Chaney (1994) developed an old-growth predictive model for northwestern Arkansas and estimated that at least 656 ha of old-growth remain in the kinds of "extreme" areas excluded from previous estimates—infertile soils on steep slopes. In Massachusetts, a heavily visited forest on Wachusett Mountain was not recognized as old-growth until 1995 because its stature and composition differed from the stereotype of eastern old-growth forests (Orwig et al. 2001).

Only recently has there been a recognition of the enormous variation among North American old-growth forests, many of which differ greatly from the classic image, in terms of site conditions, structure, and composition (Orwig et al. 2001). Based on this new awareness, researchers have begun to identify and describe previously overlooked, understudied types of old-growth forests. Published characterizations now exist for most areas of North America in which old-growth forests remain (e.g., Pacific Northwest [Franklin & Spies 1991], southern Michigan [Hammitt & Barnes 1989], northern lake states [Barnes 1989], northern Sierra Nevadas [Ansley & Battles 1998], southwestern Pennsylvania [Smith 1989; Downs & Abrams 1991], Florida [Greenberg & Simons 1999], western Maryland [McCarthy & Bailey 1996], Ohio [McCarthy et al. 2001], southeastern Alaska [Alaback & Juday 1989], Canadian Rocky Mountains [Achuff 1989], Illinois [Fralish et al. 1991], and central hardwoods [Parker 1989]). Even in some of these areas, however, quantitative characterizations do not exist for old-growth forests that occur outside protected areas or on xeric uplands (Achuff 1989).

Descriptions of surviving old-growth forests are essential for identifying priority areas for conservation and core areas for restoration, as well as for establishing appropriate management regimes and generating hypotheses about ecological processes in old-growth forests (Greenberg & Simons 1999; Johnson 1992; McCarthy et al. 2001). Characterizations of surviving old-growth forests also provide benchmarks that identify natural vegetation and disturbance regimes (McCarthy et al. 2001), and serve as points of reference to gauge land-use changes, other anthropogenic disturbances, and effects of management practices (Barnes 1989; Swetnam et al. 1999; McCarthy et al. 2001).

We identified 16 old-growth forest sites on dry, infertile, steep slopes in the western Cross Timbers of north-central Texas (Chapter 2). We examined their structure and composition to identify common characteristics of old-growth forests in this region, and to evaluate possible explanations for differences among old-growth forests.

Specifically, we hypothesized that some variation in forest structure and composition would be related to slope and aspect, although the influence of these topographic parameters has rarely been considered for old-growth forests (McCarthy et al. 2001). We used tree-ring data to assess old-growth forest history, and we considered the future of old-growth forests in the region by addressing hypotheses about succession, invasion, and regeneration. We hypothesized that the relatively undisturbed old-growth sites we studied were protected from invasion by mesquite (*Prosopis glandulosa*) and Ashe juniper (*Juniperus ashei*), and that post oak was not being successionally replaced in old-growth forests.

Because of considerable geographic variation in forest composition, human disturbance history, and ages of trees considered "old," attempts to develop specific, widely applicable criteria for old-growth status have largely given way to regional criteria, such as for the central Appalachians or Pacific Northwest (Hunter 1989; Franklin & Spies 1991; Spies & Franklin 1996; McCarthy et al. 2001). For our study area, no such criteria existed, and we sought to provide data that could serve as the basis for development of old-growth indicators for the western Cross Timbers. Additionally, all of our study sites are on private land, and the ecosystem in which they occur is threatened by suburban encroachment and clearing of woody vegetation for expansion of cattle range (Francaviglia 2000; Fitzgerald et al. 2000). A primary objective of our research was to provide baseline data for use in conservation and management decisions, and to identify research questions relevant to conservation of old-growth forests in the western Cross Timbers.

STUDY AREA

The Cross Timbers once spanned nearly 8 million ha along the ecotone between eastern deciduous forests and Great Plains grasslands. Extending from southeastern Kansas through eastern Oklahoma, and into north-central Texas, the Cross Timbers comprise a mosaic of forests, prairies, and savannahs (Küchler 1964; Figure 3.1a). Throughout the Cross Timbers, boundaries between vegetation types are often sharply defined, and occur at transitions between sandstone-derived soils (which support forests) and clay soils derived from limestone (which support prairie vegetation) (Diggs et al. 1999; Hoagland et al. 1999). Forests in the Cross Timbers are dominated by relatively small (≤15 m tall, 30-60 cm diameter at breast height [DBH]), slow-growing post oaks (*Quercus stellata*), whose diminutive stature and gnarled form result from marginal climate conditions and infertile soils (Therrell & Stahle 1998).

The larger of two zones of Cross Timbers vegetation in Texas is the western Cross Timbers, which varies in width from 50 km at the north to 160 km farther south (McCluskey 1972; Figure 3.1a). Cretaceous, sandy Woodbine and Trinity strata intermixed with sections of clay and sandy clay underlie much of the western Cross Timbers, with the exception of rocky Pennsylvanian strata near the westernmost edge (Diggs et al. 1999). The climate of the western Cross Timbers is subtropical-subhumid, and annual rainfall increases along a west-east gradient from 625-875 mm. Most precipitation occurs in April and May, whereas July and August are often marked by drought (mean evaporation-precipitation deficit is 175-250 mm) (Dyksterhuis 1948; McCluskey 1972). Average annual temperature in the western Cross Timbers is 18°C, but temperatures can be extreme: highs in July and August sometimes exceed 43°C, and temperatures below -18°C have been recorded in January (Dyksterhuis 1948; Diggs et al. 1999). The last frost of spring generally occurs from March 20-25, and the first frost of fall usually occurs from November 5-15 (Dyksterhuis 1948). The average freeze-free period is 225-240 days (USDA 1981).

European settlement of the western Cross Timbers began in the 1850s, and most forests on level ground were quickly cleared for grazing or for cultivation of corn and cotton (Dyksterhuis 1948; Grubbs 1953). Steep, rocky slopes were not farmed, and large-scale commercial logging was not economically viable in the Cross Timbers (McCluskey 1972; Jordan 1973; Bernardo et al. 1992, Francaviglia 2000). Some post oaks were cut for fuel, fence posts, railroad ties, and rough lumber; however, the steep, remote terrain and stunted, gnarled form of the trees led to the survival of large tracts of old-growth forest in the western Cross Timbers (Dyksterhuis 1948; Stahle & Hehr 1984).

METHODS

Field and Laboratory Methods

We developed a predictive model to locate old-growth forests in the western Cross Timbers (Chapter 2), and we identified 16 old-growth sites (Figures 3.1b & 3.2) while field testing the model at randomly located points. Our model criteria included steep slopes (≥8%); sandy or rocky, infertile soils; lack of historical clearing (indicated by U.S. Geological Survey topographic maps); presence of deciduous forest (determined through analysis of recent satellite imagery); and 16-hectacre (40-acre) minimum parcel size. The 16 sites we identified as old-growth in the field met all these criteria; additionally, signs of direct human disturbance—such as stumps, roads, and fences—

were absent. Grazing had occurred at some sites; overall, however, the old-growth sites we identified were relatively undisturbed and probably representative of the vegetation present before European settlement (Barnes 1989; Hunter 1989; McCarthy & Bailey 1996).

The 16 sites were not uniformly distributed throughout the western Cross Timbers; instead, they were located in rugged terrain where the largest areas of old-growth forest remain (Chapter 2). Slopes ranged from 9.4%-41.9%, and mean slope of the 16 old-growth sites was 24.2% (Table 3.1). Twelve sites occurred on soils of the Shatruce series—bouldery or very bouldery, sandy loams. Boulders made of silica and iron oxide-cemented conglomerates or sandstone covered 3-20% of the surface of Shatruce soils, and stones covered 25-50% (NRCS 2004). The remaining four sites occurred on well-drained, stony or very stony soil complexes formed from sandstone or interbedded sandstone and clay (Darnell-Exray, Truce-Bonti, Bonti-Exray, and Bonti-Exray-Truce complexes) (NRCS 2004). Nine sites were on north-facing slopes, five were on south-facing slopes, and two sites were on slopes facing due west.

At each site, we established a randomly oriented, 200 x 50 m transect (10,000 m^2; 1 ha). At 10 nodes along a transect (nodes spaced 20 m apart), we conducted point-quarter vegetation sampling (Cottam & Curtis 1956; Downs & Abrams 1991). For sampling purposes, we defined trees as stems $\geq$10 cm DBH; saplings were stems reaching breast height, but <10 cm DBH (Johnson & Risser 1975; Roovers & Shifley 1997). For each of the four quadrants around a node, we collected the following data: (1) distance to the nearest tree (m); (2) DBH of the nearest tree (cm); (3) species of the nearest tree; (4) distance to the nearest sapling (m); and (5) species of the nearest sapling. In all, we recorded data for 40 trees and 40 saplings per transect. We also recorded the azimuth of each transect and the GPS position (UTM zone 14) of each transect starting point (Table 3.1). All sampling was conducted between 3 April and 12 June 2003.

In each quadrant at each node, we used a Swedish increment borer to extract a small (5-mm diameter) core at breast height from the nearest post oak $\geq$10 cm DBH (we also measured DBH of these post oaks). Following standard methodology, cores were dried, glued into wooden mounts, sanded to a high polish, and dated (by assigning calendar years to annual rings through cross-dating) (Stokes & Smiley 1968).

Data Analysis

Because we obtained cores from randomly selected post oaks, we used their ages to construct post oak age structures and size structures representative of each old-growth site, and we constructed an overall age-structure diagram for the 16 sites. We corrected for missed pith and heart rot by performing linear regression (age vs. DBH) using only cores that reached pith or were near pith, and then applied the regression equation to the remaining cores (Hett & Loucks 1976; Lorimer 1980; Clark 2003). We incorporated adjusted ages into the age structure for each old-growth site.

For each transect, following Cottam and Curtis (1956), we used our point-quarter sampling data to calculate (for all species combined) (1) tree absolute density (stems/ha), (2) sapling absolute density (stems/ha), (3) total basal area (m^2), and (4) total basal area/ha. For each species separately at each transect, we calculated (1) tree relative density, (2) sapling relative density, (3) tree absolute density (stems/ha), (4) sapling absolute density (stems/ha), (5) total basal area (m^2), (6) relative dominance (incorporates basal area and density), and (7) basal area/ha. For each old-growth site, we also recorded tree species richness and calculated the sapling:tree ratio for each species (using absolute numbers of trees and saplings per hectare). We determined the percent slope and aspect of each site from a seamless digital elevation model, using the Spatial Analyst extension of ArcMap (ArcGIS version 8.3) (Table 3.1).

We used a G-test of independence (with Williams' correction; Sokal & Rohlf 1995) to assess whether post oak age structure was dependent on aspect (i.e., to compare post oak age structures on north- and south-facing slopes) for age intervals ≤50 years, 51-100 years, 101-150 years, 151-200 years, and 201-250 years (we excluded the interval 251-300 years because its expected frequency was too low) (Cuevas 2000). We also used G-tests of independence to determine whether tree species composition and sapling species composition were dependent on aspect (i.e., were there differences in tree and sapling species composition between north- and south-facing slopes?). To detect other stand-level differences between north- and south-facing slopes, we used Mann-Whitney U-tests (Sokal & Rohlf 1995) to compare (for all species combined) (1) mean absolute density of trees, (2) mean absolute density of saplings, and (3) mean total basal area. We also compared mean post oak sapling:tree ratios by aspect.

We used G-tests of independence to address our hypotheses about (1) invasion by Ashe juniper and mesquite, and (2) successional persistence of post oak as the dominant tree species in old-growth forests of the western Cross Timbers. Specifically, we assessed whether species composition was dependent on canopy layer (i.e., whether there were differences in species frequencies between the tree and sapling layers) for all sites combined, and for each site separately, but only for species whose expected frequency was ≥5. We used U-tests to compare the mean relative density of each species in the tree and sapling layers. To examine factors that might be related to differences in post oak regeneration across sites, we used linear regression to assess relationships between the ratio of post oak saplings to trees and (1) percent slope, (2) tree species richness, and (3) stand age (age of the oldest tree cored; Tyrrell & Crow 1994).

RESULTS

Post Oak Age Structure and Size Structure

We dated cores from 648 randomly selected post oak trees ≥10 cm DBH at 16 sites (approximately 40 trees per site). The youngest post oak we cored was 21 years old, and the oldest was 261 (mean=130 years, SD=46). After adjustment for heart rot and missed pith (based on linear regression of age vs. DBH), we projected the age of the oldest tree to be 278 years. The relationship between age and DBH of post oak trees was degraded by the presence of many small, old trees and some large, young trees (r^2=0.38 for the regression of age against size; Figure 3.3).

For the 146 post oak trees whose ages we adjusted, the mean adjustment was 47 years. Of the post oaks we dated, 73.5% were ≥100 years old, 30.5% were ≥150 years old, and 7.2% were ≥200 years old (Table 3.2). On average (based on mean post oak density of 343 stems/ha), one hectare of old-growth forest in the western Cross Timbers would have 252 post oaks ≥100 years, 105 post oaks ≥150 years, and 25 post oaks ≥200 years (Figure 3.4). Four sites had trees ≥250 years old; 9 sites had trees ≥200 years old; and at all sites but one, at least 12.5% of post oak trees were ≥150 years old. Nearly half of all cored post oaks were 151-200 years old.

The year of greatest post oak recruitment to breast height was 1877, and "pulses" of recruitment have occurred (e.g., around 1817, 1848, and 1877-1890) (Figures 3.5 & 3.6). Post oak recruitment to breast height was lower (or absent) at these sites during severe droughts in the mid-19th century (1850s-1860s) and 1950s (Stahle & Cleaveland 1988). Overall, recruitment to breast height has declined since the late 1800s, although not uniformly across all sites. Recruitment to breast height after 1982 was not evident because we sampled only post oaks ≥10 cm DBH.

Most post oak trees at old-growth sites were <40 cm DBH (93.6%; Figure 3.7 [we did not measure DBH of saplings]). Only 5.6% of post oaks were 40-49 cm, and 0.8% were 50-69.9 cm DBH. Nearly half of all post oak trees were 20-29.9 cm DBH. Mean post oak DBH was highest at Site 10 (32.0 cm) and lowest at Site 7 (20.8 cm). Post oak had the highest mean DBH of any tree species we recorded at the 16 old-growth sites.

Old-Growth Forest Composition: Tree Layer

In all, we recorded 10 tree species at the 16 old-growth sites: post oak, blackjack oak (*Quercus marilandica*), cedar elm (*Ulmus crassifolia*), Texas ash (*Fraxinus texensis*), mesquite, Ashe juniper, sugar hackberry (*Celtis laevigata*), chittamwood (*Sideroxylon lanuginosum*), Mexican plum (*Prunus mexicana*), and Texas red oak (*Quercus buckleyi*) (Figure 3.8; Table 3.3). The 10 species never occurred together at a single site; mean tree species richness was 4, and ranged from 2 (Sites 4 and 7) to 7 (Site 13). For all species combined, Site 6 had the highest tree density, with 1000 stems/ha. Three other sites had total densities >600 trees/ha, and Site 9 had the lowest total tree density (319.3 trees/ha). Mean tree density was 534.1 trees/ha (SD=204.9).

On average, post oak was the dominant tree species. Post oak was the only species present at all 16 old-growth sites, and it accounted for more than 50% of total trees/ha at 13 sites. Mean absolute density of post oak was 342.7 trees/ha (SD=170.1); however, Sites 6 and 4 had 600-700 post oaks/ha, and Sites 13 and 9 had ≤100 post oaks/ha. Post oak relative density (number of post oaks/*n* randomly sampled trees of all species) ranged from 0.20 (3 of 40 trees sampled were post oak; Site 13) to 0.98 (39 of 40 trees sampled were post oak; Site 4). Mean post oak basal area was 19.2 m^2/ha (SD=9.4), and ranged from 5.47 m^2/ha to 33.4 m^2/ha. Post oak relative dominance ranged from 0.49-0.99.

Blackjack oak trees were present at 13 sites, and mean absolute density at those sites was 101.8 stems/ha (SD=122.2). Blackjack oak relative density ranged from 0.05-0.63. Mean blackjack oak basal area was 1.7 m^2/ha (SD=2.1). At Site 14, where blackjack oak was twice as abundant as post oak (461.6 stems/ha for blackjack vs. 230.8 stems/ha for post oak), blackjack oak basal area (8.5 m^2/ha) was less than that of post oak (9.9 m^2/ha). Blackjack oak relative dominance ranged from 0.01-0.1. Basal area and dominance values were disproportionately low (with respect to relative density) because blackjack oak is a comparatively small tree, even by the standards of the western Cross Timbers (mean DBH=14.6 cm, SD=4.2). Of the 95 randomly selected blackjack oaks we measured, 86.3% were <20 cm DBH, and all others were <30 cm DBH.

Cedar elm was present at nine sites, and mean absolute density at those sites was 81.3 trees/ha (SD=53.2, range 12.0-111.8). Mean cedar elm relative density was 0.2 (SD=0.1), although at Site 9, cedar elm accounted for 35% of trees sampled. Cedar elm basal area ranged from 0.5-3.3 m^2/ha (mean=2.0, SD=1.1), and relative dominance ranged from 0.02-0.3. Mean DBH of the 56 cedar elms we measured was 17.1 cm (SD=5.1).

Texas ash—a Texas and south Oklahoma endemic—was present at eight sites, and was most abundant at Site 13 (absolute density=106.6 trees/ha). Mean absolute density of Texas ash was 53.8 trees/ha (SD=30.5), and mean relative density was 0.1 (SD=0.09, range 0.05-0.3). Mean basal area of Texas ash was 1.1 m^2/ha (SD=0.6), and ranged from 0.4-1.8 m^2/ha. Relative dominance ranged from 0.01-0.2. We measured 41 Texas ash trees; mean DBH was 15.1 cm (SD=4.7).

Mesquite was present at seven sites, and usually accounted for only a small proportion of the tree layer. Mean absolute density was 37.1 trees/ha (SD=30.6), and ranged from 12.6-82.9 trees/ha. Relative density of mesquite ranged from 0.02-0.2, and basal area ranged from 0.03-0.1 m^2/ha. Mesquite relative dominance was low (0.03-0.1).

Ashe juniper trees were present at only three sites, and were relatively common at only one (Site 8). Absolute density ranged from 8.0-122.4 trees/ha, and relative density ranged from 0.03-0.15. Ashe juniper basal area ranged from 0.8-5.6 m^2/ha (mean DBH=26.3 cm), and relative dominance was low (0.07-0.1).

Chittamwood, sugar hackberry, and Mexican plum were each present at three sites, although never simultaneously. Their maximum absolute densities were 16.6, 25.2, and 23.1 stems/ha, respectively. For each species, basal area was <0.35 m^2/ha, and all three species had low dominance values (0.01-0.02). We recorded Texas red oak only at Site 13—the site with the highest species richness—and it was uncommon (7.1 stems/ha).

Old-Growth Forest Composition: Sapling Layer

For all species combined, mean absolute sapling density was 1433.2 stems/ha (SD=780.5). Site 7 had the highest recorded sapling density (>3000 stems/ha), and lowest sapling densities occurred at Sites 11, 12, and 10 (<500 saplings/ha at each site). On a species-by-species basis, there was wide variation across sites in absolute numbers of saplings, and no species was present in the sapling layer at all 16 old-growth sites (Figure 3.9). Post oak saplings were present at 14 sites, and mean post oak sapling density was 157.1 stems/ha (SD=138.0, range 6.8-419.0). Blackjack oak saplings were present at 13 sites, and were the most abundant saplings, on average (555.7 stems/ha, SD=471.1). Sites 3 and 7 had more than 1300 blackjack oak saplings/ha, but Sites 11 and 2 had <30 saplings/ha. Twelve sites had chittamwood saplings, and mean absolute density was 113.7 stems/ha (SD=111.3, range 21.2-303.4). Cedar elm saplings were present at 10 sites; mean absolute density was 107.2 saplings/ha (SD=106.2, range 9.1-280.8). Nine sites had sugar hackberry saplings (mean density=195.4 stems/ha, SD=201.8, range 9.1-654.9). Texas ash was present in the sapling layer at eight sites; mean density was 266.7 saplings/ha (SD=266.7, range 9.1-756.6). Ashe juniper and mesquite seedlings were each present at seven sites; mean sapling densities were 228.2 stems/ha (SD=258.6, range 32.2-775.0) and 80.0 (SD=58.4, range 21.5-191.2), respectively. Six sites had Mexican plum saplings (mean density=106.1 stems/ha, SD=106.2, range 21.5-294.3). Texas red oak saplings were present only at Site 13 (29.1 stems/ha).

Canopy Layer Differences

On a site-by-site basis, species present as trees were not always represented by saplings (e.g., cedar elm at Site 6, post oak at Sites 12 and 13). The opposite was also true—some sites had saplings of species not present as trees (e.g., chittamwood and sugar hackberry at Site 16, Ashe juniper at Site 11).

Although dominant in the tree layer (on average and at most sites), post oak was not the most common sapling species at any site. On average, 26% of saplings recorded were blackjack oak, 13% were Ashe juniper, and 10% were Texas ash. The remaining 51% of saplings we recorded were divided evenly among cedar elm, chittamwood, mesquite, Mexican plum, post oak, sugar hackberry, and fragrant sumac (*Rhus aromatica* [not a true "sapling" because it does not enter the tree layer]).

Species composition was dependent on canopy layer (i.e., species were present in significantly different proportions as trees and saplings) for all sites combined (G-test; $G_{adj}=496.0$, $p<0.005$), as well as for all individual sites except Site 14. Although the G-test does not allow conclusions about where significant differences are located (Cuevas 2000), we calculated expected frequencies and made informal species-by-species comparisons of observed and expected frequencies to assess the basis for the dependence of species composition on canopy layer (Anderson et al. 1994). For all sites combined, observed post oak sapling frequency was one-fifth of the expected value, whereas sapling frequencies were greater than expected for every other species (approximately two times greater for Ashe juniper, blackjack oak, chittamwood, and sugar hackberry).

We also informally examined differences between canopy layers for each site. At all sites for which we rejected the null hypothesis of independence of composition and canopy layer, observed post oak frequencies were higher than expected in the tree layer, and lower than expected in the sapling layer. Observed frequencies of blackjack oak saplings were twice as great as expected at six sites. Cedar elm sapling frequency was twice the expected value at two sites (10 and 11); however, at Sites 9 and 12, cedar elm *tree* frequencies were higher than expected. Ashe juniper saplings were twice as abundant as expected at three sites. Two sites (1 and 2) had at least twice as many Texas ash saplings as expected. Observed and expected mesquite sapling frequencies were equivalent at Sites 9 and 15 (the only sites with expected mesquite frequencies ≥ 5). The sugar hackberry expected frequency was high enough to test at only Site 15, and the observed sapling frequency was twice as great as expected.

For some species, there were differences in mean relative density (proportional abundance) between the tree and sapling layers (Figure 3.10). Post oak mean relative density in the tree layer was 0.65 (65% of randomly selected trees were post oak), but <0.10 in the sapling layer (<10% of all saplings we recorded were post oak) (U-test; U=255, $p<0.001$). In contrast, densities of chittamwood (U-test; U=214, $p<0.001$) and sugar hackberry (U-test; U=183, $p=0.02$) were significantly higher in the sapling layer. Overall, in the tree layer, the four most abundant species (as indicated by relative density) were (1) post oak, (2) blackjack oak, (3) cedar elm, and (4) Texas ash. In the sapling layer, the most abundant species were (1) blackjack oak, (2) Ashe juniper, (3) Texas ash, and (4) cedar elm.

Old-Growth Forest Composition and Topography

For all species combined, mean absolute tree density was significantly higher on south-facing slopes (n=5) than on north-facing slopes (n=12): on average, south-facing sites had 642.7 trees/ha, whereas north-facing sites had 473.8 trees/ha (U-test; U=37, p=0.03). Mean absolute sapling density at north-facing slopes (1561.4 saplings/ha) and south-facing slopes (1003.1 saplings/ha) did not differ significantly (U-test; U=30, p=0.18). Neither mean total basal area (north, 1.79 m^2/ha; south, 2.07 m^2/ha) nor mean species richness (north, 4.3; south, 4.0) differed significantly between north- and south-facing slopes.

Tree species composition and sapling species composition depended significantly on aspect (G-test; for trees, G_{adj}=40.9, p<0.005; for saplings, G_{adj}=64.2, p<0.005). North-facing slopes had more saplings of post oak, blackjack oak, and Texas ash than expected; however, on south-facing slopes, saplings of Ashe juniper, cedar elm, mesquite, and sugar hackberry were more abundant than expected. Observed and expected frequencies were roughly equivalent for saplings of both chittamwood and Mexican plum. In the tree layer, blackjack oak and Texas ash were more abundant than expected on north-facing slopes. South-facing slopes had more Ashe juniper, cedar elm, and mesquite trees than expected. Frequencies of post oak trees were not different than expected on north- and south-facing slopes. Expected tree frequencies were too low to test for chittamwood, sugar hackberry, and Mexican plum.

Post oak age structure was also dependent on aspect (G-test; G_{adj}=39.9, p<0.005). On north-facing slopes, there were more trees than expected in the age intervals 151-200 and 201-250 years. South-facing slopes had higher than expected frequencies of post oaks in the intervals ≤50, 51-100, and 101-150 years.

There was no significant relationship between percent slope and any of the forest composition variables we calculated (based on linear regression between slope and total trees/ha, total saplings/ha, species-by-species relative density, species-by-species absolute density, species richness; all $p>0.05$, $n=16$).

Post Oak Regeneration

We used the post oak sapling:tree ratio as a measure of post oak regeneration at old-growth sites (Table 3.4). For all 16 sites, the mean sapling:tree ratio was 0.28 (SD=0.24). At two sites (12 and 13), we recorded no post oak saplings, although post oak was present in the tree layer. Among sites with post oak saplings, Site 3 had the highest sapling:tree ratio (0.79), and Site 11 had the lowest ratio (0.03). Mean sapling:tree ratios for all other tree species were ≥1.0 (Ashe juniper, 16.1; Texas ash, 10.7; blackjack oak, 6.6; sugar hackberry, 5.2; Mexican plum, 3.6; chittamwood, 3.1; mesquite, 1.9; and cedar elm, 1.6).

Post oak regeneration was significantly lower at steeper old-growth sites (F=5.04; $p=0.04$). Site 3, which had the highest sapling:tree ratio, had the lowest slope (9.4%). Sites 8 and 13 were the steepest old-growth sites (slopes >40%) and had low sapling:tree ratios (<0.07). Post oak regeneration was also significantly lower at sites with higher tree species richness (F=12.4; $p=0.003$). Of six sites with sapling:tree ratios ≥0.45, five had three or fewer tree species. Mean post oak regeneration did not differ significantly between south-facing slopes (0.14) and north-facing slopes (0.36) (U-test; U=31.5, *p*=0.12). There was no relationship between post oak regeneration and stand age, measured as the age of the oldest tree cored (F=0.02, *p*=0.9).

DISCUSSION

Assessing Old-Growth Status in the Western Cross Timbers

Empirically derived criteria for assigning "old-growth" status to forests in the western Cross Timbers have not existed previously; however, for mesic forests in the central hardwoods region, Parker (1989) defined old-growth forests as having trees in all age classes, some canopy trees >150 years old, and little or no anthropogenic disturbance of the understory during the last century. All 16 old-growth forests we studied had post oaks in all age classes, many of which were ≥150 years old (9.4% of randomly sampled post oaks, on average), and evidence of direct anthropogenic disturbance was absent.

Pasture is the dominant land cover on level terrain in the western Cross Timbers. On slopes ≥8%, second-growth forests are more common than old-growth forests, and cull forests (cut-over forests having scattered, old trees considered undesirable when logging occurred) also exist in the region, although they are much less common than old- or second-growth (Chapter 2). Our regionally extensive sample of post oak ages is useful for distinguishing these three forest types in the western Cross Timbers. At each of the 16 old-growth sites we studied, <20% of post oak trees (≥10 cm DBH) were younger than 100 years. Cull forests, which might be mistaken for old-growth, differ in having a much higher proportion of trees <100 years old (73% at one cull forest [K.C. Peppers, unpublished data]), and evidence of historical logging is present. We did not collect data on second-growth forests, but based on our field observations, most post oaks there are

<100 years old; trees >150 years old are absent; and stumps, roads, fences, and other signs of human disturbance are common.

The overall post oak age structure of old-growth forests in the western Cross Timbers differs strikingly from that of the Oklahoma Cross Timbers. Proportions of trees ≥200 years old were similar in the two regions (7.2% in Texas vs. 6.9% in Oklahoma [M. Mangione, unpublished data]); however, in Oklahoma, only 26.1% of post oak trees were ≥100 years old (vs. 73.5% in Texas). The large difference in proportions of younger trees could be a sampling artifact if post oaks were smaller in diameter, on average, in Texas than Oklahoma (i.e., most trees <100 years old in Texas may be <10 cm DBH, so we would have recorded them as saplings instead of trees). There was not a significant difference, however, between the mean DBH of randomly sampled post oaks in Texas (25.4 cm) and Oklahoma (24.2 cm; M. Mangione, unpublished data). Moreover, this metric is not sufficient to determine the source of the discrepancy in proportions of young trees in old-growth forests in Oklahoma and Texas. Future research to explore our sampling hypothesis could involve (1) comparing ages of similar-sized post oaks in Oklahoma and Texas to determine if, as it appears, trees of a given DBH are older in Texas than in Oklahoma; (2) directly comparing post oak growth rates (i.e., ring widths) between sites in Oklahoma and Texas; and (3) selectively coring post oaks <10 cm DBH in Texas to determine their age range. An alternative explanation for the difference in numbers of young trees is that post oak regeneration is lower in Texas than in Oklahoma, and our data provide some support for this hypothesis (discussed in detail below).

Neither post oak size structures nor DBH measurements of individual trees are particularly useful for identifying old-growth forests in the western Cross Timbers.

Although Clark (2003) found that linear regression of age against DBH was the best available method for estimating ages of hollow post oaks in the Oklahoma Cross Timbers, the relationship between DBH and age of post oaks is not strong (Clark 2003; Figure 3.3). In general, smaller post oaks (10-20 cm DBH) are younger; however, relatively small, but old trees do occur. For example, at our study sites, a 163-year-old post oak had a DBH of only 17.5 cm, and a 225-year-old post oak had a DBH of only 23.0 cm. Generalizations are not possible for ages of larger trees. For example, we dated a 261-year-old post oak with a DBH of 30.2 cm; at the same site, a larger tree (31.8 cm DBH) was less than half as old (125 years).

Difficulty in using DBH to predict age is not unique to post oaks. Greenberg and Simons (1999) found more DBH variation with respect to age in oaks than pines, especially among the oldest trees. In an old-growth forest in Florida, the oldest turkey oak (*Quercus laevis*; 123 years) had a DBH of 50.0 cm, whereas the largest turkey oak (51.3 cm DBH) was only 56 years old (Greenberg & Simons 1999). Small, but relatively old trees were common in old-growth forests of Michigan and Wisconsin, as were large, but young trees (Tyrrell & Crow 1994). Although size, per se, does not necessarily distinguish older post oaks in the western Cross Timbers, the oldest trees do possess several reliable external characteristics, such as longitudinally twisted stems (spiraling of bark up and down the trunk), old branch scars on the lower trunk, dead limbs or broken tops, and a canopy consisting of only a few heavy, craggy limbs (Stahle & Chaney 1994).

Old-Growth Forest Composition

Prior to our research, forest composition had not been described for the rough, rocky terrain that characterizes most remaining old-growth forests in the western Cross Timbers. In the only published study of old-growth forests in the western Cross Timbers, Kroh and Nisbet (1983) presented data from one old-growth site near Fort Worth, which is 80 km east of our easternmost study site and located on relatively level terrain. Kroh and Nisbet (1983) recorded 14 tree species, and total basal area was 24.6 m^2/ha. Although we did not record more than seven tree species at a single site, our mean total basal area was only slightly lower (23.3 m^2/ha). At the Fort Worth site, the tree layer was composed of post oak (54%), blackjack oak (25%), sugar hackberry (14%), cedar elm (5%), and red mulberry (3%; *Morus rubra*; not recorded at our sites). All relative densities reported by Kroh and Nisbet (1983) were within the ranges we recorded for these species, except for that of sugar hackberry, which never made up more than 5% of the tree layer at our sites.

Roovers and Shifley (1997) recorded 23 tree species in an old-growth forest in Illinois, and an old-growth forest in Ohio had 14 co-dominant tree species (McCarthy et al. 2001). Comparatively low tree species richness in the western Cross Timbers is due to a marginal environment characterized by extreme temperatures, low annual precipitation, and steep slopes (Risser & Rice 1971). In eastern Oklahoma, tree species richness and total basal area declined along an east-west moisture gradient (Risser & Rice 1971); however, among our study sites, there was no east-west trend in tree species richness or basal area. Instead, the two sites with the lowest and highest species richness values were both found near the center of the east-west range of our study sites. Sites 8 and 10 had the highest values for total basal area, but there were several sites east of those. Total basal area at the easternmost site was slightly below the mean, and we did not find a significant relationship between species richness and total basal area. The east-west range of our old-growth sites was probably too small (93 km) to expect moisture-related differences in forest composition, as all but two of our study sites are found in the same precipitation zone, which is marginal for tree growth. The two sites that occur in a zone of higher precipitation had species richness and basal area values near the respective means.

We hypothesized that aspect would influence old-growth forest composition and structure in the western Cross Timbers because of microclimatic modifications in wind speed, soil and air temperatures and moisture, and light intensity (Cantlon 1953; McCarthy et al. 2001). In southwestern Texas, south-facing slopes had 5-16% less soil moisture, 22-40% higher evaporation, 5-11°C higher temperatures (5 cm deep), 5-11% lower humidity, and higher wind speeds (Cottle 1932). North-facing slopes also had twice the plant cover of south-facing slopes (Cottle 1932). Reported differences in vegetation on neighboring north and south slopes included the presence of different species, as well as more subtle differences in relative abundances of species (Cantlon 1953). For example, south-facing slopes in Idaho were treeless (although adjacent north-facing slopes had trees; Gail 1921), and Douglas-fir distribution in Washington was controlled by aspect (Turesson 1914). Although aspect may have more pronounced effects on understory plants, southern aspect has been associated with differences in tree stands, such as lower stand basal area (Fralish et al. 1991), fewer individuals of large size classes, and lower tree density (Cantlon 1953).

Contrary to our expectations, at old-growth sites in the western Cross Timbers, mean absolute tree density was significantly higher at sites on south-facing slopes than at sites on north-facing slopes. This difference is difficult to explain, but may be related to differences in age structures and, ultimately, to the frequency of disturbances such as fire (i.e., if fires were more frequent on south-facing slopes, coppices of younger stems might result). Proportionally more post oaks on south-facing slopes were from younger age classes (≤50, 51-100, 101-150 years), so the larger numbers of trees on south-facing slopes primarily reflect larger numbers of young trees, only some of which will live to enter older age classes. Relatively more old post oaks (151-200 and 201-250 years) occur on north-facing slopes. We do not know whether this pattern occurs in tree species other than post oak in the western Cross Timbers. Mean absolute density of all saplings was higher on north-facing slopes, but not significantly so. We did not find a significant difference in either mean total basal area or mean species richness on north- versus south-facing slopes. Perhaps even north-facing slopes in out study area are such harsh environments (due to the climate of the western Cross Timbers and extreme slope), that differences between north- and south-facing slopes are less pronounced than in more mesic environments. Future research might involve comparisons of the sizes of similar-aged post oaks on north- and south-facing slopes to determine whether the hotter, drier conditions of southern exposures are reflected in the growth of post oak.

We found that north- and south-facing slopes also differed in the composition of their tree and canopy layers, and differences were generally consistent for each species. For example, blackjack oak and Texas ash were more abundant than expected in both the sapling and tree layers on north-facing slopes. They may require relatively more favorable conditions for survival and growth than some co-occurring tree species. In contrast, post oak was more abundant than expected as a sapling on south-facing slopes (but post oak frequencies in the tree layer appeared unrelated to aspect). In both the sapling and tree layers, Ashe juniper, cedar elm, and mesquite were more abundant than expected on south-facing slopes. Mesquite may fare well on southern exposures because of its deep roots, which can reach moisture 30 m below the soil surface in some parts of Texas (Diggs et al. 1999). Ashe juniper is also well adapted to the harsh conditions of south-facing slopes, with roots that can penetrate limestone bedrock and reach water contained in cracks and caves (Jackson et al. 1999).

Post oaks >12.5 cm DBH made up, on average, 64% of the tree layer at upland forest sites in the Oklahoma Cross Timbers (Johnson & Risser 1975). At our study sites in Texas, post oak also accounted for 64% of all trees, on average. Despite that similarity, important differences occur between old-growth forests in the Oklahoma and Texas Cross Timbers. For example, blackjack oak was half as common at our study sites (mean relative density=0.15) as at sites in the Oklahoma Cross Timbers (mean relative density=0.29) (Johnson & Risser 1975). In Oklahoma, species other than post oak or blackjack oak accounted for only 7% of all trees, whereas 22% of all trees (on average) in the western Cross Timbers were of other species. Clark (2003) found that post oak and blackjack oak together made up >80% of the tree layer at three old-growth forest sites in Osage County, Oklahoma. This was true at 10 of 16 sites in the western Cross Timbers of Texas; however, post oak and blackjack oak accounted for <60% of the tree layer at four sites (<40% at two of those). The relative importance of post oak in old-growth forests is one of the most striking differences between the Oklahoma and Texas Cross Timbers: although many of our study sites were overwhelmingly dominated by post oak, the degree of post oak dominance appears much more variable in Texas than in Oklahoma.

Johnson and Risser (1975) reported that total tree density in Oklahoma Cross Timbers forests was only 255 trees/ha. On average, our sites were twice as dense (534 trees/ha), but the sites studied by Johnson and Risser (1975) were not necessarily old-growth. For old-growth forests in the Oklahoma Cross Timbers, M. Mangione (unpublished data) reported a mean density of 587 trees/ha, which approximates the density we recorded.

Post Oak Regeneration in Old-Growth Forests

In mesic North American ecosystems, oak regeneration is declining, and oaks are being replaced by shade-tolerant species (Abrams 1992; Loftis & McGee 1993). Late-successional oak-dominated forests appear to persist, however, on dry, infertile sites in the eastern United States and along the western edge of the deciduous forests, including in the Oklahoma Cross Timbers (Abrams 1992; Johnson 1992). Even without the occurrence of fire, which is thought to have increased oak dominance in some presettlement forests (Abrams 1992), oaks appear to maintain relatively stable population sizes on xeric sites with low nutrient availability (Mikan et al. 1994).

Climatic, edaphic, and topographic characteristics of old-growth forests in the western Cross Timbers parallel those of ecosystems in which stable oak dominance has been reported; however, we found a low mean sapling:tree ratio for post oak (0.28), and none of the randomly selected old-growth sites had a post oak sapling:tree ratio ≥ 1.0. In addition, we found that post oak recruitment to breast height has been in decline since the late 1800s. Even if post oak sapling mortality were zero, the current degree of post oak dominance seems unlikely to continue even at Site 3, which had the highest sapling:tree ratio (0.79) of all 16 old-growth sites. At some old-growth sites, Ashe juniper, blackjack oak, sugar hackberry, and Texas ash appear poised to become more important components of the tree layer if post oak dominance declines. Although our results suggest that post oak may become less dominant in old-growth western Cross Timbers forests in the future, other factors (both methodological and biological) bear on this interpretation.

We assessed post oak regeneration based only on the ratio of saplings (<10 cm DBH) to trees (≥10 cm DBH). This metric may be flawed in two ways. First, the 10-cm constraint may be inappropriate; perhaps post oaks should be considered saplings up to 15 or 20 cm DBH. For example, Site 12 had no post oak saplings, based on our original 10-cm rule. When we redefined saplings as stems <20 cm DBH, the sapling:tree ratio for Site 12 was 1.0. Sapling:tree ratios would probably increase at other sites, as well, although even with the revised 20-cm DBH maximum, Site 13 still had no post oak saplings.

Second, the sapling layer may not accurately reflect population dynamics in the Cross Timbers if episodic recruitment—following a large-scale disturbance such as fire—is important in the life history of post oak (Russell & Fowler 1999; Clark 2003). In south-central Texas, *Quercus fusiformis* and *Quercus buckleyi* were much more numerous as adults than as saplings or sapling-sized root sprouts; by itself, recruitment of saplings appeared too low to maintain current population sizes of the two oak species (Russell & Fowler 1999). Russell and Fowler (1999) speculated that episodic recruitment on a time interval shorter than an adult's life span could maintain adult numbers. Applied to the western Cross Timbers, this suggests that even where post oak saplings are relatively uncommon, post oak tree populations could be maintained if periodic pulses of regeneration result in abundant seedlings. We did not record seedlings, but Clark (2003) found high densities (2400-8000 stems/ha) of post oak seedlings (≤1 m tall) in the Oklahoma Cross Timbers. Because of post oak's long life span (approximately 300 years in the western Cross Timbers), there is a relatively long window in which a pulse of recruitment might occur to result in continued dominance of post oak trees. It is unknown, however, what magnitude and frequency of episodic recruitment would be required to maintain current numbers of adults.

Our data provide evidence of historical pulses and declines in recruitment to breast height for post oak in old-growth forests in the western Cross Timbers (Figures 3.5 & 3.6). Relatively short recruitment episodes appear to have occurred around 1817, 1848, and 1932, and a 30-year recruitment pulse occurred in the late 1800s (evident overall and for at least nine individual sites). During severe droughts in the 1850s-1860s and 1950s, recruitment declined at these sites; however, there is no historical precedent (in our data) for the continued decline in recruitment after the late 1800s, which is unlikely to be a result of climatic phenomena. Instead, this decline may be related to European settlement and subsequent changes in fire frequency and grazing regimes. Increased browsing by wildlife—including exotic species—may also be a factor in declining post oak recruitment.

For three old-growth stands along a ridgeline in the Oklahoma Cross Timbers, Clark (2003) defined post oak saplings just as we did (<10 cm DBH), but found an average of 753.3 saplings/ha (approximately seven times as many, on average, as at our study sites [109.2 saplings/ha]). Moreover, the mean post oak sapling:tree ratio was 0.28 at our sites in Texas, but 1.6 in the Oklahoma Cross Timbers (Clark 2003). M. Mangione (unpublished data) reported a mean post oak sapling:tree ratio of 1.3 for old-growth forests in the Oklahoma Cross Timbers, but site-specific ratios ranged widely (0.2-4.2); five of 13 sites had ratios ≤ 0.79 (the maximum we reported). Total sapling:tree ratios (for all tree species combined) did not differ between Texas (2.5) and Oklahoma (2.6 [Clark 2003]).

We expected to find relatively high post oak regeneration at the old-growth sites we studied because they are similar—in topography and climate—to other xeric uplands in which stable, late-successional oak dominance has been reported. In contrast, we found that post oak regeneration in the western Cross Timbers seems consistent with the more general, continent-wide pattern of declining oak regeneration (Mikan et al. 1994). Our results are not definitive with regard to post oak regeneration in old-growth forests in the western Cross Timbers; however, our findings suggest that determining the importance of episodic recruitment in post oak and evaluating post oak's trajectory in these old-growth forests should be research priorities. Data on sapling mortality of post oak and other tree species, as well as post oak seedling abundance, for the western Cross Timbers would be useful in assessing potential changes in old-growth forest composition. Fire is probably implicated, to some degree, in declining post oak regeneration, but we do not know whether settlement resulted primarily in fire suppression or increased fire frequency. Analysis of historical fire regimes should be a top research priority for the region.

Successional replacement of oaks by other species is thought to be less likely on low-quality sites (dry, nutrient-poor), and oak regeneration may also be influenced by topographic factors such as slope and aspect (Johnson 1992). We found that post oak regeneration in the western Cross Timbers was lowest on steeper sites, but there was no significant difference in regeneration between north- and south-facing slopes. Perhaps this harsh environment produces conditions on the steepest slopes that are too poor for even post oak to regenerate in high numbers. We also found that post oak regeneration is lowest on sites with the highest tree species richness. On more diverse sites, especially, post oak dominance may be based on bursts of regeneration that follow climate catastrophes, such as severe droughts.

Invasion and Succession in Old-Growth Forests

We hypothesized that mesquite and Ashe juniper—although considered highly invasive species elsewhere in north-central Texas—were not problematic in relatively undisturbed old-growth sites in the western Cross Timbers. Before European settlement of the western Cross Timbers, mesquite was either uncommon and restricted to riparian areas and rocky slopes (Diggs et al. 1999), or altogether absent from the region (Dyksterhuis [1948] notes that the species was not recorded before 1849). Whatever its origins, mesquite has become abundant since European settlement and has invaded grasslands throughout the state, especially where overgrazing has occurred (Diggs et al. 1999). Mesquite was present at seven old-growth sites, but our results suggest that mesquite is not an important component of the tree layer, and that it is not increasing in abundance. Where mesquite trees were present, they made up only 8% of all trees sampled, on average; mean absolute density of mesquite trees was also low (37.1 trees/ha). Relative density of mesquite trees was highest at Site 8 (0.2), and sapling relative density (0.2) was essentially the same, suggesting that mesquite abundance will remain roughly stable. Site 12 had the highest absolute density of mesquite trees (82.9

stems/ha), but had no mesquite saplings, so mesquite numbers may decline there. Site 5 also had mesquite trees, but no saplings. Mesquite saplings were present at two sites (4 and 6) where there were no mesquite trees, but at low relative densities (0.03 and 0.05, respectively). Mesquite basal area was never higher than 0.11 m^2/ha, and dominance never exceeded 0.10. Lack of mesquite invasion is likely due to the absence (or limited nature) of historical grazing in rough, rocky old-growth forests.

Ashe juniper, on the other hand, appears poised to become a much more important component of old-growth forests in the western Cross Timbers. Ashe juniper was present in the tree layer at only three sites (8, 9, and 13) in one county, and Ashe juniper density was highest at Site 8 (15% of tree layer; 122.4 stems/ha). At that site, Ashe juniper was more abundant than Texas ash (81.6 trees/ha), but much less abundant than post oak (469.4 stems/ha) and slightly less abundant than blackjack oak (142.86 stems/ha). Ashe juniper saplings, however, were present at seven sites (in three counties), and made up 30% of the sapling layer at those sites, on average. Ashe juniper made up 60% of the sapling layer at Site 8 (775 stems/ha), whereas absolute density of cedar elm—the second most-common sapling species there—was 291 stems/ha. At Site 9, where Ashe juniper trees made up only 3% of the tree layer (8.0 stems/ha), 58% of the sapling layer was accounted for by Ashe juniper (312.2 stems/ha). At Site 12, Ashe juniper was not present in the tree layer, but made up 48% of the sapling layer (172.7 trees/ha). The presence of Ashe juniper saplings in all three counties where sizeable blocks of old-growth forest remain in north-central Texas, as well as its greater abundance in the sapling layer, suggest that Ashe juniper invasion is emerging as an important conservation/management issue in remnant old-growth forests of the western Cross Timbers.

In the Oklahoma Cross Timbers, Clark (2003) found a high density of another *Juniperus* species (eastern redcedar [*J. virginiana*]) at one old-growth site (including some very old redcedar trees). In some parts of Texas, Ashe juniper forms thickets ("cedar brakes") and is known to have adverse effects on native plants (Diggs et al. 1999). Fire suppression is cited as an important factor in the spread of *Juniperus* species in Texas (Diggs et al. 1999), although the historical role of fire as a disturbance in the western Cross Timbers is unknown. In eastern hardwood forests, differences in understory and overstory tree composition were attributed to the effects of 20th-century fire suppression (Foster et al. 1996), and fire suppression was cited as having caused conversion of savannahs to forests in the Oklahoma Cross Timbers (Johnson & Risser 1975). Clark (2003), however, found that fire frequency *increased* after European settlement and statehood in the Oklahoma Cross Timbers.

None of the other tree species we recorded is considered invasive; however, four species—blackjack oak, chittamwood, sugar hackberry, and Texas ash—were much more common in the sapling layer than the tree layer at particular old-growth forest sites. Blackjack oak relative density was at least twice as high in the sapling layer at seven sites in two counties. Texas ash relative abundance was twice as high in the sapling layer at Sites 1 and 10, and 16 times greater at Site 2, where it made up nearly half the sapling layer (but only 3% of the tree layer). Sugar hackberry was present in the tree layer at three sites, but occurred as a sapling at nine sites. Relative density of hackberry trees was always <3%, but hackberry saplings made up one-fourth of the sapling layer at two sites

(15 and 16) and more than 10% at three other sites. Chittamwood presented an unusual case: of three sites with chittamwood trees, saplings were present at only one, but saplings were also present at 11 sites where chittamwood was not part of the tree layer. Where chittamwood trees did occur, their relative density was always <3%, but chittamwood sapling relative density was always ≥3% (and reached 20% at two sites). Perhaps the harsh environment of the western Cross Timbers makes it unusual for chittamwood to grow larger than 10 cm DBH (i.e., it would rarely enter the tree layer); however, Diggs et al. (1999) report that the species reaches 15 m tall and 30 cm DBH in northcentral Texas.

Relative importance of these subordinate species seems likely to remain stable in old-growth forests only if they have high sapling mortality, or if post oak recruitment occurs in pulses. Otherwise, succession may lead to increased abundance of these species in some old-growth forests, as post oak dominance declines. Repeated, long-term monitoring is an appropriate way to detect successional changes in these old-growth forest sites and to determine what factors mediate differences in sapling and tree species composition—whether differences in survival, life span, climate, topography, or disturbance.

Conclusions

We estimated that approximately 6,210 ha of old-growth forest remain in the western Cross Timbers (Chapter 2). Although the 16 transects we surveyed encompass only 16 ha, they were randomly selected within the area predicted to retain old-growth and are probably representative of surviving old-growth forests in the region. Our results address an important, but heretofore unanswered question: what constitutes an old-growth forest in the western Cross Timbers? We believe our findings will be useful for (1) identifying other old-growth sites in the region for conservation and management purposes; (2) setting research priorities for old-growth forests in the western Cross Timbers; and (3) serving as baseline data for comparison with future research findings.

Foster et al. (1996) suggested that, because surviving old-growth forests often occupy unusual sites that are inaccessible and inhospitable, they may not be indicative of presettlement forests across the landscape. We do not propose that our data accurately describe forests that once existed on level terrain in the western Cross Timbers; in fact, Dyksterhuis (1948) found that savannahs, rather than forests, blanketed most of the flat lands that were cleared for grazing and row-crop production in the region. In those areas, tall prairie grasses were the dominant plant species, and post oaks were scattered, not dense (Dyksterhuis 1948). In much of the western Cross Timbers, however, rough, rocky, steep sites are not unusual—rather, they typify the landscape—and we believe that our results do characterize presettlement forests in those areas.

In addition to identifying common components, or average conditions, that characterize these old-growth forests, we have identified parameters (such as post oak dominance) that vary widely across sites. Whereas we have described *patterns* in old-growth forests of the western Cross Timbers, *processes* that control these patterns (e.g., regeneration, recruitment, fire as a disturbance, browsing by wildlife, seed rain of invasive species, climate change) will be most observable through long-term, repeated measurements at these sites (Foster et al. 1996; Ansley & Battles 1998). We believe our findings can serve as the point of reference for such long-term studies.

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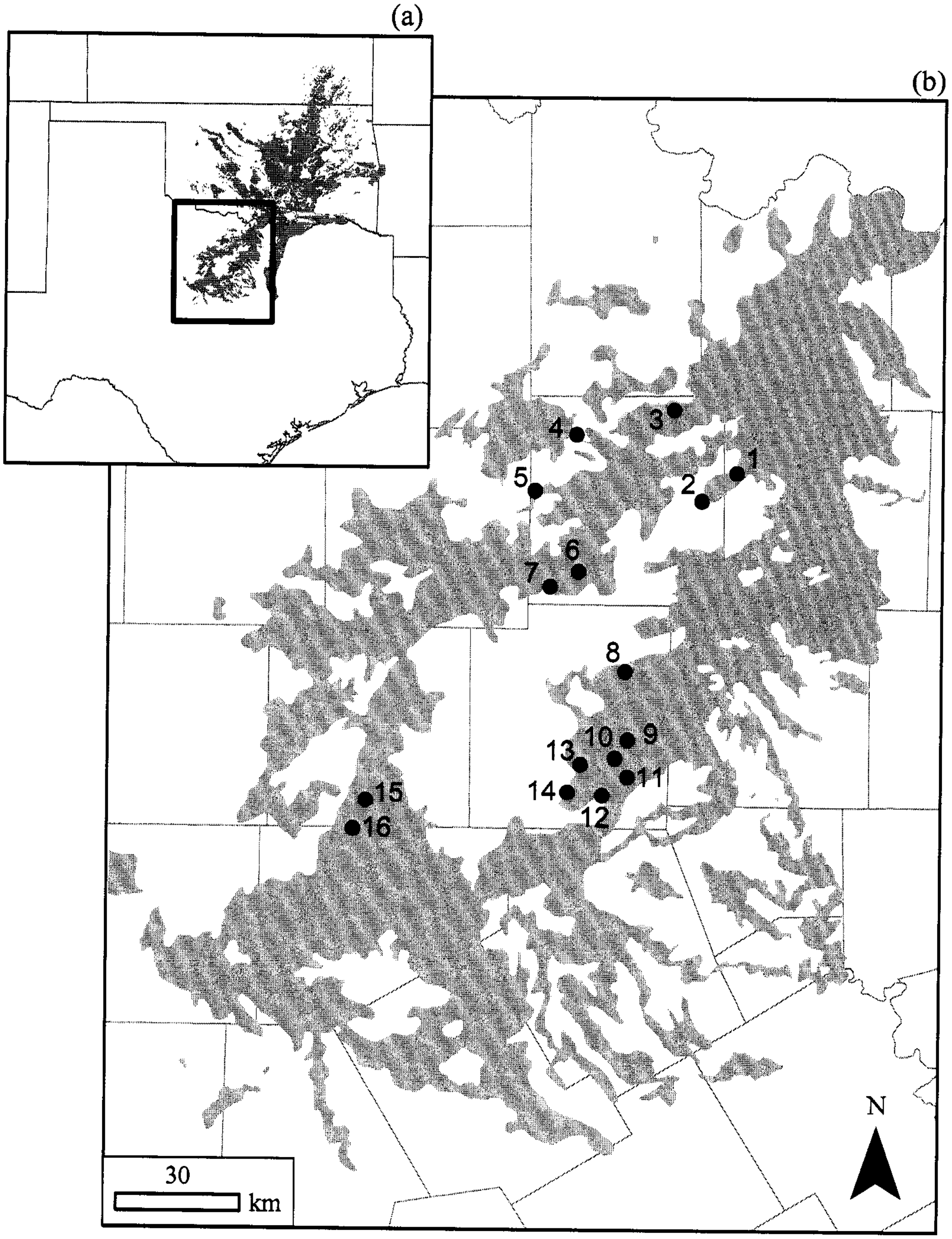

Figure 3.1. (a) Historical extent of the Cross Timbers (8 million ha, Küchler 1964) and western Cross Timbers of north-central Texas (boxed area) (1.5 million ha, Dyksterhuis 1948); and (b) 16 old-growth forest sites in the western Cross Timbers. Sites were identified and sampled in 2003 during random field-testing of an old-growth predictive model. Cross Timbers forests are dominated by post oak (*Quercus stellata*), many of which are 150-300 years old.

Figure 3.2. Old-growth forest study sites in the western Cross Timbers. In general, old-growth forests in the region are dominated by post oaks, many of which are 150-250 years old, and are located on rocky or bouldery, steep slopes. Most randomly sampled post oaks were <40 cm DBH and <15 m tall.

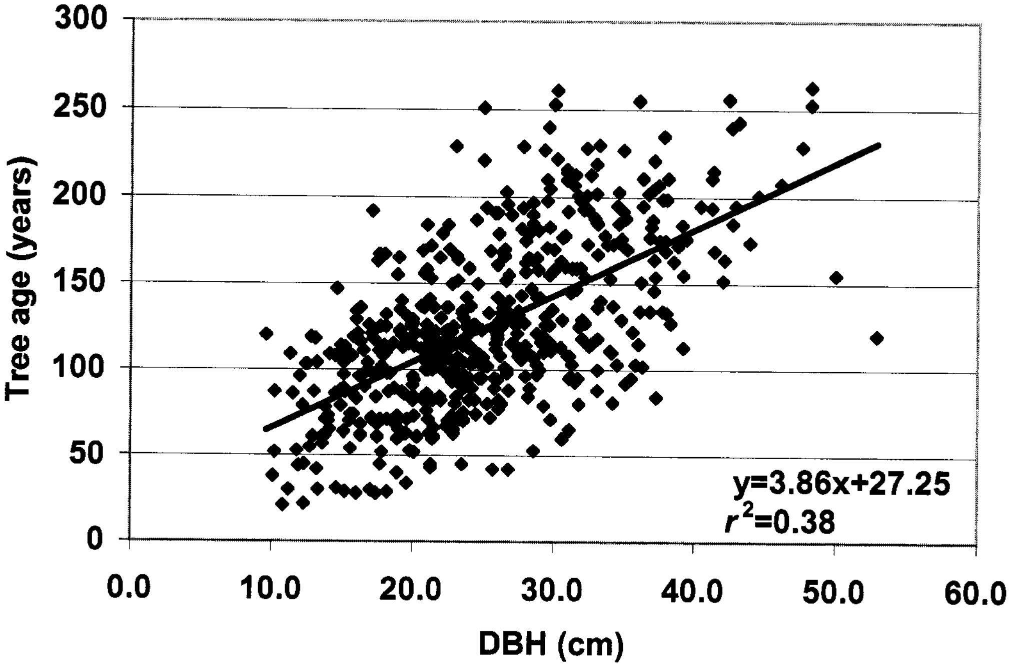

Figure 3.3. Linear regression of tree age against DBH for post oak at old-growth forest sites in the western Cross Timbers (F=325.6, p <0.001).

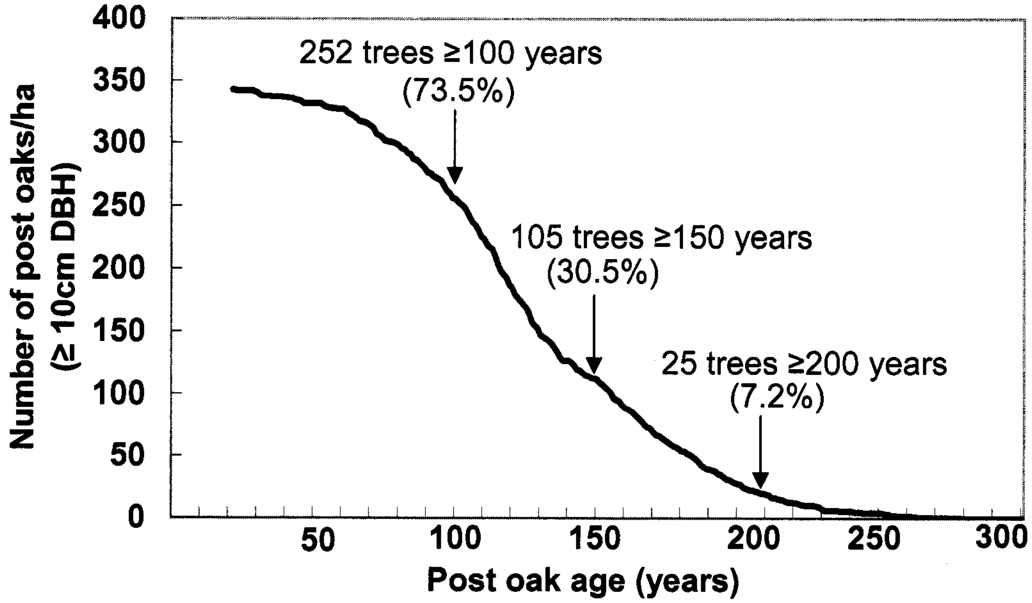

Figure 3.4. Number of post oak trees per hectare by age, on average (based on mean post oak density of 343 trees/ha) for 16 old-growth sites in the western Cross Timbers.

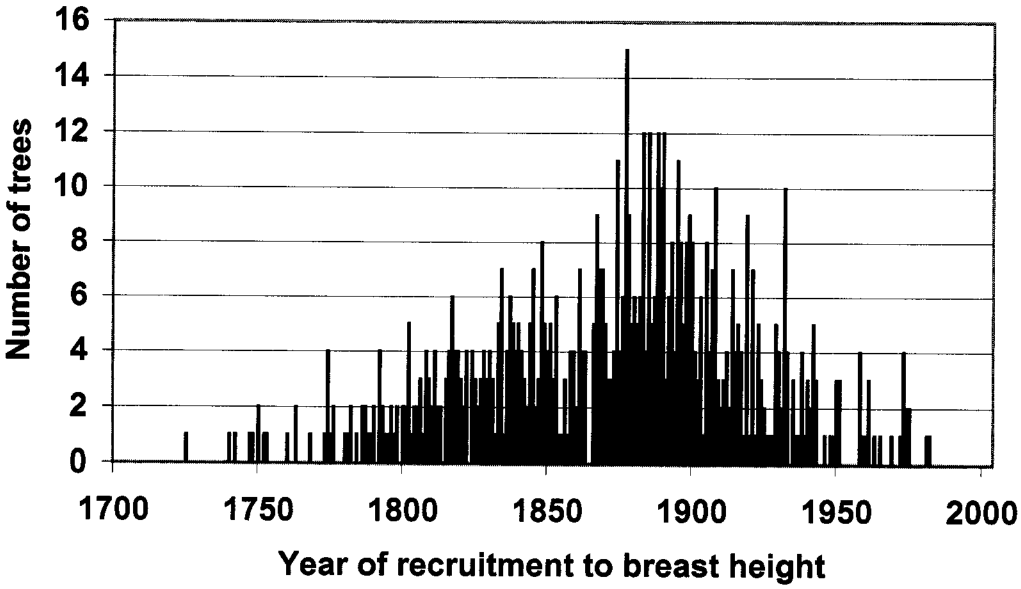

Figure 3.5. Frequency distribution of recruitment years for randomly selected post oaks at 16 old-growth forest sites in the western Cross Timbers of Texas. Linear regression was used to adjust ages of 146 cores that missed pith or were taken from trees with heart rot. Apparent lack of recruitment since 1982 is a sampling artifact that reflects a 10-cm DBH minimum for coring and dating of trees.

Figure 3.6. Site-specific recruitment (to breast height) of randomly selected post oak trees in old-growth forests in the western Cross Timbers, from 1700-2000. Recruitment to breast height since 1982 is not apparent because only trees ≥10 cm DBH were cored and dated.

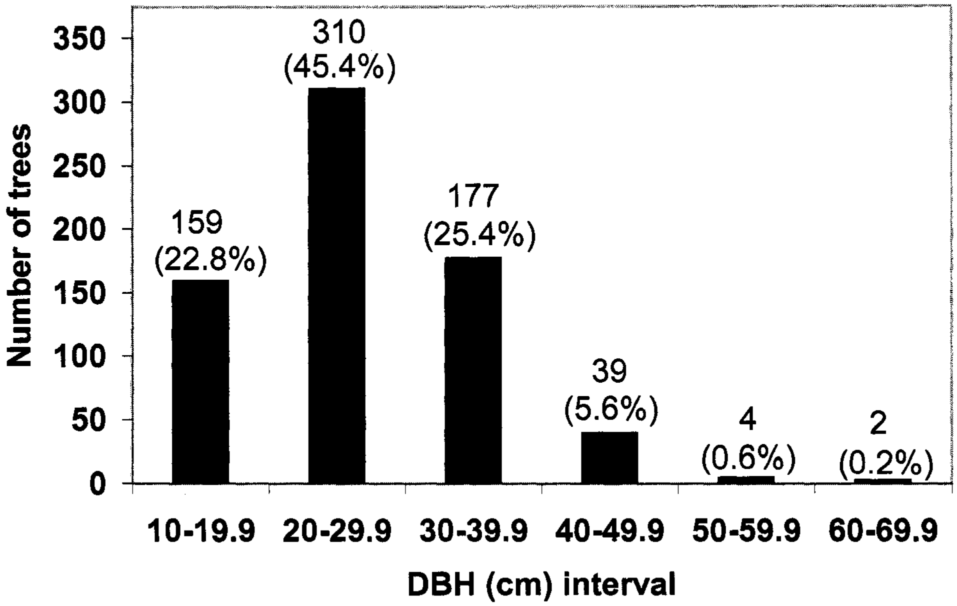

Figure 3.7. Overall size (DBH) structure for post oak trees (≥10 cm DBH) at 16 old-growth forest sites in the western Cross Timbers. We measured approximately 40 randomly selected post oak trees at each site.

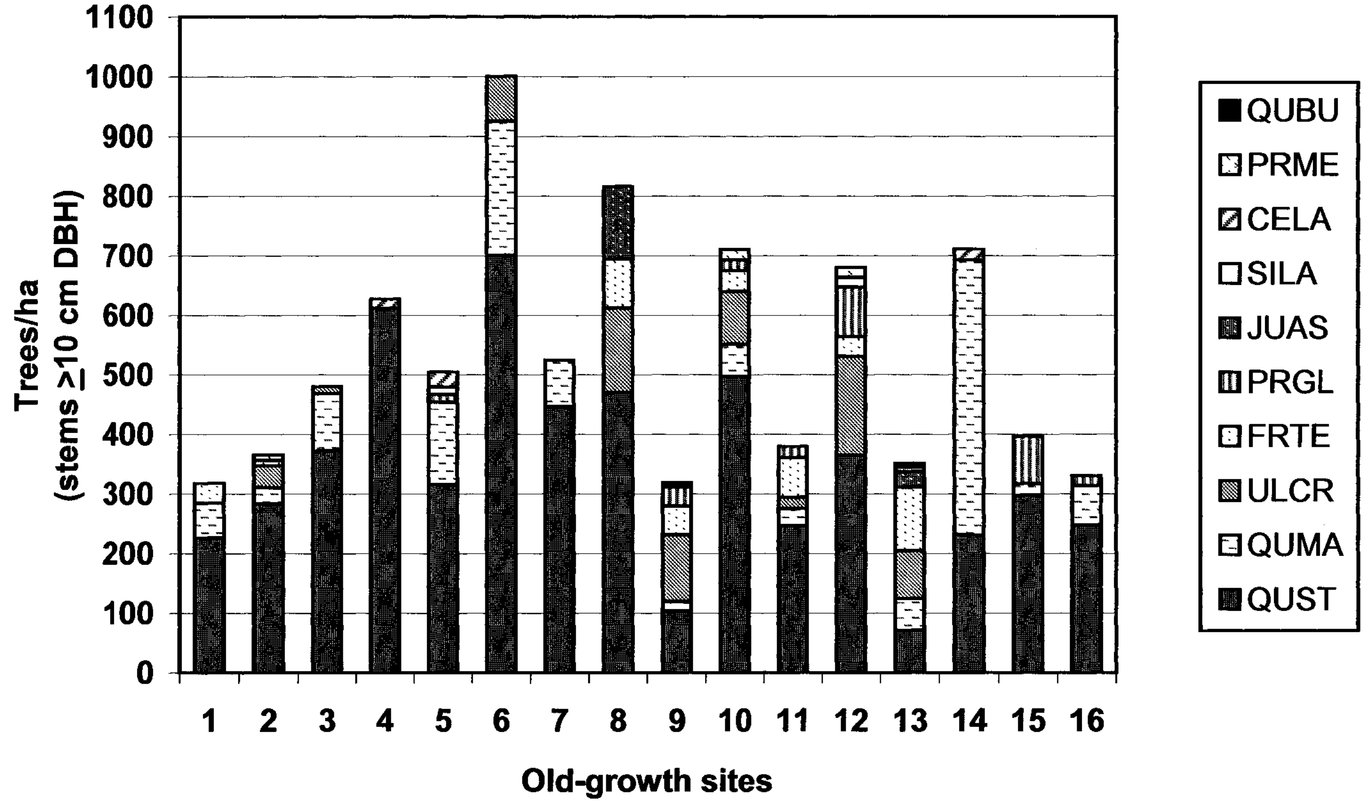

Figure 3.8. Absolute density (stems/ha) of trees (≥10 cm DBH) for each species recorded at 16 old-growth sites in the western Cross Timbers of Texas. QUST, *Quercus stellata* ; QUMA, *Quercus marilandica* ; ULCR, *Ulmus crassifolia* ; FRTE, *Fraxinus texensis* ; PRGL, *Prosopis glandulosa* ; JUAS, *Juniperus ashei* ; SILA, *Sideroxylon lanuginosum* ; CELA, *Celtis laevigata* ; PRME, *Prunus mexicana* ; and QUBU, *Quercus buckleyi.*

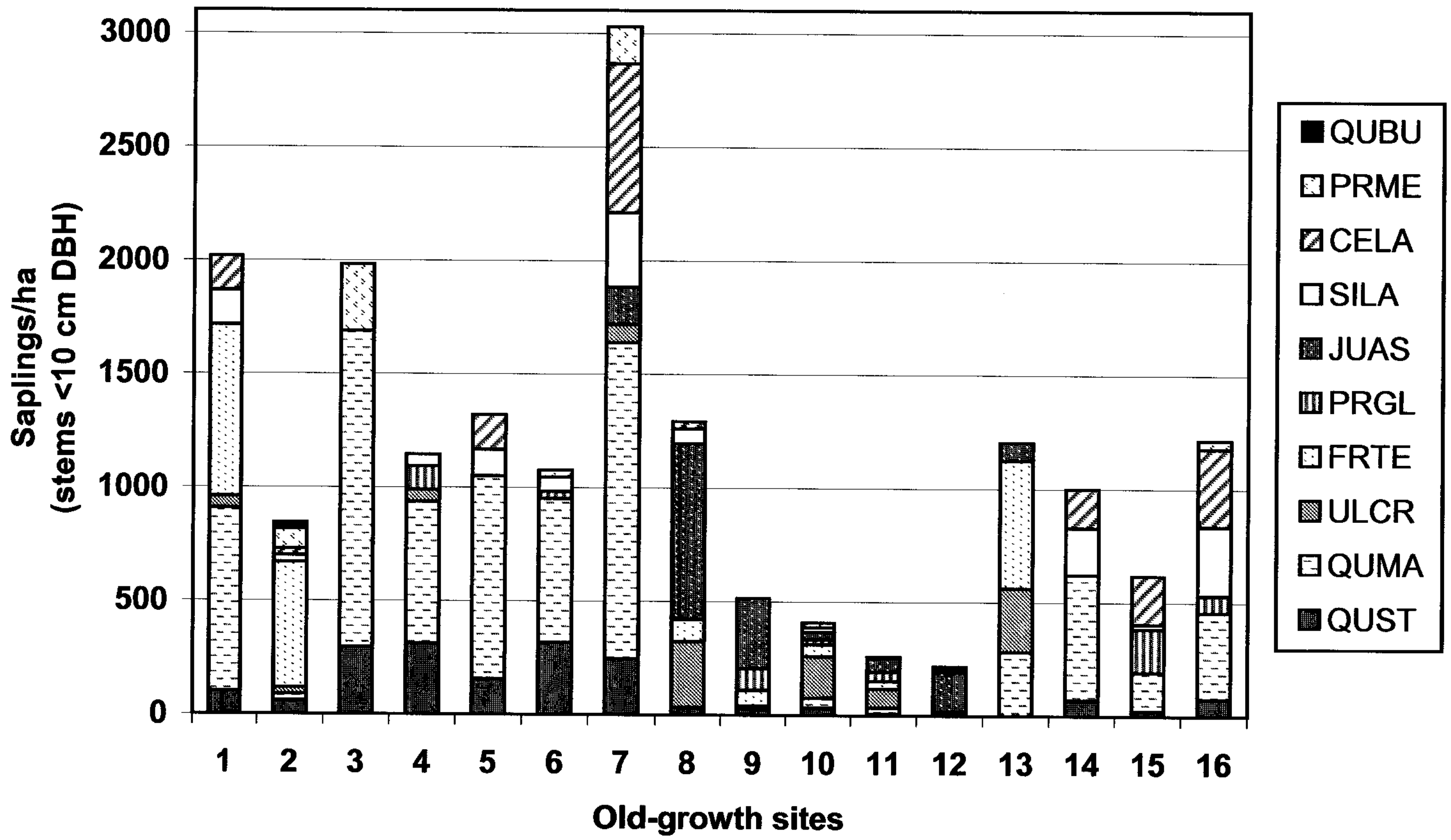

Figure 3.9. Absolute density (stems/ha) of saplings (<10 cm DBH), by species, at 16 old-growth sites in the western Cross Timbers of Texas. Species codes given in Figure 2.7.

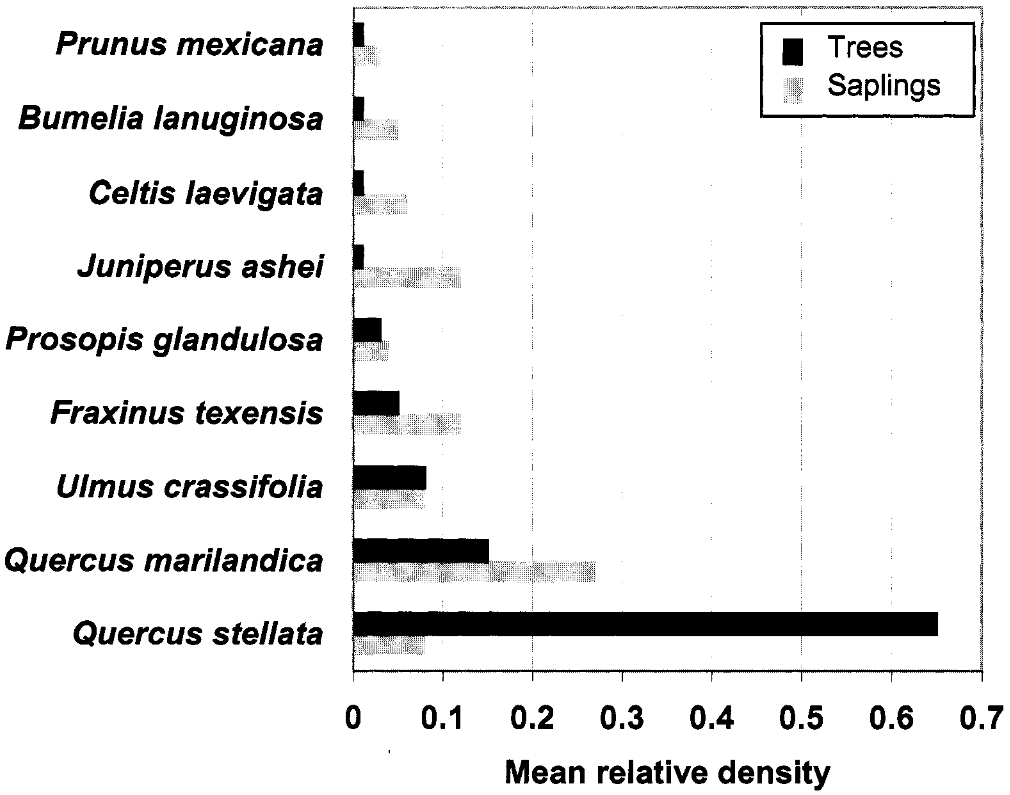

Figure 3.10. Mean relative density of each species in the tree (≥10 cm DBH) and sapling (<10 cm DBH) layers at 16 old-growth forest sites in the western Cross Timbers of Texas.

Table 3.1. Location, slope, and aspect of 16 old-growth forest sites in the western Cross Timbers of Texas. At each site, we conducted point-quarter vegetation sampling along a randomly oriented, 200 x 50 m transect (10,000 m^2) between 3 April and 12 June 2003. Old-growth sites are mapped in Figure 2.1b.

Site number	UTM coordinates (zone 14) North	UTM coordinates (zone 14) East	Slope (%)	Aspect
1	3684837	604322	30.9	N
2	3678162	595821	26.6	N
3	3699670	589137	9.4	N
4	3694029	565657	26.3	S
5	3680002	555992	19.8	N
6	3657442	562491	21.8	N
7	3656945	560268	20.0	N
8	3636062	578078	40.6	S
9	3618936	578405	10.8	N
10	3611824	569888	21.8	S
11	3606262	571326	24.7	N
12	3611130	571103	33.6	S
13	3611572	568807	41.9	N
14	3606353	565166	22.3	W
15	3599728	513489	14.1	S
16	3597978	512413	22.1	W

Table 3.2. Ages, per 50-year interval, of post oak ≥10 cm dbh at old-growth transects in the western Cross Timbers. At 10 points along a 200-m transect, the nearest post oak in each quadrant was cored. Ages are adjusted (by linear regression) for missed pith and heart rot.

Old-growth site	Post oak cored	Number of post oak ≥10 cm dbh (%)					
		≤50 yr.	51-100 yr.	101-150 yr.	151-200 yr.	201-250 yr.	251-300 yr.
1	43	3 (7.0)	4 (9.3)	12 (27.9)	20 (46.5)	4 (9.3)	
2	40	1 (2.5)	9 (22.5)	7 (17.5)	15 (37.5)	8 (20.0)	
3	40	2 (5.0)	7 (17.5)	11 (27.5)	10 (25.0)	8 (20.0)	2 (5.0)
4	40		10 (25.0)	22 (55.0)	7 (17.5)		1 (2.5)
5	40	1 (2.5)	8 (20.0)	20 (50.0)	11 (27.5)		
6	40		10 (25.0)	25 (62.5)	5 (12.5)		
7	44		3 (6.8)	30 (68.2)	8 (18.2)	3 (6.8)	
8	40		7 (17.5)	24 (60.0)	7 (17.5)	2 (5.0)	
9	40		5 (12.5)	15 (37.5)	14 (35.0)	4 (10.0)	2 (5.0)
10	48		9 (18.8)	27 (56.3)	11 (22.8)		1 (2.1)
11	42		15 (35.7)	15 (35.7)	9 (21.4)	3 (7.2)	
12	40		16 (40.0)	17 (42.5)	7 (17.5)		
13	40	6 (15.0)	6 (15.0)	10 (25.0)	11 (27.5)	7 (17.5)	
14	30		18 (60.0)	11 (36.7)	1 (3.3)		
15	41	1 (2.4)	10 (24.4)	21 (51.2)	8 (19.6)	1 (2.4)	
16	40	9 (22.5)	12 (30.0)	12 (30.0)	7 (17.5)		
Total	648	23 (3.5)	149 (23.0)	279 (43.0)	151 (23.3)	40 (6.3)	6 (0.9)

Table 3.3. Relative density (RDEN[a]), absolute density (DEN; stems/ha), basal area (BA; m^2/ha), and relative dominance (RDOM[b]), by species, of trees (≥10 cm DBH) at 16 old-growth sites in the western Cross Timbers of north-central Texas.

Site	*Quercus stellata*	*Quercus marilandica*	*Ulmus crassifolia*	*Fraxinus texensis*	*Prosopis glandulosa*	*Juniperus ashei*	*Sideroxylon lanuginosum*	*Celtis laevigata*	*Prunus mexicana*	*Quercus buckleyi*
1										
RDEN	0.68	0.18		0.15						
DEN	225.88	58.56		50.20						
BA	18.36	0.91		1.44						
RDOM	0.89	0.04		0.07						
2										
RDEN	0.78	0.08	0.10	0.03					0.03	
DEN	283.20	27.41	36.54	9.14					9.14	
BA	19.34	0.47	0.66	0.10					0.04	
RDOM	0.93	0.02	0.03	<0.01					<0.01	
3										
RDEN	0.78	0.20	0.03							
DEN	372.06	96.01	12.00							
BA	27.97	1.44	0.52							
RDOM	0.93	0.05	0.02							
4										
RDEN	0.98							0.03		
DEN	611.67							15.68		
BA	32.39							0.18		
RDOM	0.99							0.01		
5										
RDEN	0.63	0.28			0.02		0.02	0.05		
DEN	315.19	138.68			12.61		12.61	25.22		
BA	12.42	1.71			0.04		0.16	0.35		
RDOM	0.81	0.11			0.04		0.01	0.02		

Site	*Quercus stellata*	*Quercus marilandica*	*Ulmus crassifolia*	*Fraxinus texensis*	*Prosopis glandulosa*	*Juniperus ashei*	*Sideroxylon lanuginosum*	*Celtis laevigata*	*Prunus mexicana*	*Quercus buckleyi*
6										
RDEN	0.70	0.23	0.07							
DEN	700.34	225.11	75.04							
BA	25.24	2.78	2.52							
RDOM	0.83	0.09	0.08							
7										
RDEN	0.85	0.15								
DEN	446.12	78.73								
BA	25.86	0.97								
RDOM	0.96	0.04								
8										
RDEN	0.58		0.18	0.10		0.15				
DEN	469.39		142.86	81.63		122.45				
BA	28.50		3.32	1.30		5.58				
RDOM	0.74		0.09	0.03		0.14				
9										
RDEN	0.33	0.05	0.35	0.15	0.10	0.03				
DEN	103.78	15.97	111.77	47.90	31.93	7.98				
BA	5.47	0.73	3.07	1.28	0.05	0.80				
RDOM	0.46	0.06	0.26	0.11	0.05	0.07				
10										
RDEN	0.70	0.08	0.13	0.05	0.03				0.03	
DEN	497.11	53.26	88.77	35.51	17.75				17.75	
BA	33.44	1.64	1.88	0.64	0.03				0.19	
RDOM	0.85	0.04	0.05	0.02	0.03				<0.01	

Site	*Quercus stellata*	*Quercus marilandica*	*Ulmus crassifolia*	*Fraxinus texensis*	*Prosopis glandulosa*	*Juniperus ashei*	*Sideroxylon lanuginosum*	*Celtis laevigata*	*Prunus mexicana*	*Quercus buckleyi*
11										
RDEN	0.65	0.08	0.05	0.18	0.05					
DEN	246.68	28.46	18.98	66.41	18.98					
BA	10.44	0.75	1.27	1.56	0.03					
RDOM	0.72	0.05	0.09	0.11	0.03					
12										
RDEN	0.55		0.25	0.05	0.13		0.03			
DEN	364.73		165.79	33.16	82.89		16.58			
BA	13.48		3.33	0.40	0.08		0.22			
RDOM	0.71		0.18	0.02	0.08		0.01			
13										
RDEN	0.20	0.15	0.23	0.30		0.08	0.02			0.02
DEN	71.03	53.27	79.91	106.55		26.64	7.10			7.10
BA	6.03	1.18	1.49	1.84		1.31	0.09			<0.01
RDOM	0.49	0.10	0.12	0.15		0.11	0.01			<0.01
14										
RDEN	0.31	0.63						0.03	0.03	
DEN	230.80	461.59						18.46	23.08	
BA	9.88	8.46						0.27	0.01	
RDOM	0.53	0.45						0.01	0.01	
15										
RDEN	0.75	0.05			0.20					
DEN	297.26	19.82			79.27					
BA	26.30	0.32			0.11					
RDOM	0.88	0.01			0.10					

Site	*Quercus stellata*	*Quercus marilandica*	*Ulmus crassifolia*	*Fraxinus texensis*	*Prosopis glandulosa*	*Juniperus ashei*	*Sideroxylon lanuginosum*	*Celtis laevigata*	*Prunus mexicana*	*Quercus buckleyi*
16										
RDEN	0.75	0.20			0.05					
DEN	247.82	66.09			16.52					
BA	11.70	0.91			0.04					
RDOM	0.91	0.07			0.04					

[a] number of trees of a species, divided by total number of trees of all species (40 at most sites)

[b] total basal area of a species, divided by total basal area of all species

Table 3.4. Post oak regeneration (calculated as the ratio of saplings to trees) at 16 old-growth forest sites in the western Cross Timbers.

Site	Post Oak Sapling:Tree Ratio
1	0.45
2	0.21
3	0.79
4	0.51
5	0.49
6	0.45
7	0.55
8	0.07
9	0.26
10	0.06
11	0.03
12	0.00[a]
13	0.00[a]
14	0.30
15	0.07
16	0.31

[a] no post oak saplings recorded

Chapter 4

Canopy and Understory Dynamics in Old-Growth Forests of the Western Cross Timbers: Succession, Invasion, and Recruitment

ABSTRACT

At two relatively undisturbed old-growth forests (sites A and B) in the western Cross Timbers of Texas, we assessed overstory and understory dynamics through point-quarter sampling; understory sampling; coring, crossdating, and determining age structures for tree species; and computing tree-ring chronologies for post oak (*Quercus stellata*). The two sites were 16 km apart in southeastern Palo Pinto County, Texas, and occupied steep slopes (≥10%) on the same soil series. Post oak made up more than 83% of the canopy at site B, but only 33% at site A. At randomly selected old-growth sites in the western Cross Timbers, sapling:tree ratios <1 indicated post oak recruitment was declining (Chapter 3); however, at site B, we found a sapling:tree ratio of 1.16 for post oak. Age structures for post oak and Ashe juniper (*Juniperus ashei*) did not differ significantly between the two sites, but cedar elm (*Ulmus crassifolia*) age structures were significantly different. At both sites, Ashe juniper age structures were consistent with sapling:tree ratios that suggested invasion; all Ashe junipers sampled were ≤51 years old. Mesquite (*Prosopis glandulosa*) age-structure data, however, did not support an invasion hypothesis. In general, post oak recruitment, ring-width index values (from tree-ring chronologies), and historical climate data displayed similar patterns. Ring-width index values for post oak identified major historical drought periods, and roughly corresponded with pulses and absences of recruitment to breast height, although some recruitment occurred in drought years at site A. For site B, superposed epoch analysis indicated that mean ring-width index values were significantly higher than normal ($p<0.05$) three years prior to recruitment events. Understory composition at two forest locations and two savannah locations at site B resembled the vegetation composition of "relict" sites

assessed in the 1930s-1940s, but an invasive grass had become an important component of the understory, and species indicative of historical overgrazing or other disturbances were also present. Future research in the region should emphasize understanding and managing invasion of old-growth forest overstories and understories.

INTRODUCTION

Old-growth forests in the western Cross Timbers of Texas are characterized by the presence of post oaks that predate European settlement of the area (Chapter 3). Although individual trees have persisted for centuries, old-growth forests are not static (Davison & Forman 1982; Shugart 1984). Succession, variations in recruitment and mortality, anthropogenic and natural disturbances, invasion, climatic fluctuations and trends, and variations in rates of tree growth lead to temporal and spatial changes in the composition and structure of the canopy and understory of old-growth forests (Oliver & Larson 1990).

Most western Cross Timbers forests are dominated by post oak, a slow-growing, long-lived species with annual growth rings that preserve a high-quality climate signal due to extreme sensitivity to temperature and precipitation, particularly along the deciduous forest-prairie ecotone (Stahle & Hehr 1984; Stahle & Cleaveland 1988). Correlation of post oak chronologies with climate data has indicated that a strong, positive radial growth response to increasing precipitation is characteristic of the species, as is a negative growth response to increasing temperature, especially from March through July (the growing season in north Texas; Stahle & Hehr 1984). Sensitivity of post oak to climate makes this species suitable for the development of chronologies, which offer insight into climatic influences on forest dynamics. In addition, other tree species that occur in the western Cross Timbers, though perhaps not as sensitive to climate as post oak, can be crossdated to compute site-specific age structures, which provide additional information about succession in old-growth forests (Shotola et al. 1992). Age structures are also useful in assessing whether invasion—spread of a species into habitats in which it did not historically occur, or increased abundance in habitats in which it was once uncommon—is occurring in old-growth forests (Shotola et al. 1992; Martin 1999; Honnay et al. 2002).

Although analysis of the tree-ring record preserved by relatively old trees can provide one line of evidence for assessing old-growth forest dynamics, there is more to an old-growth forest than just old trees (Johnson 1992). Trees are one part—albeit a conspicuous part—of an old-growth ecosystem, but most of the plant diversity in old-growth deciduous forests occurs in the herbaceous understory (Braun 1950; McCarthy et al. 2001). The woody understory may be the first indicator of changes in forest composition, and interactions between the canopy and understory may determine old-growth forest dynamics (Gilliam & Turrill 1993; Foré et al. 1997; Pacala 1997). Whereas canopy structure and composition have been documented for most types of old-growth forests, relatively little research attention has been directed to quantitative investigations of old-growth forest understories, which are thus poorly understood worldwide (Barnes 1989; Hanley & Brady 1997) (but see Alaback & Juday 1989; McCarthy & Bailey 1996; Small & McCarthy 2002).

Characterizing the herbaceous and woody understory of a relatively unaltered old-growth forest establishes baseline conditions for future assessments of natural and human-induced disturbances and analyses of the mechanisms through which such disturbances alter community composition and structure, and can also be used in assessing changes in composition that have already occurred (if historical data are available) (Miller et al. 2002). In the western Cross Timbers, Dyksterhuis (1948) collected quantitative understory data in the 1930s and 1940s at an array of anthropogenically disturbed sites and "relict" tracts, which were thought to be representative of presettlement vegetation.

Our characterization of old-growth forest structure and composition (Chapter 3) at 16 randomly selected old-growth sites in the western Cross Timbers suggested five questions—all related to forest dynamics—that we sought to address using point-quarter sampling (Cottam & Curtis 1956), tree-ring dating of randomly selected post oaks, development of post oak chronologies, and understory sampling. Based on our sampling of forests throughout the western Cross Timbers and our observations of the diversity that exists among old-growth sites, we selected two study sites within our predictive model area (Chapter 2) that appeared to be among the best representatives of remaining old-growth forests in the region. Research questions were as follows:

1) Do the two high-quality old-growth sites we selected differ in structure or composition from the averages we calculated for 16 randomly selected old-growth sites (Chapter 3)? Does post oak recruitment appear to be in decline at these two high-quality old-growth sites?
2) If post oak recruitment appears to be declining (based on evaluation of sapling:tree ratios and age structures) and successional replacement of post oak as the dominant species appears possible, do the age structures

of any co-occurring tree species indicate the opposite trend—increasing establishment? (i.e., Which species are poised to increase in relative density as succession results in changes in the composition of the tree layer?)

3) Do age-structure data support our preliminary assessment (Chapter 3) that, whereas Ashe juniper appears to be invading old-growth forests in the western Cross Timbers, mesquite does not appear to be increasing in relative abundance?

4) Does post oak recruitment in old-growth forests exhibit patterns that reflect historical variations in radial growth? (i.e., Do episodes of recruitment and lack of recruitment correspond to episodes of above- and below-average radial growth?)

5) What woody and herbaceous understory species currently characterize old-growth forests in the western Cross Timbers? What changes in understory composition have occurred since sampling by Dyksterhuis (1948)?

STUDY AREA

The two old-growth study sites (designated as sites A and B; Figure 4.1) that we selected for forest characterization, development of age structures for post oak and other tree species, and sampling of woody and herbaceous understory vegetation were located within large, contiguous tracts of old-growth forest. Standing, dead trees were common, and neither site showed evidence of grazing by domestic livestock or of direct human disturbance, such as stumps, roads, or fences. Both sites were located on steep (>10%) slopes in southeastern Palo Pinto County, a core area for old-growth forests in the region, according to our predictive model (Chapter 3). Soils at both sites were bouldery sandy loams of the Shatruce series.

Site A, located approximately 1 km from a bend in the Brazos River, included a northwest-facing slope and portions of a rocky creek bed at the bottom of a forested canyon (Figure 4.2). Old-growth forest was the dominant land cover in the canyon, and cliffs and rocky knobs occurred on both sides of the canyon. Six tree species occurred in the canopy of site A—cedar elm, post oak, Texas ash (*Fraxinus texensis*), mesquite, blackjack oak (*Quercus marilandica*), and Ashe juniper.

Site B, located 16 km southwest of site A (Figure 4.3) was situated on a west-facing slope, adjacent to an open-canopy, savannah-like ridgetop forest. The site formed part of an extensive tract of old-growth forest, in which sandstone and conglomerate boulders were abundant on the surface. Only three tree species—post oak, blackjack oak, and cedar elm—occurred in the canopy.

METHODS

Overstory Composition and Dynamics

At each site, we conducted point-quarter sampling (Cottam et al. 1953; Cottam & Curtis 1956; Walters & Williams 1999) of trees (≥10 cm diameter at breast height [DBH]) and saplings (reaching breast height, but <10 cm DBH) at 10 nodes along a 200-m transect and used the resulting data to calculate species-specific and overall forest characterization metrics (e.g., relative density, absolute density, basal area, and sapling:tree ratio), as detailed in Chapter 3. We used a G-test of independence, with Williams' correction (Sokal & Rohlf 1995), to determine whether canopy composition was dependent on site. We also followed the methods described in Chapter 3 to obtain at least 40 cores per site from randomly selected post oak trees ≥10 cm DBH and from additional tree species, which we selected based on their relative abundances at each site (i.e., some species were too infrequent to obtain 40 cores per site). For two potentially invasive species—mesquite and Ashe juniper—we did not restrict our sampling to trees above a minimum DBH threshold because we were interested in young trees, as well as old; we obtained cross sections of stems too small to core. At site A, we obtained at least 40 cores or cross-sections per species of Ashe juniper, cedar elm, mesquite, and Texas ash. At site B, we obtained at least 40 cores or cross-sections per species of Ashe juniper, blackjack oak, and cedar elm. We cored Ashe juniper and mesquite—both of which have multiple stems—as close as possible to the root collar. Other tree species were cored at breast height. All sampling was conducted in May and October, 2003.

For post oak, blackjack oak, cedar elm, and Texas ash, we used crossdating to assign exact calendar years to all annual growth rings (Douglass 1941; Stokes & Smiley 1968). With these results, we computed age structures for each species. We were not able to crossdate mesquite or Ashe juniper because of unclear rings, possible sensitivity to factors other than climate, and missing or false rings (Stokes & Smiley 1968); thus, age structures for these species reflect ring counts only. For the three species we cored at both sites (post oak, Ashe juniper, and cedar elm), we used the Kolmogorov-Smirnov test (Sokal & Rohlf 1981; Webb & Kaunzinger 1993) to compare age distributions of each species between sites.

For post oak, we used standard dendrochronological procedures to develop a tree-ring chronology for each site (Fritts 1976; Cook & Kairiukstis 1990). We used a stage micrometer to measure individual ring widths of all exactly dated annual growth rings, on all 40 post oak cores per site, to the nearest 0.001 mm. With the computer program COFECHA (Holmes 1983) we were able to detect a few errors in crossdating or ring measurement through cross-correlation of series (i.e., dated cores from a site). Errors were corrected through crossdating or re-measurement before we produced tree-ring chronologies. We calculated the mean annual ring width for each site, and we used the computer program ARSTAN (Cook 1985) to produce a mean post oak index chronology for each site (from the mid-1700s through 2000) by removing differences in growth rates and trends among individual trees (i.e., dividing by the value of the detrending curve, fit to each ring-width time series). Ring-width index values of 1.0 reflect average radial growth, and index values above and below 1.0 indicate above- and below-average radial growth, respectively. For the period 1965-2000, during which we had a relatively large sample size of ring widths, we obtained average Palmer Drought Severity Index (PDSI) data for April of each year (because of a strong growth response to temperature and precipitation in that month). We calculated the correlation between each site's chronology and April PDSI. For a given month, PDSI is a weighted average of temperature and precipitation data for that month and preceding months (Stahle & Cleaveland 1988); in general, PDSI values range between -6 (extreme drought) and 6 (extremely wet conditions).

We used superposed epoch analysis (SEA; e.g., Therrell et al. 2004) to compare post oak recruitment and tree-ring chronologies for Sites A and B. Using multiple bootstrap iterations, we compared mean ring-width index values during recruitment years, the ten previous years, and the one following year with all remaining index values. In other words, we determined whether radial growth was significantly above normal in each of the 10 years preceding recruitment events, the year of recruitment, or the year after recruitment, for the period 1763-1959 at site A and 1750-1952 at site B.

Understory Composition

In November, 2003 and April, 2004, we sampled herbaceous and woody understory plant cover in 10 x 10 m quadrats located near the point-quarter sampling transect we established at site B (Peet et al. 1998; Walters & Williams 1999; Verheyen et al. 2003). We established five permanent plots at each of four locations—two old-growth savannah-like sites located on a ridgetop (10-60% canopy cover, on average; Rebertus & Burns 1997), and two steeply sloping, closed-canopy old-growth forest sites. The five, 10 x 10 m plots we established at each of the four sites were contiguous and formed transects 50 m long. For each transect, a random azimuth was selected from the range of bearings that would extend into the old-growth community (Russell & Fowler 1999). Within each 10 x 10 m quadrat, we identified all herbaceous and woody understory species and estimated percent cover (relative amount of surface covered; Dyksterhuis 1948) for each species, on a scale from 1-8: 1=trace (<1%), 2=1-5%, 3=5-10%, 4=10-25%, 5=25-50%, 6=50-75%, 7=75-95%, 8=95-100% (Qian et al. 1997; Peet et al. 1998). We also assessed percent cover by bare rock and bare soil/leaf litter, separately. Herbaceous species for which diagnostic characters were not visible at the time of sampling were identified to genus only. Nomenclature follows Diggs et al. (1999). We deposited voucher specimens of species characteristic of each quadrat at the University of Arkansas Herbarium.

RESULTS

Overstory Composition

At site A, there were 319 trees/ha, for all species combined. Thirty-four percent of the trees we recorded were cedar elm (112 stems/ha), and post oak made up a slightly smaller proportion of the tree layer (33% [104 trees/ha]) (Table 4.1). Texas ash made up 15% of the canopy (48 trees/ha), and mesquite accounted for 10% of all the trees we recorded (32 trees/ha). Blackjack oak and Ashe juniper were uncommon in the tree layer, accounting for 5% (16 trees/ha) and 3% (8 trees/ha), respectively. Post oak accounted for nearly half (5.5 m^2/ha) of the total basal area (11.8 m^2/ha) at site A. As a result, post oak relative dominance (0.46) was disproportionately high, in comparison with its relative density (0.33). Cedar elm, which was slightly more common than post oak in the tree layer, had a basal area of 3.1 m^2/ha; hence, its relative dominance was only 0.25. Texas ash basal area was 1.3 m^2/ha, and its relative dominance was 0.11. All other species had basal areas <1 m^2/ha and dominance values <0.10.

Site A had 543 saplings/ha; overall, there were 1.7 saplings for every tree. Nearly 60% of all saplings were Ashe juniper (312 saplings/ha; sapling:tree ratio=39.1). The next-most-common sapling species was mesquite, which accounted for 18% of all recorded saplings (95 stems/ha) and had a sapling:tree ratio of 3.0. Texas ash made up 13% of the sapling layer (68 stems/ha; sapling:tree ratio=1.4). Post oak accounted for 5% of the sapling layer and had a sapling:tree ratio of 0.5 (27 saplings/ha). Cedar elm was uncommon in the sapling layer (3% of all saplings; 14 stems/ha); its sapling:tree ratio was 0.1. Blackjack oak saplings did not occur at site A.

At site B, for all species combined, there were 436 trees/ha. We found that composition of the tree layer depended significantly on site (G-test; $G_{adj}=300$, $p<0.005$); in other words, sites A and B differed in tree species composition. At site B, post oak made up 83% of all trees (360 stems/ha). Ten percent of all trees were blackjack oak (44 trees/ha), and cedar elm made up 7% of the canopy (33 trees/ha). Total basal area at site B (28.7 m^2/ha) was more than twice that of site A. Post oak accounted for nearly all the basal area at site B (26.5 m^2/ha), and its relative dominance was correspondingly high (0.92). Relative dominance values for blackjack oak and cedar elm were 0.05 and 0.03, respectively.

There were more than three times as many saplings per hectare at site B (1676 saplings/ha) as at site A. The three species present in the tree layer were also present as saplings; in addition, we recorded four species in the sapling layer that did not occur in the tree layer (Texas ash, Ashe juniper, chittamwood [*Sideroxylon lanuginosum*], and sugar hackberry [*Celtis laevigata*]). Forty percent of all saplings at site B were blackjack oak (671 stems/ha), and the sapling:tree ratio for blackjack oak was 15.4. Post oak accounted for 25% of all saplings (420 stems/ha); there were 1.16 post oak saplings for every post oak tree at the site. Texas ash made up 18% of the sapling layer (293 stems/ha). Eight percent of all saplings at site B were Ashe juniper (126 stems/ha). Chittamwood, cedar elm, and sugar hackberry each made up less than 5% of the sapling layer.

Age Structures

For post oak, we dated 42 randomly selected trees (≥10 cm DBH) at site A and 54 randomly selected trees at site B (Figure 4.4). We used linear regression of age against DBH to adjust ages of hollow trees (due to heart rot) or had off-center pith that was missed by the increment borer. At site A, post oak ages ranged from 45 to 255 years. Thirty-nine trees (92.9%) were ≥50 years old, 31 trees (73.8%) were ≥100 years old, 19 trees (46.3%) were ≥150 years old, and five trees (11.9%) were ≥200 years old. At site B, post oak ages ranged from 52 to 263 years. All 54 trees were ≥50 years old, 35 trees (64.8%) were ≥100 years old, 17 trees (31.5%) were ≥150 years old, and eight trees (14.8%) were ≥200 years old. Post oak age structures were not significantly different between the two sites (Kolmogorov-Smirnov test; D=0.22, p=0.18).

We counted annual growth rings (but did not assign exact calendar years to rings) on 40 Ashe juniper cores and cross sections of all sizes (no minimum DBH) from each old-growth site (Figure 4.5). Ashe juniper produces annual growth rings that are typical of conifers—divided into earlywood and latewood, with a sharp boundary between the latewood of one year and earlywood of the following year (Stokes & Smiley 1968). Although our ring counts were likely within five years of the true age for Ashe juniper, crossdating was not possible, primarily due to the occurrence of false rings (Stokes & Smiley 1968). At site A, estimated Ashe juniper ages ranged from 12 to 51 years (mean=25.8, SD=9.4). Twenty-six Ashe junipers (65.0%) were ≥20 years old, and 11 trees (27.5%) were ≥30 years old. At site B, estimated ages of Ashe juniper ranged from 11 to 51 years (mean=23.4, SD=8.9). Twenty-five Ashe junipers (62.5%) were ≥20 years old, and 6 trees (15.0%) were ≥30 years old. Ashe juniper age structures were not significantly different between the two sites (Kolmogorov-Smirnov test; D=0.20, p=0.36).

For cedar elm, we dated 40 cores from site A and 36 cores from site B (Figure 4.6). At site A, cedar elm ranged in age from 48 to 201 years (mean=117.5, SD=45.8). Twenty-two cedar elms (55.0%) were ≥100 years old, and 10 cedar elms (25.0%) were ≥150 years old. At site B, cedar elms ranged in age from 55 to 198 years (mean=99.1, SD=36.5). Thirteen cedar elms (36.1%) were ≥100 years old, and three (8.3%) were ≥150 years old. Cedar elm age structures were significantly different at the two sites (Kolmogorov-Smirnov test; D=0.31, p=0.046).

Blackjack oak was not abundant enough at site A to obtain 40 cores, so we determined the age structure for this species only for site B (Figure 4.7). Blackjack oaks ranged in age from 15 to 104 years (mean=63.7, SD=19.8). Thirty-one trees (77.5%) were ≥50 years old, 6 trees (15.0%) were ≥80 years old, and three trees (7.5%) were ≥100 years old.

We determined the age structure for mesquite by counting annual rings (rather than assigning exact calendar years to rings) on 38 cores from site A only (mesquite did not occur at site B) (Figure 4.8). Mesquite ages ranged from 6-112 years (mean=42.4, SD=23.9). Twenty-six mesquite trees (68.4%) were ≥30 years old, 10 trees (26.3%) were ≥50 years old, and two trees (5.3%) were ≥100 years old. Mesquite is a ring-porous species, and although it forms annual growth rings, the rings are faint and indistinct in structure; in general, crossdating is not considered possible for mesquite (Martinez 2000).

For Texas ash, we computed the age structure using 38 exactly dated cores from site A only (Figure 4.9). Texas ash ages ranged from 44 to 115 years (mean=71.7, SD=14.9). Thirty-five trees (92.1%) were ≥50 years old, 20 trees (52.6%) were ≥70 years old, and three trees (7.8%) were ≥100 years old.

Post Oak Chronologies

For post oak at each old-growth site, during the period 1750-2000, we compared annual recruitment to breast height with 1) mean annual ring-width measurements (in mm) from all post oak cores at that site, and 2) the post oak ring-width index from the site (Figure 4.10; Villalba & Veblen 1997). At site A, our sampling indicated possible "pulses" of post oak recruitment from 1829-1850 and from 1892-1911. Post oak recruitment did not occur in our sample from site A during the intervals 1785-1801, 1818-1828, 1864-1871, 1878-1888, 1912-1927, and 1944-1959. An apparent lack of recruitment since 1959 reflects, in part, our minimum sampling size of 10 cm DBH (i.e., trees <45 years old were generally <10 cm DBH) (Webb & Kaunzinger 1993). For the period 1750-2000, overall mean ring width for site A was 0.5 mm. Annual mean ring widths were greatest in 1784, 1868-1870, 1888-1892, 1970, and 1998. Ring widths remained above average during the episode of recruitment from 1829-1850, but fluctuated around the mean during the apparent episode of recruitment from 1892-1911. A sustained gap in post oak recruitment at site A was roughly coincident with a major regional drought in the 1950s (Stahle & Cleaveland 1988), but we did record post oak recruitment during the 1850s-1860s drought. Also, from 1864-1871, no post oak recruitment occurred, but mean radial growth peaked. When the effects of variation among individual trees were removed (in the ring-width index), however, the radial growth "peak" around 1870 was less pronounced. Mean ring-width values and index values before 1800 were calculated using relatively few trees, so comparisons with recruitment should be made in the context of a small sample size.

For site A, the correlation coefficient (*r*) between the ring-width index and April PDSI was 0.73 (Figure 4.11). We used only the period 1965-2003 for this calculation because of the relatively large sample size for that portion of the chronology (38 of 42 trees). High April PDSI values were usually reflected in below-average ring-width index values (e.g., for 1968, 1975, 1982, 1992, 1995, and 1997). There was also a close correspondence between below-average index values and low April PDSI for some individual drought years, including 1971, 1984, and 1996. For other drought years, such as 1967, 1978, and 2000, April PDSI suggested conditions for tree growth were even worse than the tree-ring index values indicated.

At site B, overall mean ring width was 0.75 for the period 1750-2000. Post oak recruitment episodes apparently occurred from 1800-1819 and 1870-1906 (Figure 4.12). Ring-width index values were relatively high during most of the latter period, and the year of highest post oak recruitment (1919) occurred three years after a peak in radial growth. Sustained, above-average mean ring-width values from 1750-1780 were due primarily to our small sample size during that interval (i.e., few trees dated to years before 1780). For the same period, however, ring-width *index* values (after removal of individual variation) fluctuated around the mean, indicating a dampening of the sample-size effect. Post oak recruitment did not occur at site B from 1852 to 1865, roughly coincident with a major drought (Stahle & Cleaveland 1988) and with a prolonged period of below-average radial growth. Effects of the 1950s drought were not evident in the recruitment data for this site because we did not core any trees <52 years old; however, that drought was reflected in below-average ring-width values.

For site B, during the period 1965-2003, the correlation coefficient (r) between April PDSI and the ring-width index was 0.71 (Figure 4.13). As at site A, years of above-average index values generally corresponded to above-average April PDSI, with the exception that the magnitude of PDSI peaks sometimes exceeded the magnitude of peaks in the ring-width index (e.g., for 1982, 1992, and 1995). Years of below-average conditions for tree growth at site B were reflected in both the ring-width index and PDSI values (e.g., for 1967, 1971, 1978, 1984, 1988, 1996, and 2000).

We used superposed epoch analysis as another, more explicit way to compare radial growth by post oak with recruitment. For the period 1763-1959, superposed epoch analysis for site A did not indicate the occurrence of higher-than-normal ring-width index values in the 10 years preceding post oak recruitment events, or the year following recruitment (Figure 4.14). In contrast, for site B, during the period 1750-1952, radial growth by post oak trees was significantly above normal three years before recruitment occurred (Figure 4.14; mean ring-width index value in year -3=1.119, $p<0.05$).

Herbaceous and Woody Understory

In all, we recorded 78 herbaceous and woody understory species at site B (Table 4.2). Of those, 42 (53.8%) were forbs (erect, broad-leaved herbaceous plants [Walters & Williams 1999]), 23 (29.5%) were graminoids (grasses and sedges), and seven (9.0%) were tree seedlings or saplings. Vines, shrubs, and ferns were each represented by two species (2.6%). Six species (7.7%) were recorded only in forest quadrats, 38 (48.7%)

were recorded only in savannah quadrats, and 34 (43.6%) were recorded in at least some quadrats in both forest and savannah. The 78 species we recorded represented 33 families; the best-represented families, overall, were Poaceae (22 species [28.2%]) and Asteraceae (9 species [11.5%]).

At savannah site 1, bare rock covered 10-25% of each of the five quadrats, and bare soil and leaf litter (combined) covered an additional 10-50% (10-25% in two quadrats, 25-50% in three quadrats). Canopy cover ranged from 5-40%. We recorded 53 species at this savannah site (Table 4.3). The understory species with the highest values for percent cover were grasses: *Sporobolus pyramidatus* (whorled dropseed), *Bouteloua curtipendula* (side-oats grama), and *Eragrostis intermedia* (plains love grass). Each accounted for 5-10% cover of quadrats in which it was present; *S. pyramidatus* was present in all five quadrats, *B. curtipendula* was present in four quadrats, and *E. intermedia* was present in two quadrats. In addition to *S. pyramidatus*, five understory species were present in all five quadrats: *Allium canadense* (wild onion), *Carex microdonta* (small-tooth caric sedge), *Lepidium densiflorum* (prairie pepperweed), *Panicum hallii* (Hall's panic), and *Vicia ludoviciana* (deer pea vetch), but none made up more than 5% cover in any quadrat. Thirty-four species (64.2%) each accounted for "trace" proportions of surface cover (<1% cover in a quadrat), and of those, 16 were present in only one quadrat.

At savannah site 2, bare rock covered 5-10% of four quadrats, but was not present in one quadrat. Bare soil and leaf litter covered 5-25% of each of the five quadrats. Canopy cover ranged from 2-55%. We recorded 52 species (Table 4.4), including 22 species not present at savannah site 1 (i.e., the two savannah sites had 30 species in common). *Schizachyrium scoparium* (little bluestem) was the most common understory species, accounting for 25-50% cover in all five quadrats. Two other grasses—*Bothriochloa ischaemum* (King Ranch bluestem) and *Aristida longespica* (slim-spike threeawn)—were also relatively common, covering 10-50% and 10-25% of each quadrat, respectively. *Chaetopappa asteroides* (common least daisy; 5-10% cover in all five quadrats) was the only other species accounting for more than 5% cover in any quadrat. Ten species accounted for 1-5% cover of quadrats in which they were present; those included eight grasses, as well as seedlings and saplings of post oak and Ashe juniper. *Erigeron strigosus* (prairie fleabane), *Panicum hallii*, *Panicum oligosanthes* (Scribner's rosettegrass), *Allium canadense*, and *Verbena halei* (slender vervain) were present in all five quadrats, but none accounted for more than 5% cover. Thirty-eight species (73.0%) each accounted for <1% cover, and 19 of those were recorded in only one quadrat.

At forest site 1, bare rock and bare soil/leaf litter each accounted for 10-50% of all five quadrats. Canopy cover ranged from 65-85%. We recorded 24 understory species (Table 4.5), and 17 of those (70.8%) each accounted for less than 1% cover. The most common understory species was *Bothriochloa ischaemum*, which made up 10-25% of the cover in all five quadrats. Three other species each accounted for more than 5% cover in each quadrat—*Smilax bona-nox* (saw greenbrier) and seedlings and saplings of post oak and Texas ash. Three species—*Panicum hallii*, *P. oligosanthes*, and *Allium canadense*—each made up 1-5% cover.

In all five quadrats at forest site 2, bare rock covered 10-25% of the surface, and bare soil/leaf litter covered an additional 25-50%. Canopy cover ranged from 70-90%. Of the 34 understory species we recorded (Table 4.6), the three most common were post oak, cedar elm, and Texas ash (seedlings and saplings). Nineteen of the 34 species recorded at this site also occurred at forest site 1. Post oak seedlings or saplings were present in all five quadrats, accounting for 5-25% cover. Cedar elm and Texas ash were each present in the understory of four quadrats, accounting for 10-25% cover and 5-25% cover, respectively. Two species—Ashe juniper and *Cirsium texanum* (Texas thistle)—accounted for 5-10% cover in three quadrats and one quadrat, respectively. Four species each accounted for up to 10% cover: *Bothriochloa ischaemum*, *Panicum oligosanthes*, *Smilax bona-nox*, and *Lespedeza cuneata* (sericea). *Cynanchum laeve* (bluevine) covered 1-5% of two quadrats. *Carex microdonta*, *Cheilanthes tomentosa* (woolly lip fern), and *Oxalis stricta* (sheep showers) were present in all five quadrats, but each made up <1% cover. Twenty-one other species each accounted for <1% cover, and 11 of those were recorded only once.

DISCUSSION

Forest Composition, Succession, and Invasion

Old-growth sites A and B differed dramatically in composition of the tree and sapling layers. Whereas post oak accounted for 83% of the tree layer at site B, only 33% of randomly sampled trees at site A were post oaks. Mean relative density of post oak at all randomly sampled old-growth sites was 0.64, and the lowest relative density we recorded for post oak was 0.20 (Chapter 3). Because sites A and B occurred on the same soil series, we suspect that the difference in post oak frequency may be related to slope and/or aspect; dominance of drought-tolerant post oak may be highest under the most harsh conditions for tree growth. Trees growing at site A, which faced northwest and had a slope of 10.8%, may experience more favorable temperature and moisture conditions than those growing on the 32.9%, west-facing slope at site B. The occurrence of only three species in the canopy of site B (the other two were blackjack oak and cedar elm) supports our hypothesis that conditions for tree growth are harsh at this site.

At site A, with the exception of blackjack oak, all species present in the canopy were also present as saplings. Ashe juniper was uncommon (3%) in the tree layer, but made up 58% of the sapling layer; thus, unless sapling mortality is high or longevity is low, Ashe juniper will become more frequent in the tree layer in the future. Post oak made up only 5% of the sapling layer, and its sapling:tree ratio (0.55) suggested that the frequency of post oak in the canopy may decline in the future (unless regeneration is strongly episodic [Chapter 3]). At site B, four species not present in the tree layer were represented by saplings—Texas ash, Ashe juniper, chittamwood, and sugar hackberry. Blackjack oak, which made up only 7% of the tree layer at site B, accounted for 50% of all saplings (sapling:tree ratio of 15.4). The topographic or environmental factors responsible for the difference in frequency of blackjack oak saplings at these two sites are unclear, but might be related to the more severe conditions inferred for site B. Although post oak made up only 25% of the sapling layer at site B, there were so many saplings (three times more than at site A) that the sapling:tree ratio for post oak was 1.16. None of the randomly selected old-growth sites had post oak sapling:tree ratios >0.79; site B was the only old-growth forest we sampled in the western Cross Timbers in which succession did not appear likely to result in declines in post oak dominance.

Despite differences between sites A and B in the relative density of post oak trees and saplings, we did not find differences in post oak age structures between the sites. Post oak was much more common in the tree layer at site B than at site A, but the range of post oak ages was similar (45-255 years at site A, 52-263 years at site B). The sapling:tree ratio for post oak was lower at site A, which suggested that relatively few young post oaks would occur there; however, because we cored only post oaks ≥10 cm DBH (which were usually older than 50 years), we could not compare the ages of the youngest post oaks at the two sites. We did find a smaller proportion of post oaks <150 years old at site A, and this result is consistent with our assessment of lower post oak recruitment at the site. To address directly questions about post oak recruitment and successional changes in composition, future research priorities should include determining the absolute density of post oak seedlings in old-growth stands and dating cores from post oaks <10 cm DBH.

We hypothesized that if the relative density of post oak was in decline in old-growth forest canopies (as we suspect is the case for site A and all of the randomly selected old-growth sites), age structures of some other tree species should indicate trends toward increasing relative density in the tree layer (i.e., relatively more young trees). We believed that tree-ring data would be a valuable addition to our point-quarter sampling results in assessing possible changes in old-growth forest composition. In an undisturbed forest in New York, Martin (1999) cored trees and constructed age structures to determine whether Norway maple (*Acer platanoides*) was invading a stand and displacing sugar maple (*Acer saccharum*). In a New Jersey forest preserve, Webb and Kaunzinger (1993) combined that approach—coring trees, counting rings, and determining age structures—with sampling of seedlings and saplings to assess Norway maple invasion. Shotola et al. (1992) determined size-class distributions for species in an old-growth forest in southern Illinois to assess regeneration and changes in forest composition and structure.

Our research is the first examination of the possibility of tree invasion into old-growth forests of the western Cross Timbers, and the first to document age structures for species other than post oak in the region's old-growth forests. At old-growth study sites A and B, our point-quarter data suggested that Ashe juniper made up a larger proportion of the sapling layer than the tree layer, so we suspected Ashe juniper invasion at both sites. We also sought to evaluate the possibility of invasion by mesquite, which occurred only at site A.

At both sites A and B, 62-65% of all Ashe junipers were ≥20 years old, but the oldest Ashe junipers were only 51 years old. The relatively young age of all the Ashe junipers we sampled is consistent with our invasion hypothesis. Ashe juniper age structures did not differ between sites, but Ashe juniper was a component of the tree layer (i.e., Ashe junipers ≥10 cm DBH occurred) only at site A. Perhaps the lower slope and northwest aspect of that site resulted in conditions that favored more rapid growth than at the steeply sloping, west-facing site B.

There is no published record of the longevity of Ashe juniper; however, eastern redcedar (*Juniperus virginiana*) trees >500 years old are known to occur in the Oklahoma Cross Timbers (D. Stahle, personal communication). A relatively short life span for Ashe juniper is an alternative to our invasion hypothesis, although a life span significantly shorter than that of eastern redcedar seems unlikely. That alternative explanation could be addressed by selectively coring the largest Ashe juniper trees at old-growth sites on Shatruce soils (or similar series) in the region and determining their ages. If Ashe juniper is long-lived in the western Cross Timbers, site A may undergo a dramatic change in composition as abundant saplings recruit to the tree layer, particularly if post oak dominance is simultaneously declining (as our data suggest). At site B, the potential for changing composition due to invasion by Ashe juniper seems more modest (at least in the near future), due to the relatively low proportion of Ashe juniper in the sapling layer.

Ashe juniper is native to Texas, where it historically occurred mainly in the Edwards Plateau region (Fuhlendorf et al. 1997). On Texas rangelands, however, Ashe juniper density is increasing, and its distribution is expanding (Hicks & Dugas 1998). Together, Ashe juniper and eastern redcedar have invaded approximately 8.9 million ha in the state, and existing control measures have proved effective for only 10-20 years (Owens & Schliesing 1995). Large Ashe juniper trees are sensitive to drought (90% died on the Edwards Plateau during a major drought in the 1950s [Young 1956; Merrill & Young 1959]), but trees <2 m tall can survive drought conditions. Ashe juniper is also sensitive to fire, particularly when trees are <15 years old, and fire suppression is cited as one of the primary reasons for Ashe juniper invasion of rangelands in Texas (Diamond et al. 1995; Fuhlendorf et al. 1996). Because 95% of the seed rain from Ashe juniper trees remains within 5 m of the parent tree (Owens & Schliesing 1995), avian dispersal may be the primary source of Ashe juniper invasion into old-growth forests. In winter, frugivorous birds such as American Robins (*Turdus migratorius*) and Cedar Waxwings (*Bombycilla cedrorum*) eat Ashe juniper fruits and disperse the seeds (Owens & Schliesing 1995). The leaves, however, contain secondary chemicals that discourage browsing by wildlife and domestic cattle (Fuhlendorf et al. 1997). Ashe juniper invasion can convert savannahs to closed-canopy stands, resulting in lower understory diversity and dramatically altering the community (Fuhlendorf et al. 1997; Yager & Smeins 1999). Because two lines of evidence suggest that Ashe juniper is invading old-growth forests in the western Cross Timbers, we suggest that this phenomenon should be a top research and conservation priority for the region. Examination of historical accounts or photos might be useful in determining the longevity of Ashe juniper in the western Cross Timbers.

Mesquite, which is considered a problematic invader of grasslands in Texas (Diggs et al. 1999), made up 10% of the tree layer and 18% of the sapling layer at site A. The sapling:tree ratio for mesquite was 2.98. Whereas the oldest Ashe junipers we cored were 51 years old, we found mesquite trees more than 115 years old at site A. Although most (73.7%) of the mesquites we cored were <50 years old, that finding alone is insufficient to support a hypothesis of invasion. Moreover, we did not record mesquites of any age at site B. We suggest that mesquite invasion in Texas may be more problematic on rangelands, and that old-growth forest invasion may be less likely in the absence of overgrazing or major human disturbances.

Although cedar elm, blackjack oak, and Texas ash are not considered invasive, we determined age structures for each species for comparison with our point-quarter sampling results, and to provide baseline age-structure data for assessing future changes. If the relative abundance of post oak is declining, age structures for these species might be expected to indicate relatively large proportions of young trees.

Cedar elm age structures at sites A and B differed significantly, even though their age ranges were similar (48-201 years at site A, 55-198 years at site B). On average, cedar elms were 18 years older at site A than at site B. Whereas one-fourth of the cedar elms we cored at site A (10 trees) were ≥150 years old, only 8.3% (3 trees) of those at site B exceeded 150 years in age. In addition, nearly 20% more trees at site A were ≥100 years old. Cedar elm longevity may be lower at site B, where several lines of evidence suggest temperature and moisture conditions may be less favorable for tree growth. Because most cedar elms ≥10 cm DBH were ≥50 years old, we could not use age-structure data to evaluate our point-quarter sampling results, which suggested a scarcity of young cedar elms at site A. Including trees <10 cm DBH in the age structure would allow an evaluation of whether cedar elm is likely to become less common in old-growth forests of the western Cross Timbers.

We cored blackjack oak only at site B, where it made up 10% of the tree layer, but 40% of the sapling layer (sapling:tree ratio = 15.37). Blackjack oak does not appear to live as long as post oak (Stahle & Hehr 1984); the maximum age we recorded at site B was 104 years, and 85% of the trees we cored were <80 years old. Because we employed a 10-cm minimum DBH requirement for sampling, most (77.5%) of the blackjack oaks we cored were ≥50 years old. Although the DBH minimum prevented us from determining the proportion of relatively young trees, the age structure for blackjack oak drops off rapidly at about 65 years. Even if blackjack oaks live only to 105 or 110 years in the western Cross Timbers, it appears that the percentage of young trees is disproportionately high, and blackjack oak may be expected to increase in abundance at site B (in the absence of extreme mortality events, such as might result from drought).

We cored Texas ash only at site A, where it was present in nearly equal percentages in the sapling and tree layers (15% of the tree layer, 13% of the sapling layer). More than half of all Texas ash trees were ≥70 years old, but fewer than 10% were

≥80 years old. The oldest Texas ash was nearly 120 years old. We do not have any evidence to suggest that Texas ash is increasing in relative abundance at site A; however, at site B, where the species was not present in the canopy (and trees ≥10 cm DBH were not available for coring), Texas ash made up 18% of the understory and may become an important component of the canopy. Our data will be essential in future evaluations of forest succession at this site. To make more explicit predictions about succession and tree invasion in old-growth forests of the western Cross Timbers, future researchers will need to quantify seedling abundance for all tree species and determine complete age structures, which must include trees <10 cm DBH.

Post Oak Chronologies and Recruitment

In general, post oak recruitment, ring-width values, and April PDSI displayed similar patterns. For trees in northern Patagonia, Villalba and Veblen (1997) compared radial growth of trees in with age structures and found that overall, age-structure peaks coincided with above-average radial growth (indicating increased establishment or decreased mortality), and lack of recruitment coincided with below-average radial growth. The same may be true for the two old-growth sites we sampled. Villalba and Veblen (1997) indicated that tree growth might lag behind climatic variation, and we found that in the western Cross Timbers, "pulses" of post oak recruitment seemed to follow several years after peaks in April PDSI or radial growth. Specifically, at site B, radial growth was significantly above normal three years before post oak recruitment occurred.

The effects of major historical droughts in Texas may be seen in an examination of our post oak age structures. The most severe period of consecutive droughts since 1698 in Texas occurred from 1951-1956 (Stahle & Cleaveland 1988), and our data indicated an absence of post oak recruitment to breast height from 1950-1960 at site A (at site B, our data do not indicate any recruitment after 1950). There was also a prolonged drought in northern Texas from 1855-1864 (Stahle & Cleaveland 1988), and although post oak recruitment did not occur during that period at site A, we did record recruitment at site B. The post oak chronology for site A also indicates an absence of recruitment in the 1770s, which Stahle and Cleaveland (1988) cite as one of the three driest decades in Texas history. During the wettest decade (1791-1800; Stahle & Cleaveland 1988), however, we did not observe a peak in radial growth or a pulse in recruitment. Instead, we found episodes of recruitment from 1800-1820 at site A and from 1800-1810 at site B; we suspect that these pulses were related to increased rainfall in the 1790s, and that the biological response lagged behind the change in growth conditions. Because we recorded recruitment to breast height, rather than seedling establishment, we would expect a lag between climate signals (as evidenced by changes in radial growth) and effects on recruitment. For both sites, the recruitment, or lack thereof, that we recorded, is not well defined by our sample size of 40 post oaks per site. Overall, at site A, the connection between radial growth (and presumably climate) and post oak recruitment was more ambiguous than at site B, where we have hypothesized that relatively harsh conditions prevail, and where two lines of evidence indicated a relationship between radial growth and post oak recruitment.

Previously, we found evidence of a decline in post oak recruitment after the late 1800s in old-growth forests of the western Cross Timbers (Chapter 3). The decline was most evident when data from 16 randomly selected sites were pooled. At both sites A and B, recruitment pulses occurred in the late 1800s and early 1900s, but our age-structure data did not clearly indicate a decline in recruitment. Ring-width index values, which were highly correlated with April PDSI, did not indicate any climate trend since the late 1800s that might account for lower recruitment. If such a decline is occurring, its cause is more likely anthropogenic than climatic, and we suggested several human-induced changes that might be related to recruitment declines (Chapter 3).

We hypothesized that relatively harsh climatic conditions at site B were responsible for extreme dominance by post oak, low canopy species richness, and shorter life spans of some tree species. If conditions for tree growth were less favorable at site B, we would expect the annual growth rings of post oak to be smaller, on average, than those from trees at site A. Mean ring width was not significantly different at sites A and B, so our chronologies do not directly address that hypothesis. It remains unclear what topographic or environmental factors are responsible for the relatively species-poor canopy of site B and for the site's unusually high post oak sapling:tree ratio.

Understory Changes Since Dyksterhuis (1948)

In 1939, Dyksterhuis (1948) sampled the vegetation of the western Cross Timbers along 123 km of transects (3 sample plots/km)—including one transect that was 45.5 km long—that spanned portions of Jack, Clay, Archer, Young, and Parker counties. The results were used to describe "average floristic composition" of the region. Dyksterhuis

(1948) also identified six "relict" tracts that had not been grazed for at least 10 years, and had never been overgrazed, cultivated, or cleared. Four of the six relict tracts had burned at least once during the preceding 10 years, and Dyksterhuis (1948) reported that ring counts demonstrated the establishment of "veteran" post oak trees before European settlement (ring counts were not published). Relict sites were sampled in 1938 or 1939, and again from 1943-1945. Two of the relict sites were in areas of gentle relief, two occurred on flat relief, and two were on rough relief and had rocks and gravel on the surface—the same topography that characterized our study site B in southeastern Palo Pinto County. The two rough-relief sites sampled by Dyksterhuis were in Jack County (just north of Palo Pinto County); however, Dyksterhuis (1948) concluded that understory vegetation was similar in composition throughout the "fringe" of the western Cross Timbers (680,000 ha of rough relief, as opposed to the relatively level terrain of the "main belt," which differed in understory composition—but not overstory composition—from the fringe).

No published studies have quantified vegetation of the western Cross Timbers since 1948. We sampled understory vegetation in 20, 10 x 10 m quadrats at site B, including two steeply sloping forest locations and two savannah-like sites atop a ridge. Dyksterhuis (1948) described relict sites as having a sparse overstory, and photographs of relict sites indicated they were savannah-like; we suspect the ridgetop sites we sampled were more similar in topography to those sites than were our forest slope sites, and thus more appropriate for comparison with the historical data. Dyksterhuis sampled vegetation in 9.3-m^2 circular areas, and determined average percent cover for all species present (except those accounting for less than 0.5%). Because our sample size was small, and because Dyksterhuis (1948) did not report raw data for each sample plot or the number of sample plots that figured into the reported averages, we did not assess statistically significant differences in composition between the relict sites and our sites. Instead, we made qualitative comparisons of differences among “average” vegetation in 1939, relict vegetation in the 1930s-1940s, and the vegetation of site B in 2003-2004.

Dyksterhuis (1948) did not report cover by bare rock or bare soil/leaf litter, but one of our most notable results was that the combination of bare rock and bare soil/leaf litter accounted for a higher percent cover than the most common understory species, combined. For most quadrats, percent cover of bare rock alone exceeded percent cover by any one plant species. At the two savannah locations, seven species each made up more than 5% of the understory vegetation, and six of those were grasses. At the two forest sites, six of the nine species that accounted for more than 5% of the vegetation were trees (seedlings and saplings); the only relatively common grass (*Bothriochloa ischaemum*) within forest quadrats occurred at forest site 1. The most common species at any site, in terms of percent cover, was *Schizachyrium scoparium* (25-50% of quadrats at savannah site 1). At all four sampling locations at site B, more than half of all species made up “trace” proportions (<1%) of the understory. Only two forbs made up more than 5% of the understory at a sample site, but most “trace” species were forbs.

At the two relict sites sampled by Dyksterhuis (1948) in the region of rough relief, *Schizachyrium scoparium* made up 47-70% of the understory; the only other species that made up more than 5% of the understory were *Sorghastrum nutans* (Indiangrass), *Bouteloua curtipendula*, *Bouteloua hirsuta* (hairy grama), *Sporobolus* sp. (dropseed), and post oak seedlings. Along the transects Dyksterhuis sampled through non-relict areas (representing "average" vegetation) in the western Cross Timbers, *Schizachyrium scoparium* made up less than 1% of the vegetation, whereas annual forbs (<1% of relict sites) accounted for nearly 20%, and annual grasses accounted for 16% of the understory. Post oak and blackjack oak accounted for 26% of the vegetation (compared with 6% at relict sites). Dyksterhuis (1948) attributed this "almost complete change in composition of vegetation" primarily to overgrazing and, to a lesser extent, to fire suppression.

Our descriptions of the understory in two steeply sloping old-growth forest areas will be useful as baseline data for future assessments of the effects of human disturbance, and represent the first characterization of the understory at the steep, rocky sites on which most of the region's remaining old-growth occurs. These sloping forest sites, however, were not appropriate for comparison with either the relict or "average" vegetation sampled by Dyksterhuis (1948) because most of the understory at both forest sites consisted of tree seedlings and saplings. This does not appear to reflect a change since the 1930s, but rather differences in topography between our forest sites and the sites sampled by Dyksterhuis. At our forest sites, canopy cover was too great to allow for a grass understory.

Composition of the two savannah sites we sampled did not resemble the average, overgrazing-induced vegetation reported by Dyksterhuis (1948) from cross-country sampling. Instead, the two savannah sites had four grasses in common with the most abundant species recorded by Dyksterhuis at relict sites—*Schizachyrium scoparium*, *Bouteloua curtipendula*, *B. hirsuta*, and *Sporobolus* spp. We did not observe the other common grass at relict sites—*Sorghastrum nutans*—in any quadrat. When we omitted coverage by bare rock and bare soil/leaf litter, and considered only the vegetated area of each quadrat, the proportion of *Schizachyrium scoparium* at savannah site 2 was within the range Dyksterhuis reported for the two relict sites (47-70%). As a proportion of total vegetated areas per quadrat, *Bouteloua curtipendula*, *B. hirsuta*, and *Sporobolus* spp. percent coverages were also within the ranges reported for relict sites. Dyksterhuis (1948) reported that annual forbs were almost absent from relict sites, but did not list species present only in trace proportions; thus, we could not assess whether more annual forb species occurred at the two savannah locations we sampled than at relict sites. In the only other published study of understory vegetation in the Cross Timbers, Johnson and Risser (1975) reported that herbaceous vegetation was sparse in the understory of an open-canopy forest in Oklahoma. The herbaceous understory, which was composed of 27 species, resembled a tallgrass prairie and was dominated by *Schizachyrium scoparium*, *Andropogon gerardii*, and *Sorghastrum nutans* (Johnson & Risser 1975).

Bothriochloa ischaemum (widely known as KR bluestem), which occurred at all four sites (forest and savannah), is native to central and eastern Asia, and is considered a pernicious invasive species (Diggs et al. 1999). *B. ischaemum* did not occur in the western Cross Timbers at the time of Dyksterhuis' sampling, but we found that the species accounted for 1-5% of savannah site 1, 10-25% of savannah site 2, 10-25% of forest site 1, and 1-10% of forest site 2. In quadrats at savannah site 2, *B. ischaemum*—considered a threat to native species (Diggs et al. 1999)—was as abundant as *Schizachyrium scoparium*. The presence of this exotic grass in both forest and savannah sites should be a cause for concern among private landowners, as well as conservation and management agencies.

The only other non-native species we recorded was *Eragrostis pilosa* (India love grass), which was introduced to the United States from Europe and Asia; it occurred in trace proportions of the understory at savannah site 1. We recorded two annual species of *Aristida* (*A. longespica* and *A. oligantha* [oldfield threeawn]), which were absent from relict sites and are known to increase under grazing (Dyksterhuis 1948). *A. longespica* was one of the most common species at savannah site 2, accounting for 10-25% of the understory. We also recorded *Nassella leucotricha* (winter grass) and *Chloris verticillata* (tumble windmill grass) at savannah sites 1 and 2, respectively. Dyksterhuis (1948) noted the absence of these species from relict sites in 1939; both are characteristic of sites exposed to heavy grazing or other disturbances (Hatch & Pluhar 1993).

Our results from sampling two savannah locations at site B suggest that, although several native grasses occurred in proportions similar to those recorded from relict sites in 1939, composition of the understory has been affected by historical grazing, and both savannah understories have been invaded by *Bothriochloa ischaemum.* Future research should assess the potential for controlling *B. ischaemum* in old-growth savannah sites in the western Cross Timbers, and the potential long-term changes in the understory due to invasion.

Milbau et al. (2003) and Lodge (1993) emphasize that invasion occurs as a result of biological and ecological characteristics of exotic species, combined with the "invasibility" of the target ecosystem. Old-growth forests have been reported to resist plant invasion because of low light availability and intact substrates (Brothers & Spingarn 1992; McCarthy et al. 2001), but light availability would not limit invasive plants in the old-growth savannahs we sampled. Brothers and Spingarn (1992) suggest that xeric, upland woodlands, in which light availability is high (such as ridgetop savannahs in the western Cross Timbers) would be more susceptible to invasion than closed-canopy forests. Edge effects also play a role in determining the outcome of interactions between invasive species and forest understories (Harris 1984). Honnay et al. (2002) found that most weedy plant species did not penetrate farther than 3 m into a forest, but that some invasive species extended 20 m into a forest at south-facing edges. In the western Cross Timbers, where most savannahs on level ground have been cleared for cattle grazing, edge effects may be important in determining invasibility of upland old-growth forests.

In some old-growth forests with canopies that appear to represent presettlement composition, understory vegetation has been altered since European settlement (Davison & Forman 1982; Barnes 1989). For the western Cross Timbers, however, our data do not indicate a dramatic change in the understory of old-growth post oak savannah sites (with respect to historical data from relict sites [Dyksterhuis 1948]). Because Dyksterhuis (1948) does not appear to have sampled the understory of steeply sloping, heavily forested sites, we do not have benchmarks for directly assessing understory changes on that type of site, which characterizes most remaining old-growth. Understory species indicative of disturbance, or lack thereof, are not well known for old-growth forests in the region (i.e., most species indicative of overgrazing are grasses, which are much less abundant than forbs in old-growth forests). Hence, monitoring of old-growth forest and savannah understories should be a research priority in the western Cross Timbers. In addition, the range of variation in the understory of old-growth forests throughout the western Cross Timbers is unknown, as are the environmental and topographic factors responsible for differences among old-growth understories. Forest understory composition has been shown to be related to soil drainage (Pausas 1994; Qian et al. 1997), slope (Small & McCarthy 2002), overstory species composition (Berger & Puettmann 2000), stand age (Hanley & Brady 1997), and aspect (Olivero & Hix 1998; Small & McCarthy 2002). Future research in old-growth forests of the western Cross Timbers might consider these influences on understory composition. Aspect influenced tree and sapling composition in the western Cross Timbers (Chapter 3), and we suspect that aspect also influences herbaceous understory composition in this ecosystem. Differences in understory composition have also been recorded between "ancient and recent" (or "young and immature") forests (Qian et al. 1997; Bossuyt et al. 1999; Verheyen et al. 2003). Sampling of second-growth forests in the western Cross Timbers would be useful in evaluating understory dynamics following anthropogenic disturbances.

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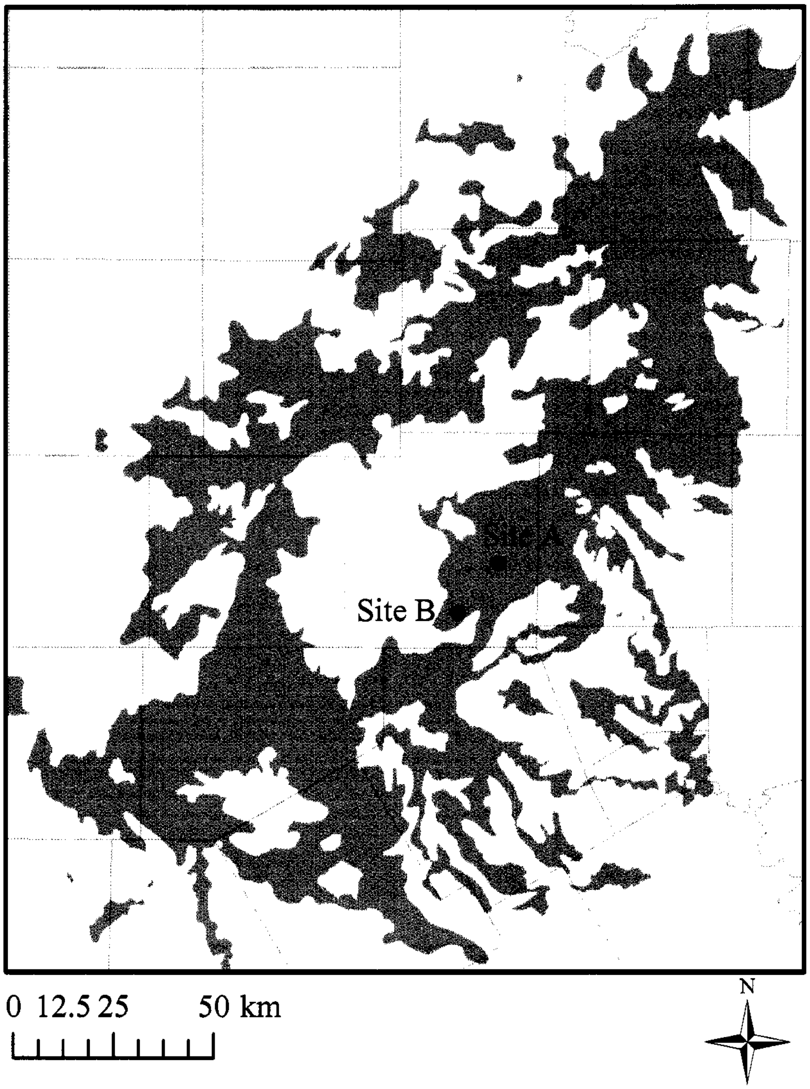

Figure 4.1. Old-growth study sites A and B (in red) in Palo Pinto Couny, Texas, and the historical extent of the western Cross Timbers of Texas (in gray; Dyksterhuis 1948).

Figure 4.2. Old-growth sample site A (in red), in Palo Pinto County, Texas. The rough topography of the western Cross Timbers is indicated by the digital raster graphic (DRG), a digital version of a 1:24,000 scale U.S. Geological Survey topographic map. Yellow areas of the map are contiguous areas predicted to retain old-growth, post-oak-dominated forests (see Chapter 2).

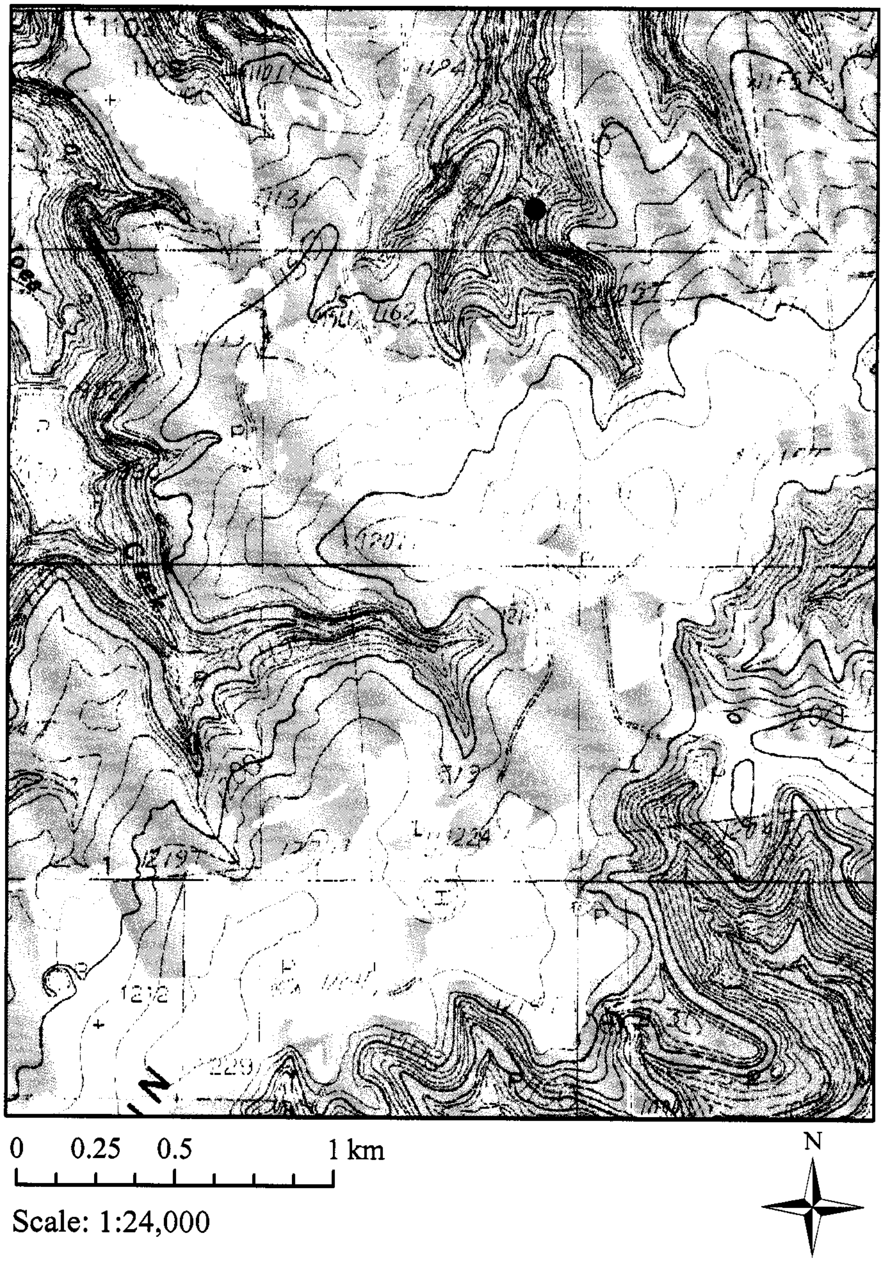

Figure 4.3. Old-growth sample site B (in red), located approximately 16 km from site A in Palo Pinto County, Texas. As in Figure 4.2, map layers include a digital version of a U.S. Geological Survey topographic map and our predictive model (in yellow) of contiguous old-growth forests.

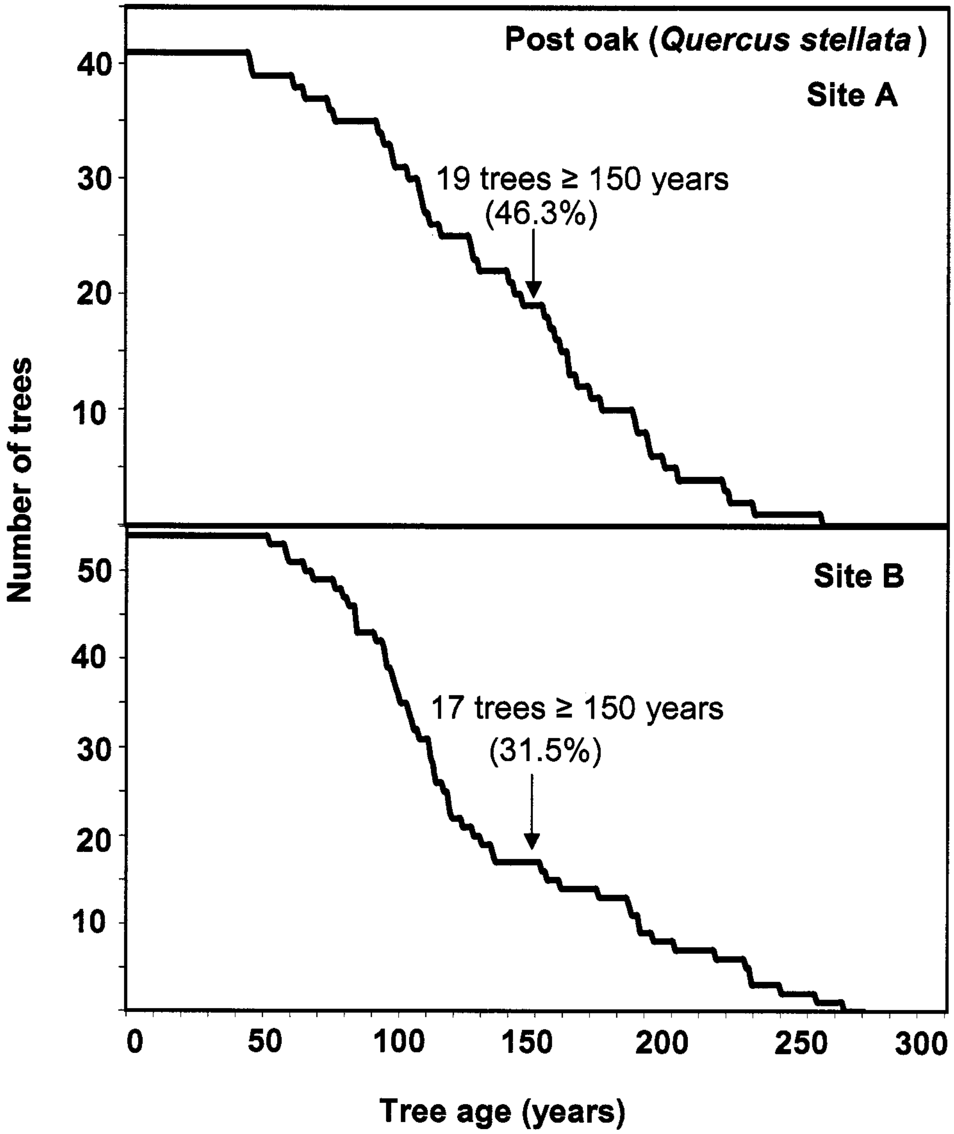

Figure 4.4. Post oak age structures for old-growth forest sites A and B in the western Cross Timbers. Post oak cores were obtained from randomly selected trees ≥ 10 cm DBH in April and May, 2003 and crossdated using standard methods.

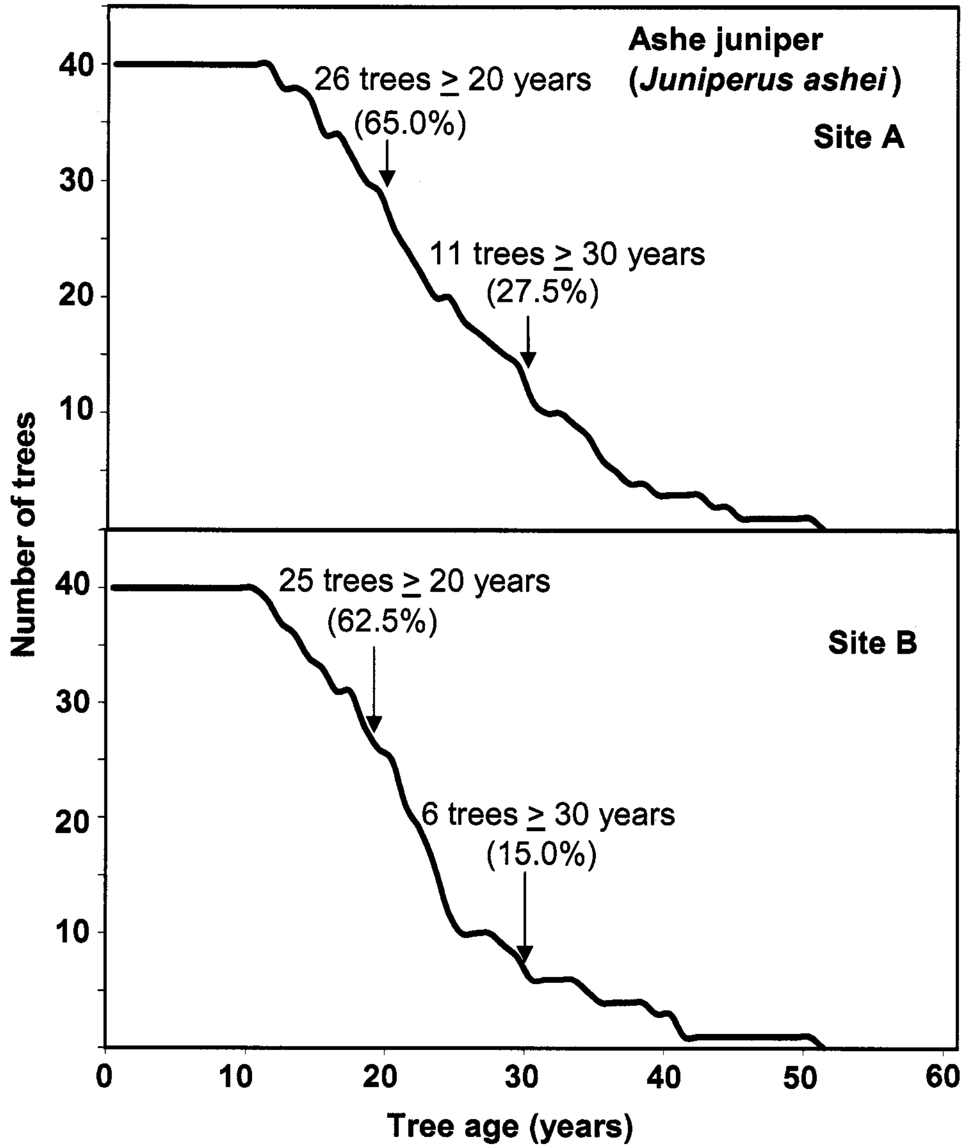

Figure 4.5. Ashe juniper age structures for old-growth forest sites A and B in the western Cross Timbers. Ashe juniper cores were obtained from randomly selected trees in October 2003, and ages were determined by counting annual growth rings.

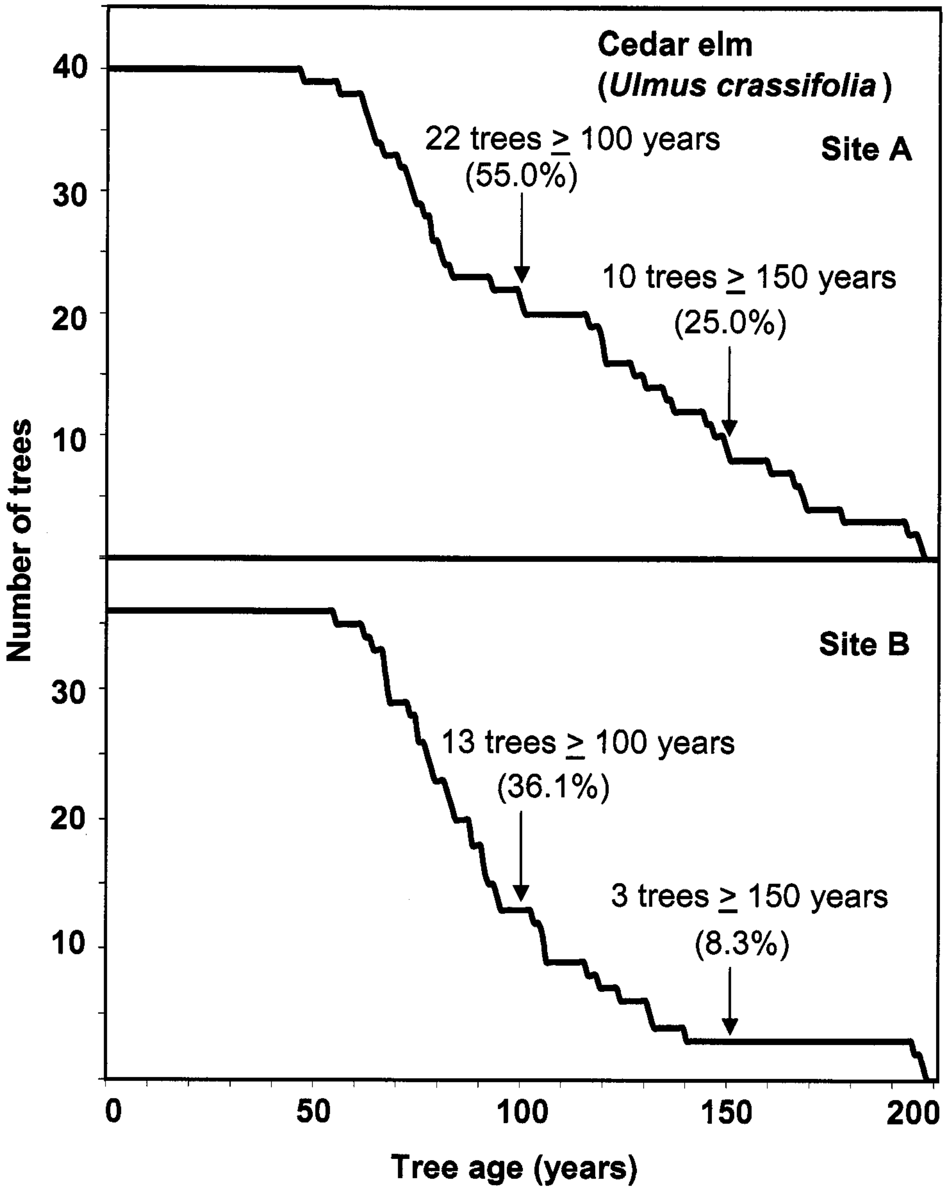

Figure 4.6. Cedar elm age structures for old-growth forest sites A and B in the western Cross Timbers. Cedar elm cores were obtained from randomly selected trees in October 2003 and crossdated using standard methods.

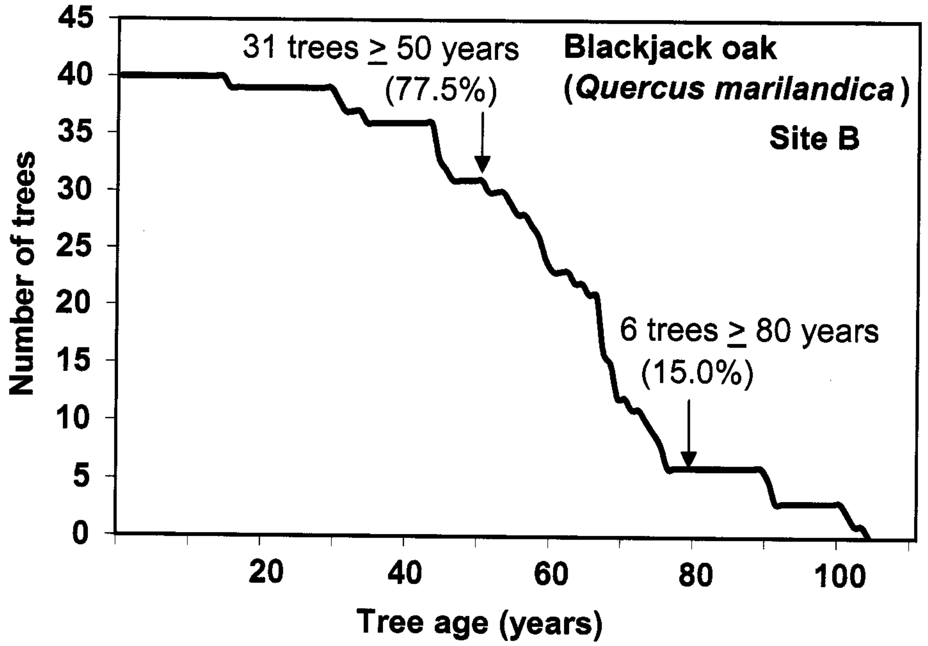

Figure 4.7. Blackjack oak age structure for old-growth forest site B in the western Cross Timbers. Blackjack oak cores were obtained from randomly selected trees in October 2003 and crossdated using standard methods.

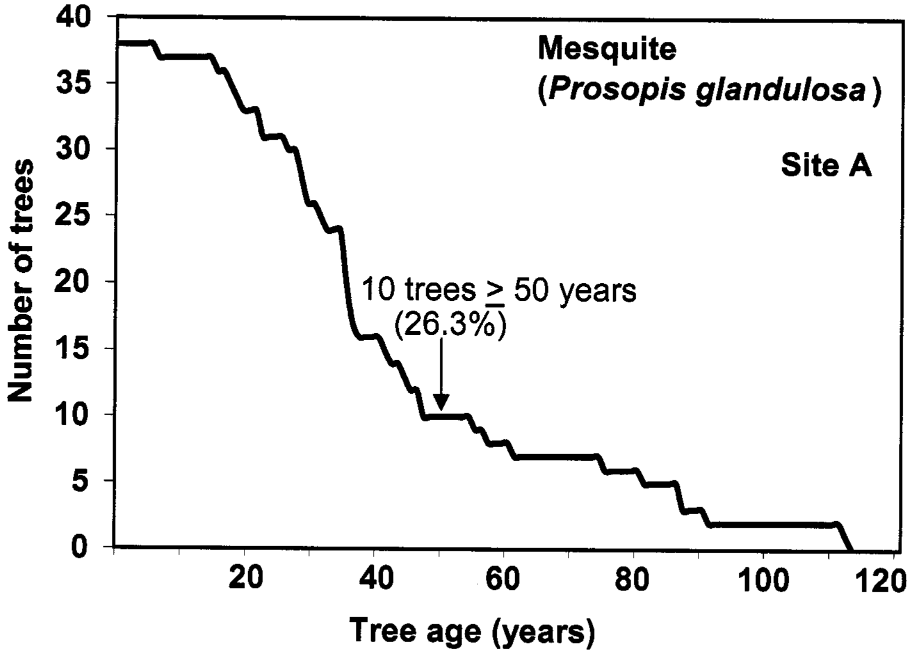

Figure 4.8. Mesquite age structure for old-growth forest site A in the western Cross Timbers. Mesquite cores were obtained from randomly selected trees in October 2003, and ages were determined by counting annual growth rings.

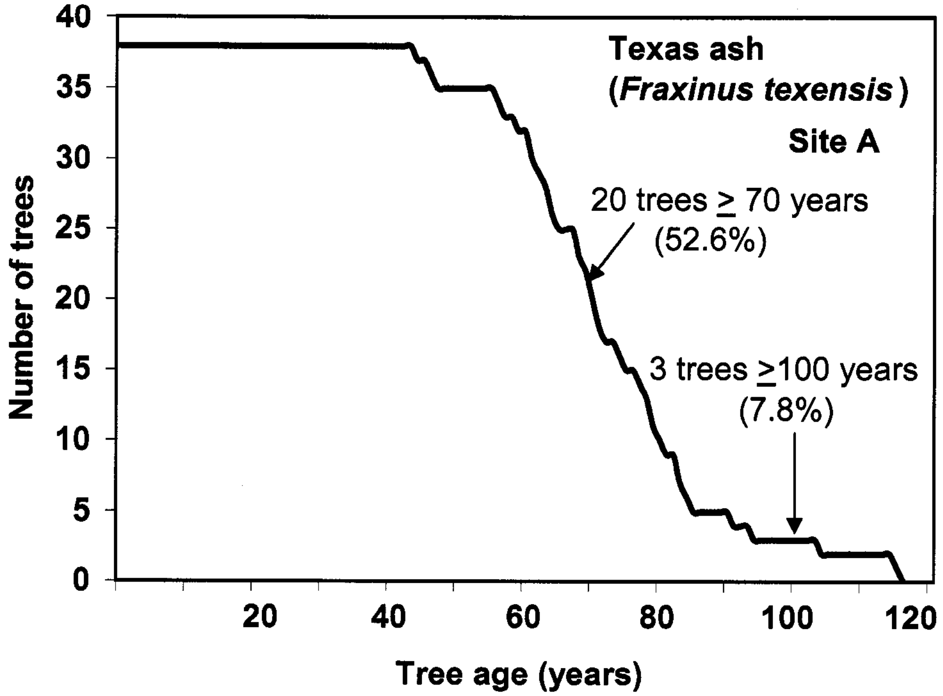

Figure 4.9. Texas ash age structure for old-growth forest site A in the western Cross Timbers. Texas ash cores were obtained from randomly selected trees in October 2003 and crossdated using standard methods.

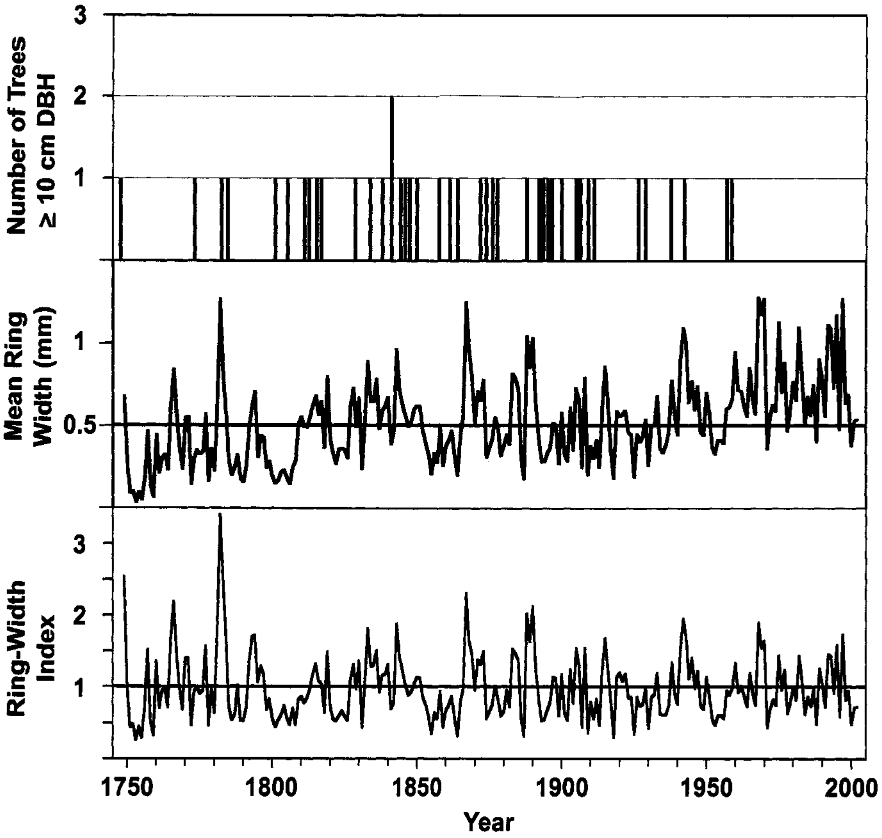

Figure 4.10. Year of recruitment to breast height for post oak trees at old-growth site A (n = 40), plotted above the mean ring widths and ring-width index for the same site. The tree-ring chronology was based on measurements of annual rings from 40 randomly selected post oak trees ≥10 cm DBH.

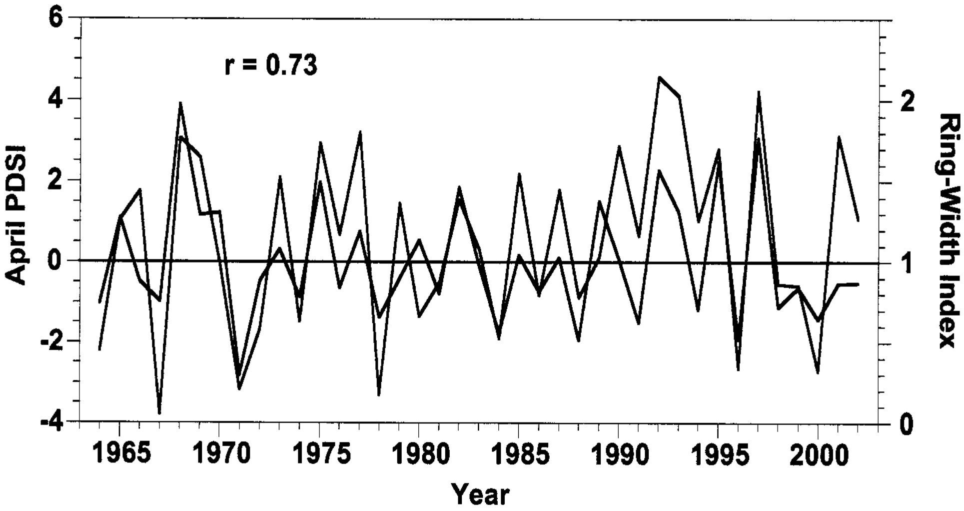

Figure 4.11. Ring-width index (black) and April Palmer Drought Severity Index (PDSI) values (red) for old-growth site A, from 1965-2000.

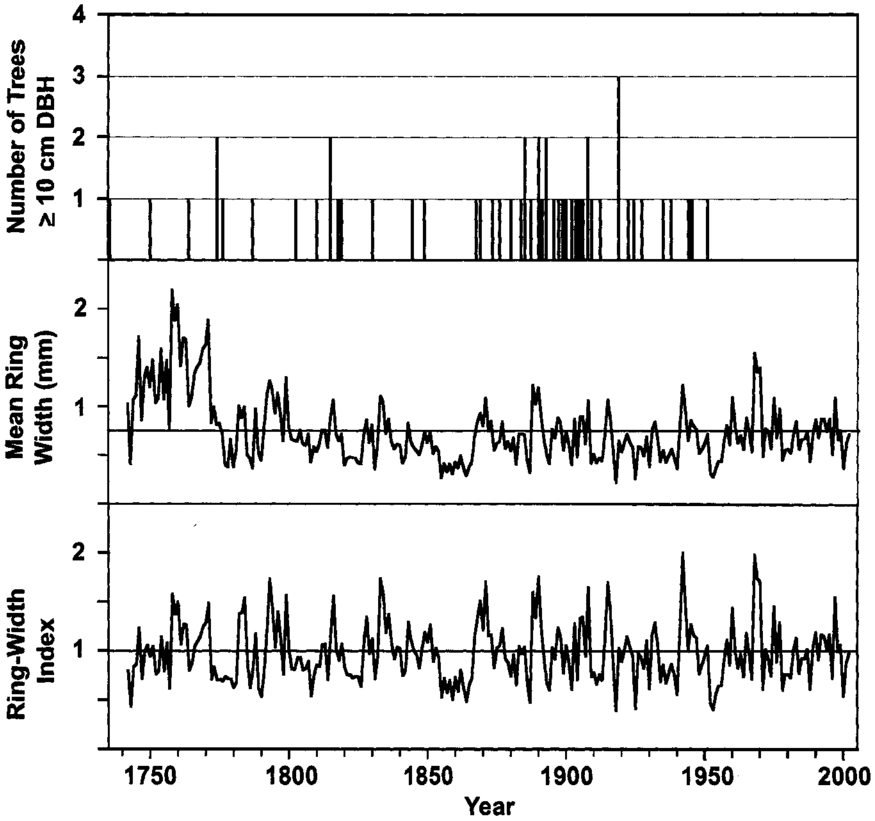

Figure 4.12. Year of recruitment to breast height for post oak trees at old-growth site B (n = 54), plotted above the mean ring widths and ring-width index for the same site. The tree-ring chronology was based on measurements of annual rings from 40 randomly selected post oak trees ≥ 10 cm DBH.

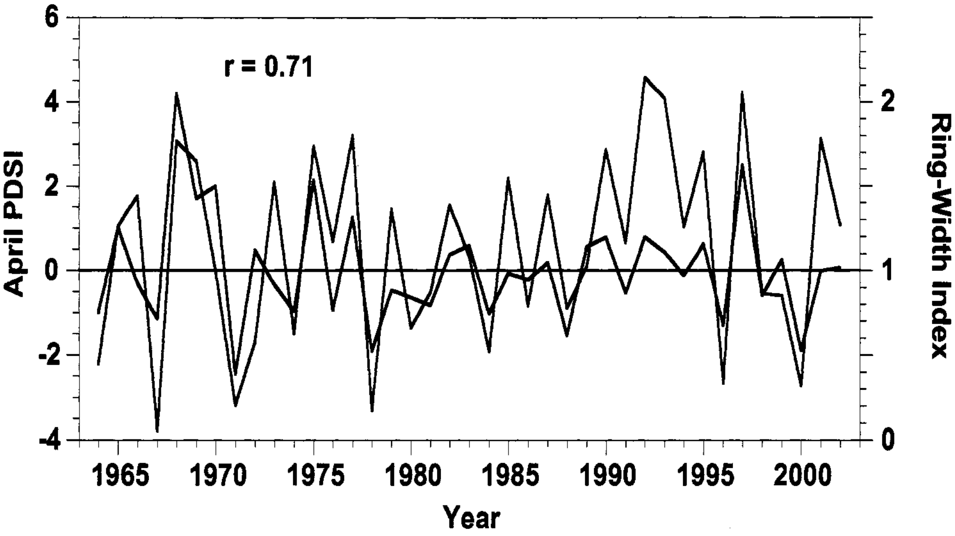

Figure 4.13. Ring-width index (black) and April Palmer Drought Severity Index (PDSI) values (red) for April at old-growth site B, from 1965-2000.

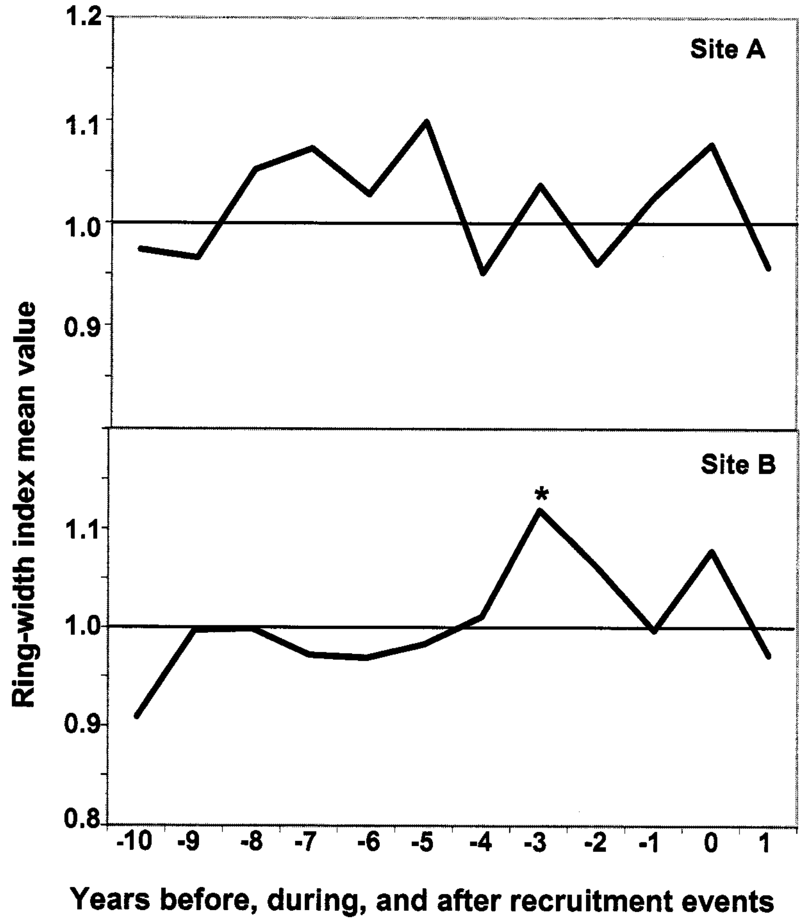

Figure 4.14. Superposed epoch analysis of tree growth for years of post oak recruitment to breast height between 1763-1959 (Site A) and 1750-1952 (Site B). For Site B, mean ring-width index values were significantly higher than normal three years preceding recruitment events (year -3=1.119, p<0.05).

Table 4.1. Tree relative density (RDEN[a]), tree absolute density (DEN; stems/ha), tree basal area (BA; m^2/ha), tree relative dominance (RDOM[b]), sapling:tree ratio, sapling relative density, and sapling absolute density of all tree and sapling species recorded at old-growth sites A and B in the western Cross Timbers of north-central Texas.

Site	*Quercus stellata*	*Ulmus crassifolia*	*Quercus marilandica*	*Fraxinus texensis*	*Prosopis glandulosa*	*Juniperus ashei*	*Sideroxylon lanuginosum*	*Celtis laevigata*
A								
RDEN (tree)	0.33	0.34	0.05	0.15	0.10	0.03		
DEN (tree)	103.78	111.77	15.97	47.90	31.93	7.98		
BA (tree)	5.47	3.07	0.73	1.28	0.55	0.80		
RDOM (tree)	0.46	0.25	0.06	0.11	0.05	0.07		
SAP:TREE	0.55	0.12		1.42	2.98	39.10		
RDEN (sapling)	0.05	0.03		0.13	0.18	0.58		
DEN (sapling)	27.15	13.57		67.86	95.01	312.18		
B								
RDEN (tree)	0.83	0.07	0.10					
DEN (tree)	359.95	32.72	43.63					
BA (tree)	26.48	0.95	1.24					
RDOM (tree)	0.92	0.03	0.05					
SAP:TREE	1.16	1.28	15.37					
RDEN (sapling)	0.25	0.03	0.40	0.18		0.08	0.04	0.02
DEN (sapling)	419.05	41.91	670.49	293.34		125.72	83.81	41.91

[a] number of trees of a species, divided by total number of trees of all species (40 at most sites)

[b] total basal area of a species, divided by total basal area of all species

Table 4.2. Understory plant species recorded at four sample sites (five, 100 m^2 quadrats in each of two savannah sites and two forest sites) at Site B, a relatively undisturbed, post oak-dominated old-growth remnant in the western Cross Timbers of Texas. Understory sampling was conducted in November, 2003 and April, 2004. Nomenclature follows Diggs et al. (1999).

Scientific name	Common name	Family	Site type
Acacia roemeriana	catclaw	Fabaceae	forest[a]
Acalypha gracilens	slender copperleaf	Euphorbiaceae	forest and savannah[b]
Achillea millefolium	milfoil	Asteraceae	forest and savannah
Allium canadense	wild onion	Liliaceae	forest and savannah
Ambrosia artemisiifolia	common ragweed	Asteraceae	forest and savannah
Antennaria parlinii	large-leaf pussy-toes	Asteraceae	forest
Aristida longespica	slim-spike threeawn	Poaceae	savannah
Aristida oligantha	oldfield threeawn	Poaceae	savannah
Aristida purpurea	purple threeawn	Poaceae	savannah
Asclepias verticillata	whorled milkweed	Asclepiadaceae	savannah
Asclepias viridis	green milkweed	Asclepiadaceae	savannah
Bothriochloa ischaemum	King Ranch bluestem	Poaceae	forest and savannah
Bothriochloa laguroides	silver bluestem	Poaceae	savannah
Bouteloua curtipendula	side-oats grama	Poaceae	savannah
Bouteloua hirsuta	hairy grama	Poaceae	savannah
Bromus pubescens	hairy brome	Poaceae	savannah
Callirhoe involucrata	purple poppy-mallow	Malvaceae	savannah
Carex microdonta	small-tooth caric sedge	Cyperaceae	forest and savannah

Scientific name	**Common name**	**Family**	**Site type**
Chaerophyllum tainturieri	smooth chervil	Apiaceae	forest and savannah
Chaetopappa asteroides	common least daisy	Asteraceae	forest and savannah
Cheilanthes tomentosa	woolly lip fern	Pteridaceae	forest and savannah
Chloris verticillata	tumble windmill grass	Poaceae	savannah
Cirsium texanum	Texas thistle	Asteraceae	forest and savannah
Coreopsis wrightii	rock coreopsis	Asteraceae	savannah
Croton monanthogynus	doveweed	Euphorbiaceae	savannah
Cynanchum laeve	bluevine	Asclepiadaceae	forest
Desmodium sp.	tick-clover	Fabaceae	forest and savannah
Diodia teres	poor-joe	Rubiaceae	savannah
Eragrostis curtipedicellata	gummy love grass	Poaceae	savannah
Eragrostis intermedia	plains love grass	Poaceae	savannah
Eragrostis pilosa	India love grass	Poaceae	savannah
Erigeron strigosus	prairie fleabane	Asteraceae	forest and savannah
Euphorbia tetrapora	weak euphorbia	Euphorbiaceae	savannah
Fraxinus texensis	Texas ash	Oleaceae	forest and savannah
Froelichia gracilis	slender snake-cotton	Amaranthaceae	savannah
Galium texense	Texas bedstraw	Rubiaceae	forest and savannah
Geranium sp.	crane's bill	Geraniaceae	forest
Hedeoma reverchonii	Reverchron's false penny-royal	Lamiaceae	savannah
Hedyotis nigricans	prairie bluets	Rubiaceae	savannah
Helenium elegans	elegant sneezeweed	Asteraceae	savannah

Scientific name	Common name	Family	Site type
Hypericum drummondii	nits-and-lice	Clusiaceae	savannah
Juniperus ashei	Ashe juniper	Cupressaceae	forest and savannah
Lactuca ludoviciana	western wild lettuce	Asteraceae	forest and savannah
Lepidium densiflorum	prairie pepperweed	Brassicaceae	forest and savannah
Lespedeza cuneata	sericea	Fabaceae	forest and savannah
Lithospermum incisum	narrow-leaf gromwell	Boraginaceae	savannah
Nassella leucotricha	winter grass	Poaceae	savannah
Nuttallanthus texanus	Texas toad-flax	Scrophulariaceae	savannah
Oenothera laciniata	cut-leaf evening-primrose	Onagraceae	forest and savannah
Opuntia engelmannii	Texas prickly pear	Cactaceae	forest and savannah
Oxalis stricta	sheep-showers	Oxalidaceae	forest and savannah
Panicum hallii	Hall's panic	Poaceae	forest and savannah
Panicum oligosanthes	Scribner's rosettegrass	Poaceae	forest and savannah
Paspalum distichum	knot grass	Poaceae	savannah
Pellaea atropurpurea	purple cliff-brake	Pteridaceae	forest
Penstemon laxiflorus	beardtongue	Scrophulariaceae	forest
Phyllanthus polygonoides	knotweed leaf-flower	Euphorbiaceae	forest and savannah
Plantago rhodosperma	tallow-weed	Plantaginaceae	forest and savannah
Poa annua	annual bluegrass	Poaceae	savannah
Prosopis glandulosa	honey mesquite	Fabaceae	savannah
Pseudognaphalium stramineum	cotton-batting cudweed	Asteraceae	forest and savannah
Quercus marilandica	blackjack oak	Fagaceae	savannah

Scientific name	Common name	Family	Site type
Quercus stellata	post oak	Fagaceae	forest and savannah
Rhus trilobata	skunkbush	Anacardiaceae	forest and savannah
Ruellia humilis	prairie-petunia	Acanthaceae	savannah
Schizachyrium scoparium	little bluestem	Poaceae	savannah
Sedum nuttallianum	yellow stonecrop	Crassulaceae	savannah
Sideroxylon lanuginosum	chittamwood	Sapotaceae	forest and savannah
Smilax bona-nox	saw greenbrier	Smilacaceae	forest and savannah
Spermolepsis inermis	spreading scaleseed	Apiaceae	forest and savannah
Sporobolus compositus	meadow dropseed	Poaceae	savannah
Sporobolus pyramidatus	whorled dropseed	Poaceae	savannah
Tridens flavus	purpletop	Poaceae	savannah
Triodanis perfoliata	hen-and-chickens	Campanulaceae	forest and savannah
Ulmus crassifolia	cedar elm	Ulmaceae	forest and savannah
Verbena halei	slender vervain	Verbenaceae	savannah
Vicia ludoviciana	deer pea vetch	Fabaceae	forest and savannah
Vulpia octoflora	common sixweeks grass	Poaceae	savannah

[a] Forest sites were steeply sloping (≥8%), old-growth forests with canopies dominated by post oak.

[b] Savannah sites had scattered, old post oaks, relatively little canopy cover, and were located on ridgetops.

Table 4.3. Understory cover at savannah site 1, ordered by percent cover, then by number of sample plots (of 5 total) at which the cover type was encountered.

Cover type	Percent cover	Number of plots
bare rock	10-25	5
bare soil/leaf litter	10-50	5
Sporobolus pyramidatus	5-10	5
Bouteloua curtipendula	5-10	4
Eragrostis intermedia	5-10	2
Allium canadense	1-5	5
Carex microdonta	1-5	5
Lepidium densiflorum	1-5	5
Panicum hallii	1-5	5
Panicum oligosanthes	1-5	4
Fraxinus texensis	1-5	3
Juniperus ashei	1-5	3
Oxalis stricta	1-5	3
Quercus stellata	1-5	3
Schizachyrium scoparium	1-5	3
Bothriochloa ischaemum	1-5	2
Chaetopappa asteroides	1-5	2
Cirsium texanum	1-5	2
Sedum nuttallianum	1-5	2
Poa annua	1-5	1
Quercus marilandica	1-5	1
Vicia ludoviciana	trace[a]	5
Lespedeza cuneata	trace	4
Cheilanthes tomentosa	trace	3
Opuntia engelmannii	trace	3
Plantago rhodosperma	trace	3
Acalypha gracilens	trace	2
Aristida oligantha	trace	2
Chaerophyllum tainturieri	trace	2
Desmodium sp.	trace	2
Erigeron strigosus	trace	2
Euphorbia tetrapora	trace	2
Hedeoma reverchonii	trace	2
Hypericum drummondii	trace	2

Cover type	**Percent cover**	**Number of plots**
Nuttallanthus texanus	trace	2
Oenothera laciniata	trace	2
Pseudognaphalium stramineum	trace	2
Smilax bona-nox	trace	2
Spermolepsis inermis	trace	2
Achillea millefolium	trace	1
Ambrosia artemisiifolia	trace	1
Aristida purpurea	trace	1
Bouteloua hirsuta	trace	1
Bromus pubescens	trace	1
Coreopsis wrightii	trace	1
Eragrostis pilosa	trace	1
Froelichia gracilis	trace	1
Galium texense	trace	1
Geranium sp.	trace	1
Lactuca ludoviciana	trace	1
Nassella leucotricha	trace	1
Sideroxylon lanuginosum	trace	1
Sporobolus compositus	trace	1
Ulmus crassifolia	trace	1
Verbena halei	trace	1

[a]trace, <1% cover

Table 4.4. Understory cover at savannah site 2, ordered by percent cover, then by number of sample plots (of 5 total) at which the cover type was encountered.

Cover type	Percent cover	Number of plots
bare rock	0-10	4
bare soil/leaf litter	5-25	5
Schizachyrium scoparium	25-50	5
Bothriochloa ischaemum	10-50	5
Aristida longespica	10-25	4
Chaetopappa asteroides	5-10	5
Erigeron strigosus	1-5	5
Panicum hallii	1-5	5
Panicum oligosanthes	1-5	5
Aristida oligantha	1-5	4
Bouteloua curtipendula	1-5	4
Bothriochloa laguroides	1-5	3
Eragrostis intermedia	1-5	3
Quercus stellata	1-5	3
Juniperus ashei	1-5	2
Sporobolus pyramidatus	1-5	2
Allium canadense	trace	5
Verbena halei	trace	5
Ambrosia artemisiifolia	trace	4
Eragrostis curtipedicellata	trace	4
Opuntia engelmannii	trace	4
Plantago rhodosperma	trace	4
Achillea millefolium	trace	3
Hypericum drummondii	trace	3
Callirhoe involucrata	trace	2
Chloris verticillata	trace	2
Croton monanthogynus	trace	2
Euphorbia tetrapora	trace	2
Galium texense	trace	2
Hedeoma reverchonii	trace	2
Hedyotis nigricans	trace	2
Lepidium densiflorum	trace	2
Oxalis stricta	trace	2
Phyllanthus polygonoides	trace	2

Cover type	**Percent cover**	**Number of plots**
Triodanis perfoliata	trace	2
Acacia roemeriana	trace	1
Aristida purpurea	trace	1
Asclepias verticillata	trace	1
Asclepias viridis	trace	1
Bouteloua hirsuta	trace	1
Diodia teres	trace	1
Fraxinus texensis	trace	1
Helenium elegans	trace	1
Lespedeza cuneata	trace	1
Lithospermum incisum	trace	1
Nuttallanthus texanus	trace	1
Oenothera laciniata	trace	1
Paspalum sp.	trace	1
Prosopis glandulosa	trace	1
Pseudognaphalium stramineum	trace	1
Rhus trilobata	trace	1
Ruellia humilis	trace	1
Tridens flavus	trace	1
Vulpia octoflora	trace	1

Table 4.5. Understory cover at forest site 1, ordered by percent cover, then by number of sample plots (of 5 total) at which the cover type was encountered.

Cover type	Percent cover	Number of plots
bare rock	10-50	5
bare soil/leaf litter	10-50	5
Bothriochloa ischaemum	10-25	5
Fraxinus texensis	5-10	5
Quercus stellata	5-10	5
Smilax bona-nox	5-10	4
Panicum hallii	1-5	5
Panicum oligosanthes	1-5	5
Allium canadense	1-5	4
Cheilanthes tomentosa	trace	4
Desmodium sp.	trace	4
Erigeron strigosus	trace	4
Oxalis stricta	trace	4
Vicia ludoviciana	trace	4
Galium texense	trace	3
Phyllanthus polygonoides	trace	3
Carex microdonta	trace	2
Cirsium texanum	trace	2
Opuntia engelmannii	trace	2
Pseudognaphalium stramineum	trace	2
Rhus trilobata	trace	2
Sideroxylon lanuginosum	trace	2
Acacia roemeriana	trace	1
Ambrosia artemisiifolia	trace	1
Chaetopappa asteroides	trace	1
Juniperus ashei	trace	1

Table 4.6. Understory cover at forest site 2, ordered by percent cover, then by number of sample plots (of 5 total) at which the cover type was encountered.

Cover type	Percent cover	Number of plots
bare rock	10-25	5
bare soil/leaf litter	25-50	5
Quercus stellata	5-25	5
Ulmus crassifolia	10-25	4
Fraxinus texensis	5-25	4
Juniperus ashei	5-10	3
Cirsium texanum	5-10	1
Bothriochloa ischaemum	1-10	5
Panicum oligosanthes	1-10	4
Smilax bona-nox	1-10	4
Lespedeza cuneata	1-10	3
Cynanchum laeve	1-5	2
Carex microdonta	trace	5
Cheilanthes tomentosa	trace	5
Oxalis stricta	trace	5
Erigeron strigosus	trace	3
Phyllanthus polygonoides	trace	3
Vicia ludoviciana	trace	3
Desmodium sp.	trace	2
Lactuca ludoviciana	trace	2
Oenothera laciniata	trace	2
Panicum hallii	trace	2
Sideroxylon lanuginosum	trace	2
Spermolepsis inermis	trace	2
Triodanis perfoliata	trace	2
Acalypha gracilens	trace	1
Achillea millefolium	trace	1
Allium canadense	trace	1
Antennaria parlinii	trace	1
Chaerophyllum tainturieri	trace	1
Geranium sp.	trace	1
Lepidium densiflorum	trace	1
Pellaea atropurpurea	trace	1
Penstemon laxiflorus	trace	1
Plantago rhodosperma	trace	1
Pseudognaphalium stramineum	trace	1

Chapter 5

Conclusions

More than 30 years ago, Harrison (1972) described the Cross Timbers as a "rapidly disappearing and irreplaceable" ecosystem. Indeed, as I noted, dramatic habitat modification has occurred throughout the Cross Timbers on level terrain; however, areas of high relief have been less subject to anthropogenic modification because of their inaccessibility and low economic value (for wood or as rangeland). Although the University of Arkansas Tree-Ring Laboratory had documented the occurrence of stands of old post oak trees in the Cross Timbers, little was known about the extent or condition of old-growth forests, particularly in the western Cross Timbers of Texas.

We identified many large, relatively undisturbed old-growth forests throughout the western Cross Timbers and produced a map of areas ≥16 ha that are likely to retain old-growth forests. The map's primary value for land managers and conservation organizations is in identifying core areas, or regions, in which old-growth forests dominate the landscape. The map also includes many areas dominated by second-growth forest, due to historical clearing of many steep, forested slopes, and also to the difficulty I encountered in attempting to distinguish old- and second-growth deciduous forests with multispectral satellite imagery. Hyperspectral imagery may prove useful in making this distinction, thereby improving the accuracy of the old-growth map for the western Cross Timbers. Also, future research may identify topographic or environmental factors that would improve predictions of old-growth forest locations, but which I did not consider in my predictive model. Ultimately, however, decision-making by private landowners about the fate of old-growth forests will never be entirely consistent or predictable.

I also produced the first characterization of the overstory of old-growth forests in the western Cross Timbers, based on sampling of 16 randomly selected old-growth sites. Simultaneously, I developed a definition of old-growth forests for the region, based on post oak age structures that I computed for old-growth, cull, and second-growth forests. Old-growth forest structure and composition were relatively well known for the Oklahoma Cross Timbers, and I found that knowledge about Oklahoma was not entirely transferable to the western Cross Timbers of Texas. In particular, I documented an apparent low level of post oak recruitment in the western Cross Timbers, although high post oak regeneration has been reported for Oklahoma (Clark 2003). Low recruitment by post oak is consistent with declines in oak regeneration throughout most of North America, but inconsistent with hypotheses that successional replacement of oaks would not occur on xeric uplands (Abrams 1992).

I tested hypotheses about effects of slope, aspect, and precipitation on old-growth forest composition, and also examined succession in old-growth overstories. I developed tree-ring chronologies for post oak, and used them to assess relationships between radial growth and recruitment, and climate and recruitment. The age structures I produced for other tree species were useful in refining the answer to the question, "What *is* an old-growth forest in the western Cross Timbers?" They also enabled me to demonstrate that Ashe juniper is invading the sapling layer of old-growth forests in the region, and will likely invade the canopy layer. Mesquite, although considered a problematic invasive species in Texas rangelands, did not appear invasive in old-growth forests.

Although this dissertation project answered many questions about old-growth forests in the western Cross Timbers, it also generated a number of new questions. For example, what percentage of old-growth forests did my map omit because of the 8% slope constraint I imposed? In other words, how large an area is occupied by old-growth forests on level terrain? I also excluded the eastern Cross Timbers from the old-growth model, but it would be valuable to identify old-growth forests in that region, as well as in the post oak savannahs ("post oak belts") farther south. Moreover, nothing is known about the potential effects of ecological restoration in the western Cross Timbers, but as land-use changes continue, that area of research may become a priority.

Determining the historical frequency and magnitude of fires in the western Cross Timbers should be a research priority for the future. Is fire suppression implicated in Ashe juniper invasion? I am also curious about the differences I found between the Oklahoma and Texas Cross Timbers (Table 5.1). Is post oak recruitment really greater in Oklahoma, or did sampling methods bias my interpretation of recruitment in Texas? For one site (site B in southeastern Palo Pinto County), I found a post oak sapling:tree ratio above 1.0. Perhaps research will identify unique characteristics of that site, in terms of topography, environment, or land-use history. At the other sites we sampled, will succession lead to a dramatically changed forest composition? My results suggest that could occur, and researchers could address the question through quantifying seedlings of all tree species, assessing seedling and sapling mortality, dating trees of all diameters, and monitoring the sites at which we have established "baseline" conditions. Notably, I found that the two longest-lived tree species had the lowest sapling:tree ratios. Is this evidence of disturbance or invasion, or rather a consequence of longevity and episodic recruitment? With regard to the relationship between climate and post oak recruitment, future research might include more detailed analyses of recruitment, with respect to drought and wetness events, as indicated by tree-ring reconstructed PDSI values.

I found that an old-growth canopy does not necessarily indicate an undisturbed understory. Where does the site I sampled fall along the continuum of understory disturbance that exists in the western Cross Timbers? Which areas retain an understory composition most similar to that documented by Dyksterhuis (1948) at relict sites? What role do pasture-forest edge effects play in determining understory composition in old-growth remnants? What effects will Ashe juniper invasion have on old-growth forest understories?

I identified 16 old-growth sites as relatively undisturbed, with respect to the degree of human activity or modification; however, exotic animal species (e.g., aoudad sheep [*Ammotragus lervia*]) have been introduced, and many species native to the western Cross Timbers no longer occur there. European settlement resulted in the near-eradication or extirpation of the prairie dog (*Cynomys ludovicianus*), bison (*Bison bison*), black bear (*Ursus americanus*), red wolf (*Canis rufus*), passenger pigeon (*Ectopistes migratorius*), and prairie chicken (*Tympanuchus* sp.). At least two of those—bison and prairie dogs—are considered keystone species (Miller et al. 1994; Knapp et al. 1999). What are the ecological results of their elimination from the western Cross Timbers?

These questions indicate the vast potential for future research in the western Cross Timbers, and for opportunities to address larger ecological questions about mechanisms of succession and invasion. The potential for interdisciplinary research—at the interface of ecology, geography, economics, and history—is particularly interesting in this region.

For example, what do economic and demographic data suggest about future incentives to clear or "develop" old-growth forests in the western Cross Timbers?

Hoagland et al. (1999) called for an evaluation of the conservation status of the Cross Timbers, and The Nature Conservancy of Texas has begun such an assessment, relying on these findings to prioritize conservation areas, articulate conservation and management issues, and identify research needs. Also, this dissertation project played an important role in the recent establishment of the Ancient Cross Timbers Consortium for Research, Education, and Conservation (http://www.uark.edu/misc/xtimber/). The Consortium—a network of cooperating public agencies, private organizations, educational institutions, and landowners—will expand opportunities for research, including long-term monitoring of old-growth sites. Such monitoring is essential for documenting natural and human-induced changes in old-growth forests and developing appropriate conservation and management strategies for this unique ecosystem.

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Table 5.1. Comparison of old-growth forests in the Cross Timbers of Texas and Oklahoma, in terms of post oak age structure, forest composition, tree and sapling density, and sapling:tree ratios.

Parameter	**TX**	**OK**	**Source of Oklahoma results**
% post oak trees ≥200 years old	7.2	6.9	(M. Mangione, unpublished data)
% post oak trees ≥100 years old	73.5	26.1	(M. Mangione, unpublished data)
Mean post oak DBH (cm)	25.4	24.2	(M. Mangione, unpublished data)
Mean post oak relative density	0.6	0.6	(Johnson & Risser 1975)
Mean blackjack oak relative density	0.1	0.3	(Johnson & Risser 1975)
Mean total tree density (stems/ha)	534.0	255.0	(Johnson & Risser 1975)
Post oak saplings/ha	109.2	753.3	(Clark 2003)
Mean sapling:tree ratio (all species)	2.5	2.6	(Clark 2003)
Mean post oak sapling:tree ratio	0.3	1.6	(Clark 2003)

OLD-GROWTH FORESTS IN THE WESTERN CROSS TIMBERS OF TEXAS

Abstract of dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

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ABSTRACT

The Cross Timbers—a mosaic of savannahs, tallgrass prairies, and post oak (*Quercus stellata*)-dominated forests—historically spanned 8 million hectares of southeastern Kansas, eastern Oklahoma, and northcentral Texas, covering the ecotone between eastern deciduous forests and grasslands of the southern Great Plains. Because of infertile soils and rugged terrain, large-scale commercial logging did not occur in the Cross Timbers, and old-growth forests remain. I developed an environmental model that predicted 19,166 hectares of remaining old-growth forests in the western Cross Timbers of Texas. Field technicians surveyed 50 randomly selected transects (500,000 m^2 in all) within the predicted old-growth area: 32.4% was old-growth, and more than 50% was second-growth. Cull forests and cleared land also occurred in the predictive model area. For old-growth sites, I constructed an overall post oak age structure, based on dating of increment cores from randomly selected trees $\geq$10 cm DBH. Point-quarter sampling at 16 old-growth sites identified during field testing of the predictive model indicated that post oak was characteristic of old-growth sites, although post oak dominance varied from 0.46 to 0.99. Approximately one-third of 648 randomly selected post oaks were $\geq$150 years old, and 7.2% were $\geq$200 years old. Forest composition differed between tree and sapling layers, and aspect was an important determinant of tree density and post oak age structure. Post oak regeneration was low in the western Cross Timbers and appeared to have been declining since the late 1800s. Ashe juniper (*Juniperus ashei*) appeared to be invading old-growth forests in the region, although there was no evidence of invasion by mesquite (*Prosopis glandulosa*). For two old-growth sites, I documented age structures of five tree species that occurred with post oak in the overstory. Post oak recruitment and

climate data from 1700-2000 were related to tree-ring chronologies developed for post oak at the two sites. I quantitatively characterized the understory of old-growth forest and savannah communities on steep slopes and ridgetops, respectively. Old-growth savannah understory vegetation resembled vegetation at “relict” sites in the western Cross Timbers sampled in the 1930s, although I identified several invasive grasses in the understory.