Composition, Structure, and Developmental Determinants of a Scrub Oak Forest in the West Cross Timbers of North Central Texas

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ABSTRACT

We evaluated composition and community determinative factors of an old-growth, scrub forest on a deep-sand habitat in the West Cross Timbers of North Central Texas. Species composition and vegetation structure were analyzed based on 1) dominance, density, and importance values of woody plants and 2) foliar cover of herbaceous species and woody seedlings or offshoots in the understory. We concluded that this was the potential natural vegetation for this deep-sand site with the sandy soil being the principal determining factor in development and stability of this natural community (i.e., an edaphic climax). We designated this as a sand post oak-saw greenbrier (*Quercus margarettiae-Smilax bona-nox*) community based on the dominant tree and shrub species. The scrub forest consisted of three layers: 1) a closed canopy of sand post oak and blackjack oak (*Q. marilandica*); 2) a shrub layer of six species, including saw greenbrier, a liana that extended into the tree canopy; and 3) an irregular understory of herbaceous plants plus seedlings and clonal shoots of oaks and greenbrier. Herbaceous plants were all native species and included six species of grasses, two of grasslike plants, and five of forbs. Most of the herbaceous cover developed in natural openings and low quantity of available soil water in the deep sandbeds of this forest was the primary phenomenon that permitted domination of this site by sand post oak. Various communities on sandy-land sites in the Gulf and Atlantic Coast regions have been described in which sand post oak and other species are important constituents. This climax scrub forest is an integral part of the landscape mosaic of the West Cross Timbers.

KEYWORDS: Sand post oak-saw greenbrier community; Edaphic Climax; West Cross Timbers

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INTRODUCTION

The Cross Timbers is a relatively large natural ecological unit distinguished by vegetation composed of hardwood trees, especially oak (*Quercus*) species, and shrubs with associated herbaceous plants, particularly panicoid and eragrostoid grasses (Diggs et al. 1999; Garrison et al. 1977; Sims and Risser 2000), that developed on soils derived from sands, sandstone, and other parent materials including shales (Byers et al. 1938; Francaviglia 2000; Hoagland et al. 1999). Cross Timbers soils were historically interpreted as being in the Red and Yellow Podzolic great groups that developed with deciduous forests (Soil Survey Staff 1938; Dyksterhuis 1948; Francaviglia 2000). They correspond to the Alfisol order in the newer soil taxonomic system (Soil Conservation Service 1990a).

The Cross Timbers—a title used since frontier times (Dale 1966; Francaviglia 2000; Hollon 1955)—has long been recognized as distinctive climax or potential natural vegetation that forms physiogonomic patterns ranging from dense forest and woodland through savanna to grassland that has patches or groves of trees (Braun 1950; Bruner 1931; Diggs et al. 1999; Dyksterhuis 1948, 1957; Hoagland et al. 1999). Tharp (1939) provided one of the first vegetational descriptions of the Cross Timbers and distinguished the Western Cross Timbers from the Eastern Cross Timbers. ("West" and "Western" have been used interchangeably in some proper names whereas in other formal designations, such as for subunits of vegetational-land resource areas or ecoregions, only one or the other adjective is part of the published name.) Historically, the two forms of East and West Cross Timbers have been designated also as Lower and Upper Cross Timbers, respectively (Diggs et al. 1999). Numerous workers (Braun 1950; Diggs et al. 1999; Dyksterhuis 1948; Hoagland et al. 1999) interpreted the Cross Timbers as a vegetational mosaic having primarily a savanna form that exists as a comparatively broad transition (ecotone) from the main or more eastern body of the oak-hickory (*Carya*) forest extending west to the tallgrass and true prairies. Francaviglia (2000) treated the Cross Timbers as more of a geographic region delineated by its vegetation much as did frontiersmen such as prominent author Washington Irving (1835), historian William Kennedy (1841), and freighter Josiah Gregg (1844).

Fenneman (1931) regarded the Cross Timbers as important in delineating physiographic units in the Great Plains and, later, Fenneman (1938) used Eastern and Western Cross Timbers as names of units of the Coastal Plain province. Maps of the vegetational or land resource areas of Texas have traditionally included the unit (region five) designated as Cross Timbers and Prairies (Correll and Johnston 1979; Diggs et al. 1999; Gould 1962). In classifying and mapping ecoregions (Bailey 1995, 1996, 1998) the name Cross Timbers was incorporated into and used as titles and descriptions for level four ecoregions in Texas (Griffith et al. 2004), Oklahoma (Woods 2005), and Kansas (S. S. Chapman et al. 2001 in litt.), the three US states in which Cross Timbers is potential natural vegetation (Hoagland et al. 1999).

Apparently all workers who studied the Cross Timbers, regardless of their emphasis or interpretation, recognized the floristic diversity along with physiogonomic and structural variation of Cross Timbers vegetation. The Cross Timbers has been studied from perspectives of human history and culture (Dale 1966; Francaviglia 2000; Richardson 1963), geology, including physiography (Fenneman 1931, 1938), as well as vegetation (Diggs et al. 1999; Dyksterhuis 1948; Hoagland et al. 1999). Foreman (1947) related geology and vegetation of the Cross Timbers to early history, especially of exploration, commerce, and military expeditions. Reports concerning vegetation and community ecology of the Cross Timbers have included brief descriptions (Braun 1950; Bruner 1931), summary reviews (Diggs et al. 1999; Hoagland et al. 1999), and a detailed monograph (Dyksterhuis 1948). Even with this long-standing study of the Cross Timbers, most of the diverse forms of this regional natural community have received remarkably little evaluation.

This dearth of vegetational evaluation for most native plant communities in Texas and areas adjacent to it was recognized by Elliott (2013). We recently conducted a quantitative study of a mixed hardwood floodplain-riparian forest in the West Cross Timbers (Rosiere et al. 2013) that had been indicated (Elliott 2013) as in need of quantification. We next directed our efforts toward analysis of a scrub oak forest on deep sand in the West Cross Timbers that Elliott (2013) designated as "Crosstimbers: Sandyland Oak Woodland." In his brief description, Elliott (2013) specified that this sandyland plant community was in need of vegetational verification in anticipation of it being "sufficiently distinct to require a separate vegetation type." It was emphasized that field data was "largely lacking" for this distinctive form of Cross Timbers vegetation (Elliott 2013). In a later version of these vegetation descriptions, Elliott (2013) had not amended his previous brief treatment of the sandyland oak woodland. Apparently, the type still had not been verified.

Indeed, almost no description, let alone quantitative evaluation, of this native plant community was found. In his classic monograph, Bruner (1931) alluded to a "chaparral" community of sand or scrub post (*Quercus stellata* [var.] *margaretta*) and dwarf plants of blackjack oak (*Q. marilandica*) in the transition zone between oak-hickory forest and prairie in Oklahoma. Little (1939) briefly described a dwarf woodland of blackjack oak and post oak in southwestern Oklahoma comprised of trees having heights of 3 to 4.5 meters and diameters (diameter breast height) of 10 to 15 centimeters. The shrubland mentioned by Bruner (1931) and the dwarf woodland of Little (1939) was consistent with the Cross Timbers sandyland oak woodland that Elliott (2013) described as dominated by post oak and blackjack oak with characteristic presence of sand post oak, which is also known as dwarf post oak, margaretta oak, and runner oak, (*Q. margarettae* = *Q. margarettiae* = *Q. margaretta*). The closest specific descriptions of scrub oak communities in the Cross Timbers were brief and mostly conjectural notes on range sites associated with descriptions of soil series in county soil surveys (Soil Conservation Service 1973, 1977a, 1977b, 1978, 1980).

Descriptions of major North American shrublands as rangeland cover types by the Society for Range Management (Shiflet 1994) did not include sand post oak-dominated scrub types or make reference to this species under description of the two Cross Timbers cover types (SRM 731, SRM 732). Forest cover types recognized by the Society of American Foresters (Eyre 1954, 1980) did not include sand post oak in descriptions of post oak-blackjack oak upland forest (SAF 40) though sand post oak was named as one of the scrub oak species in an oak-pine type (SAF 71).

Vegetation in which sand post oak is a dominant or, at least, major species in south-central North America is not limited to the Cross Timbers as there are similar natural plant communities with sand post oak in the Texas Post Oak Savanna (Texas vegetational area 3) that occurs east of the West Cross Timbers (Gould 1962; Correll and Johnston 1979), including the Xeric Sandylands or Deep Sands Ecosystem (Diggs et al. 2006). Sand post oak has a species range extending from southeastern Virginia across the length of the Gulf Coastal Plain into central Texas and south-central Oklahoma (Burns and Honkala 1990; Correll and Johnston 1979; McGregor et al. 1986; Sargent 1933) so as to occur in various native plant communities including Coastal Plain pine savannas in Florida (Rebertus et al. 1989, 1993), an oak-pine cover type (Eyre 1980), and western sandhill xeric woodland in Louisiana (Louisiana Natural Heritage Program 2009). Such tree-defined vegetation notwithstanding, sand post oak-dominated dwarf forest that develops on deep sands in the West Cross Timbers is distinctly different from other plant communities. Thus, this distinctive vegetation warrants analysis and description necessary for its recognition as a natural community type.

Sandyland scrub oak vegetation is one of the most widely dispersed and distinctive—though least described—natural plant communities in the Cross Timbers. It is also one of the variants (subtypes) of Cross Timbers vegetation that is relatively limited in total area and that has been and continues to be lost in conversion to home sites, row crops, especially peanuts (*Arachis hypogaea*), orchards, and, most frequently, introduced forage species, especially agronomic forage crops like Coastal bermudagrass (*Cynodon dactylodon* Pers. 'Coastal') and exotic range grasses such as weeping lovegrass (*Eragrostis curvula*).

On its deep-sand environment, this native scrub oak community develops into such dense vegetation that it is nearly impenetrable to humans and livestock. This sandyland vegetation supports only limited herbaceous understory, much of which is inaccessible as forage for grazing animals. In *Commerce of the Prairies*, Josiah Gregg (1844:361) described such Cross Timbers vegetation as "almost impenetrable 'roughs.'" Farmers and ranchers know this woody vegetation as "sandrough" or "sandtangle" and, cost-permitting, replace areas of this native sandyland community with crop monocultures (type conversions) capable of producing greater yields of commodities or, more commonly, forage for hay and pasture. Most remaining tracts of "sandrough" are used as loafing areas by cattle (*Bos taurus*, *B. indicus*) that graze conterminous type conversions of introduced grasses. Smaller, remaining remnants and the perimeters of larger tracts of "sandtangle" become overgrazed, often to the extent that the surface of the sandy soil is severely disturbed, commonly resulting in elimination of the limited herbaceous layer.

The following investigation on the quantitative composition, structure, and successional status of this deep-sand, native scrub oak community in the West Cross Timbers was an initial effort to provide field data that was deemed essential to classification and mapping of natural plant communities (Elliot 2013). Ultimately, such analysis should aid in preservation and management of remaining parcels of this distinctive natural vegetation.

MATERIALS AND METHODS

The area under investigation was in the Western Cross Timbers portion of the Cross Timbers unit of potential natural vegetation (Diggs et al. 1999; Hoagland et al. 1999). It was in the West Cross Timbers ecoregion (29c on the ecoregion map of Griffith et al. 2004) and Cross Timbers and Prairies vegetational area (Correll and Johnston 1979). The study area was in the Texan biotic province of Dice (1943). The Western Cross Timbers developed at the borders of two physiographic units: 1) Coastal Plains and Piedmont and 2) Comanche Plateau of the Great Plains (Fenneman 1931, 1938). Climate was classified by the modified Koppen system as mesothermal in all years, dry season in winter, with occasional desert years (Russell 1945).

Preliminary explorations were conducted on eight tracts (varying from approximately 0.1 to 36 hectares) of natural vegetation in north-central Texas (Erath and

Eastland counties, Texas) that was dominated by sand post oak with a shrub layer made up overwhelmingly of saw or greenbrier (*Smilax bona-nox*) which extended into crowns of oaks. Plant communities in these tracts included an herbaceous layer of varying development that was made up of perennial, cespitose grasses, grasslike plants, and miscellaneous forbs.

All eight tracts had developed on deep-sand soils that were included in the Nimrod-Arenosa-Patilo complex, Patilo-Nimrod, or Patilo mapping units (Soil Conservation Service 1973, 1977b). The Patilo soil series consist of loamy, siliceous, semiactive, thermic Grossarenic Paleustalfs, whereas the Nimrod series consist of loamy, siliceous, active, thermic Aquic Arenic Paleustalfs and the Arenosa series consist of thermic, uncoated Ustic Quartzipsamments (Soil Conservation Service 1990a; Soil Survey Staff 2018). The range site was Deep Sand or Deep Sandy (Soil Conservation Service 1973, 1977a, 1977b, 1978, 1980).

Physiochemical properties of soils were determined from Soil Survey Geographic data retrieved from the Web Soil Survey, National Cooperative Soil Survey (http://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm). Soil data was retrieved for each component of the representative map units underlying the study area. The available water-holding capacity (Dane and Topp 2002) was hand calculated for each soil in the map unit using soil textural class, reported coarse fragment content, and modal soil description depths (maximum depth of 152 cm). Cation exchange capacity (Soil Science Society of America 2001) was used as an indication of soil fertility (Brady and Weil 2008; Lal 2006).

All but the smallest tract of vegetation, a remnant parcel near a highway intersection, had been grazed continually for years by cattle and white-tailed deer (*Odocoileus virginianus*). Wild turkey (*Meleagris gallopavo*) were also commonly observed to use these deep-sand habitats. None of these tracts had burned in the last half century. These parcels had never been treated with mechanical or chemical brush control.

Two of these tracts (approximately 3 and 8 hectares; both in Erath County, Texas) that appeared to have the most advanced state of vegetation development were selected for vegetational analyses. These two tracts had the largest trees (maximum height of about 10 meters, maximum trunk diameter at breast height of approximately 0.3 meter), the largest clumps of trees (those with greatest number of boles per clonal tree; as many five to nine shoots in one modular plant), the greatest frequency of natural canopy openings that were populated primarily by herbaceous plants, and the most species diversity (which was related to occurrence of openings under gaps in the tree canopy).

Vegetation of study tracts consisted of a mostly closed canopy of sand post oak with a few blackjack oaks (Figure 1).

Plants of both oak species were small trees or large shrubs that had an aggregated dispersion in which oak shoots, especially those of sand post oak, grew in clumps. There was a seemingly open (i.e. sparse cover) understory except for saw greenbrier with occasional plants of other shrub species and localized areas of herbaceous cover. Difficult entry and passage beneath and among oak clumps revealed not an openness, but instead fence-like barriers of numerous and largely leafless shoots of saw greenbrier that inflicted shallow lacerations and puncture wounds and restricted through travel by larger animals to established trails or paths. Grazing and browsing by large mammals like ruminants was limited to edges of these trails and the natural openings in the canopy.

An herbaceous layer consisting of native, perennial bunchgrasses; grasslike plants; and forbs had developed sporadically. This herbaceous layer was better developed in well-lit microsites and absent in areas where shade from the closed canopy was most dense. The natural opening or gaps in the otherwise closed-canopy community supported smaller plants of saw greenbrier along with the herbaceous plants. These openings or natural "clearings," which were often found on low mounds or hummocks, were to be randomly distributed throughout the vegetation. The soil surface was covered almost exclusively by a layer of oak leaves with minor components of leaves from other plant species. This leaf cover consisted of an upper portion of raw or undecayed leaves, a middle portion of partly decayed leaves, and a bottom layer of more-or-less fully decomposed leaves laying on O horizons (Oi, Oe, Oa) of the soil. It was a characteristic forest floor of organic matter (Perry et al. 2008).

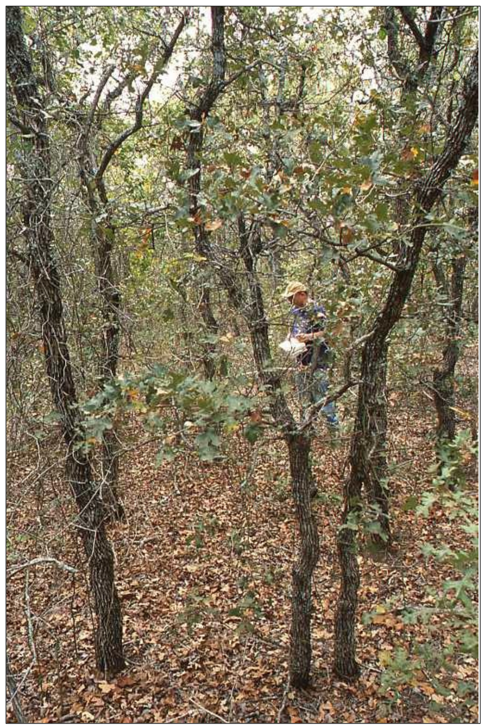

Figure 1. Closed canopy of sand post oak at the study site.

Species composition of the herbaceous-low woody layer was determined from measurements of foliar cover using the step-point method (Bonhan 1989). A sharp-tipped pin was used to randomly sample all plants, detritus, and bare ground occurring within the layer of vegetation delineated by the tallest grass species which was generally little bluestem (*Schizachyrium scoparium*) or sand lovegrass (*Eragrostis trichodes*). We recorded total number of hits for each herbaceous species, shoots of woody plants (both seedlings and vegetative offshoots), dead plant material, and exposed soil surface in the grass-defined layer of vegetation. A total of 5172 points was recorded.

Absolute and relative cover were derived from the total number of point hits. Relative composition of herbaceous species was expressed as both 1) percentage of all plants (including woody species) within the herbaceous zone and 2) of only herbaceous plants.

For woody vegetation, four transects were placed through the study sites. Woody vegetation >1.0 cm in diameter was sampled in 30 randomly chosen quadrats, (5 by 5 m) along the four transects. For herbaceous vegetation and woody vegetation <1.0 cm in diameter, 30 random quadrats (2 by 5 m) were sampled. Species of plants were identified and classified using Diggs et al. (1999), which also served as the reference for common and scientific names. Voucher specimens were deposited in the herbarium at Tarleton State University in Stephenville, Texas. We identified all woody plants in each quadrant and measured diameter at breast height (dbh) of all that were >1.0 cm. The dbh was used to calculate basal area. Density (plants/ha), dominance (basal area/ha) was calculated, and relative-importance values were calculated as described in Rosiere et al. (2013). Vegetational analysis was done at annual peak standing crop and fruit-ripening stage of warm-season species (i.e. early autumn).

RESULTS

The composition and structure of this deep-sand vegetation (Tables 1 and 2) consisted of 1) a canopy made up of crowns of scrubby mature trees of sand post and blackjack oak along with upper shoots of saw greenbrier; 2) an intermediate woody layer of various shrub species and shorter shoots of the two oak species; 3) a lower layer consisting of an herbaceous component of native grasses, grasslike plants, and forbs along with a woody component (mostly seedlings and offshoots of saw greenbrier and the two oak species) that formed a mixed understory of sporadic cover. From perspectives of physiogonomy and dominance, this West Cross Timbers vegetation was a forest community.

Table 1. Density, dominance, and relative-importance values for woody vegetation >1 cm diameter at breast height and saw greenbrier stems in Erath County, Texas.

Taxon	Density (plants/ha)	Dominance (plants/ha)	Importance Value (%)
Trees			
Sand post oak (*Quercus margarettiae*)	2810	48,744.1	54.1
Blackjack oak (*Quercus marilandica*)	70	90.7	0.2
Shrubs			
Saw greenbrier (*Smilax bona-nox*)	28,425	299.1	45.4
Eastern prickly-pear (*Opuntia humifusa*)	80	8.5	0.2
Ashe’s juniper (*Juniperus ashei*)	50	15.4	0.1
Southern blackhaw (*Viburnum rufidulum*)	50	0.5	0.1
Chittamwood (*Sideroxylon lanuginosu*)	10	0.3	0.02
Prickly-ash (*Zanthoxylum hirsutum*)	10	0.3	0.02
Total	31,505	49,158.9	100.1

This forest vegetation was made up overwhelmingly of sand post oak and saw greenbrier (Table 1) with miscellaneous scattered shrubs and an erratic, sparse cover of herbaceous species (Table 2). Herbaceous cover occurred primarily in natural openings found irregularly within the forest vegetation. These openings typically existed on low mounds or hummocks that were a characteristic feature of such deep-sand habitats as described for these soil series, especially the Patilo (Soil Conservation Service 1990a).

Plant communities of these tracts consisted primarily of closed canopies from mature plants of scrub oaks (overwhelmingly sand post oak) the interlocking crowns of which had considerable cover of saw greenbrier. The interrupted or erratic understories consisted of both herbaceous species as well as immature, woody plants such as seedlings-saplings of oaks and smaller shoots of saw greenbrier. The intermediate woody layer was composed primarily of adults of various shrub species. Shrubs were of diverse heights and growth forms. These forms included scraggly bushes; small, single shoots such as those of chittamwood (*Sideroxylon lanuginosum* subsp. *oblongifolium*); and cladophylls of eastern prickly-pear (*Opuntia humifusa*).

Table 2. Species Composition (absolute and relative foliar cover) of herbaceous and woody plants (below 1 cm diameter) in herbaceous/low woody layer of scrub oak forests (including natural openings) at peak standing crop in the Western Cross Timbers, Erath County, Texas as determined by step-point method in mid-October 2012. The letter "T" represents trace amounts of plants.

Category	Hits (number of)	Relative Cover (of herbaceous spp. only; %)	Absolute Cover (all spp. in herbaceous layer; %)
Grasses			
Sand lovegrass (*Eragrostis trichoides*)	13	9.1	3.3
Little bluestem (*Schizachyrium scoparium*)	15	10.6	3.8
White-hair panic (*Panicum acuminatium* var. *villosun*)	32	22.5	8.1
Arrow-feather threeawn (*Aristida purpurascens*)	1	0.7	T
Thinseed paspalum (*Paspalum setaceum*)	3	2.1	0.8
Purple sandgrass (*Triplaisis purpurea*)	2	1.4	0.5
Total	66	46.5	16.8
Grasslike			
Bracted caric-sedge (*Carex cephalophora*)	21	14.8	5.3
Slender flatsedge (*Cyperus lupulinus*)	9	6.3	2.3
Total	30	21.1	7.6
Forbs			
Horseweed (*Conyza canadensis*)	22	15.5	5.6
Heart-sepal wild buckwheat (*Eriogonum multiflorum*)	7	4.9	1.8
Texas bullnettle (*Cnidoscolus texanus*)	2	1.4	0.5
Frostweed (*Verbesina virginica*)	1	0.7	T
Spotted beebalm (*Monarda punctata*)	14	9.9	3.6
Total	46	32.4	11.7

Table 2 (cont.)

Category	Hits (number of)	Relative Cover (of herbaceous spp. only; %)	Absolute Cover (all spp. in herbaceous layer; %)
Trees and Shrubs (seedlings, shoots)			
Sand post oak (*Quercus margarettiae*)	41	10.4	
Saw greenbrier (*Smilax bona-nox*)	192	48.7	
Eastern pricklypear (*Opuntia humifusa*)	6	1.5	
Mustang grape (*Vitis mustangensis*)	1	T	
Chittamwood (*Sideroxylon lanuginosu*)	4	1.0	
Ashe's juniper (*Juniperus ashei*)	4	1.0	
Sugarberry (*Celtis laevigata*)	4	1.0	
Total	252	64.0 (% of cover of herbaceous layer)	
Total plant cover in herbaceous layer	394	7.6 (% of total hits)	
Litter			
Leaf litter	4,241	82.0 (% of total hits)	
Downed tree trunks/crowns	99	1.9 (% of total hits)	
Total	4,340		
Bare ground	438	8.5 (% of total hits)	
Total	5172		

Some sand post oaks grew as single or paired shoots, but more commonly scrub trees of this species existed in clumps of at least three, though typically four or five, up to nine boles. In most cases, it could not be determined if these shoots were of individual plants (different genotypes) or if they were clonal offshoots of the same tree (Figure 2).

In a few instances boles rose from horizontal shoots on or just below the soil surface. Berg and Hamrick (1994) reported that clustering in sand post oak was from both asexual reproduction (shoot proliferation or "suckering") and sexual reproduction from acorns. Acorn production by sand post oak occurred on both sample locations. Given that most trunks of sand post oak grew in clumps or clusters, it seemed likely that asexual reproduction was the predominant mode of regeneration at these locations, but it was also likely that some trunks in clusters had originated from seed. New shoots of sand post oak growing in a power line clearing adjoining one of the study tracts were all from low stumps or rootstocks immediately below the soil surface (i.e., re-establishment was by coppicing and not seedling establishment).

Blackjack oak was the third-most important woody species based on dominance, but blackjack oak had lower density (plants/ha) than eastern prickly-pear. These two species had the same importance value but given the larger size and greater cover of individual plants, we interpreted blackjack oak as the associate woody species of this plant community. Trees of blackjack oak in this deep-sand community almost always consisted of a single trunk although infrequently paired trunks and, rarely, three shoots were encountered. Otherwise, blackjack oak did not form clumps or clusters of shoots in the examined tracts.

Figure 2. Sand post oaks growing in clumps of five boles. Note the exposed, horizontal shoots.

Cover and density of the woody species other than adult oaks were at size and habit of shrubs with the more common species, aside from eastern prickly-pear and saw greenbrier, being southern blackhaw (*Viburnum rufidulum*), lime prickly-ash (*Zanthoxylum hirsutum*), immature plants of the conifer, Ashe's juniper (*Juniperus ashei*), and chittamwood. All of these shrubs or shrub-like plants except saw greenbrier were minor compared to oak species, but they comprised a second or intermediate woody layer. Saw greenbrier, growing as seedlings and young clonal shoots up to adult age-size plants, extended from the soil surface to the crowns of oaks so as to be present in all layers of the plant community. These shrub species, except for eastern prickly-pear in the Cross Timbers, have wide distribution, adaptation to diverse habitats and, perhaps most importantly, are not restricted to deep sand. Two woody species were recorded only as seedlings or asexual shoots in the herbaceous layer: sugarberry (*Celtis laevigata*), a tree species, and mustang grape (*Vitis mustangensis*), a liana. Adults of these two species were seen infrequently on all eight forest tracts, mostly on outer edges of the scrub forest.

White-haired panic (*Panicum acuminatum* var. *villosum*), little bluestem, and sand lovegrass were the major grasses. Little bluestem and sand lovegrass were of approximately the same relative cover (Table 2). White-haired panic had greater cover than that of little bluestem and sand lovegrass combined. Bracted caric-sedge (*Carex cephalophora*) measured slightly greater cover than little bluestem or sand lovegrass and considerably less than white-haired panic. Bracted caric-sedge and slender flat sedge (*Cyperus lupulinus*) together had less measured cover than white-haired panic, but more than little bluestem and sand lovegrass combined.

Grasses made up 46% of the relative cover of the herbaceous-small woody plant layer (the understory) of the forest vegetation. This exceeded the relative cover of forbs which was 32% of the understory. Cover of horseweed (*Conyza canadensis*) varied sporadically throughout the understory, but it was the forb with greatest cover. Cover of horseweed exceeded than that of any herbaceous species except for white-haired panic. Grasslike plants comprised slightly over 20% of the understory cover.

Some herbaceous species occurred at extremely low cover and density. These included such forbs as frostweed (*Verbesina virginica*) and Texas bullnettle (*Cnidoscolus texanus*) and the native annual grass, purple sandgrass (*Triplasis purpurea*). It could be argued that presence at trace amounts versus absence amounted to small differences, but of equal validity is the argument that presence at any amount was important from an indicator plant standpoint. For example, although Texas bullnettle and purple sandgrass are widely distributed their preferred natural habitat is open forests and woodlands that develop on sandy soils. Even trace amounts of cover (i.e., mere presence) of additional species increased biological diversity of the forest community.

Most of the herbaceous cover of this plant community was in natural openings, but plants of all herbaceous species also grew erratically in less shaded spots under the scrub oak-saw greenbrier canopy. Several species of herbaceous species frequently grew together especially where greenbrier shoots and closely spaced oak trunks appeared to offer protection from grazing by cattle and white-tailed deer.

DISCUSSION

Findings about vegetation of a West Cross Timbers scrub oak forest were organized into five major topics: 1) community characterization and successional status, 2) possible factors involved in determining community development, 3) soil and plant relations, 4) affinity with other natural communities, and 5) conclusions with management applications.

Community characterization and Successional Status. Categorization of this Cross Timbers vegetation was problematic. Physiogonomy and species composition of this plant community were subject to interpretation, if not perception. Both sand post oak and blackjack oak typically had the shrub feature of small shoots and, in case of sand post oak, of multiple (generally, four to nine) boles per plant yet with heights up to approximately 10 or more meters and breast height diameters of 20-25 centimeters. With these dimensions the terms “shrub” or “tree” were alternatively appropriate based on criteria of Society of American Foresters (Helms 1998). The term “brush or scrub tree” was seemingly more descriptive, so that “scrub forest” (Helms 1998) was the most consistent term for this woody plant-dominated vegetation. The potential natural plant community for the Patilo soil series was described by the Soil Conservation Service (1978) as “scrub forest.”

Reich and Hinckley (1980) applied the designation of “pygmy forest” to woody vegetation dominated by blackjack oaks that were naturally dwarfed or stunted on sandstone bluffs in the Ozark Plateau. These blackjack oaks were stunted so as to have a distorted habit or growth form (Reich and Hinckley 1980) much like elfin-wood or krumholtz vegetation (Barbour et al. 1999). The label of “pygmy forest” was first applied to coniferous forests of stunted, sometimes distorted, and, in general, small-sized trees on infertile soils in the Coast Range of northern California (Jenny et al. 1969; McMillan 1956; Westman 1975). The concept of pygmy forest was later expanded to include climax vegetation dominated by coast live oak (*Quercus agrifolia*) that develops on deeper sand dunes as described by McBride and Stone (1976). Habit of sand post oak and physiogonomy of vegetation it dominated on deep-sand sites in the West Cross Timbers were consistent with those of pygmy forests. Blackjack oak, the associate tree species, also had a scrubby, stunted appearance on deep-sand sites in contrast to larger trees of more typical arborescent form on other Cross Timbers habitats. Perceptions of Cross Timbers trees as recorded in various frontier-era journals and military reports included such descriptions as "stunted trees," "small, gnarled," "dwarfish," "short stunted oak," and "low, shrubby timber" (Foreman 1947, pp. 49, 62, 81, 103, 113).

Pygmy forest was also applied to old-growth woodlands comprised of dwarfish, stunted, and twisted (and ancient) trees of conifers, especially Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*), that developed on shallow soils and volcanic parent material in lava flow badlands such as those of the El Malpais National Monument in western New Mexico (Wayman 2015). This unique malpais vegetation and its edaphic habitat was first described by Lindsey (1951) and later appraised by Grissino-Mayer et al. (1997).

Although many plants of pygmy forest species have gnarled, twisted, or otherwise grotesque habits this morphology is not a consistent feature. Many plants are just smaller versions of regular-sized and -shaped plants as, for example, conifers in the pygmy forest of the California Coast Range studied by Jenny et al. (1969) and Westman (1975). This was consistent with the meaning of "pygmy" or the synonym, "dwarf" (Merriam-Webster 2003). The twisted and gnarled habits of normal-sized trees is a notable feature of Cross Timbers oaks (Diggs et al. 1999; Francaviglia 2000; Hoagland et al. 1999) such that this characteristic is not a morphological form that designates a scrub or dwarf tree. Shoots of sand post oak were typically twisted, crooked, and knotty as well as being of diminutive size at maturity. It was not known if sand post oak had the genetic potential to grow to size of post oak. Blackjack oak, with either single or multiple shoots, on deep sand exhibited this habit, though less consistently (Fig. 3).

Figure 3. Shoots of sand post oak showing their twisted, crooked, and knotty growth as well as their diminutive size at maturity.

It would be appropriate to interpret the scrub blackjack and sand post oaks growing on deep sand in the Western Cross Timbers as dwarf trees, and the woody plant community they form as a pygmy, dwarf, or scrub forest. This scrub tree-dominated vegetation with its closed canopy was not "woodland" as labeled by Elliott (2013) because by definition (Helms 1998), woodland is a tree-dominated community with an open canopy (even though it may consist of small, short-trunked trees). As with previous studies of pygmy forests (Jenny et al. 1969; McBride and Stone 1976; Reich and Hinckley 1980), we concluded that woody vegetation dominated by sand post oak in the Western Cross Timbers constituted a scrub or pygmy forest, the adult oak trees of which were dwarfs.

According to the native vegetation classification system developed by Daubenmire (1966), the Cross Timbers scrub forest dominated by sand post oak and with saw greenbrier as the dominant shrub, would be a Sand Post Oak-Saw Greenbrier habitat type. As a cover or dominance type in the system used by the two leading US scientific societies dealing with management of natural vegetation, this dwarf forest would be a variant of the Cross Timbers types (SRM 731, SRM 732) recognized by the Society for Range Management (Shiflet 1994) while it would have to have a new designation, a title, of Sand Post Oak followed by an SAF number for inclusion in the forest types described by the Society of American Foresters (Eyre 1954, 1980). For the natural plant communities of Texas proposed by Elliott (2013), this vegetation would be Sandyland Scrub Oak Forest for the West Cross Timbers.

It was proposed (and explained below) that this dwarf forest is the potential natural vegetation for certain deep-sand habitats. It was further concluded that the soils of such environments were the principal determining factor in development of this forest community. These sand post oak-dominated dwarf forests comprise an edaphic climax. Below we reviewed possible determinative habitat variables and elaborated on our designation of soil-based climax vegetation.

Consistent with climax community is the concept that each climax is part of a fully evolved, mature, and dynamically stable ecosystem (Odum 1969; Orians 1975). The limited species richness and comparatively consistent composition and structure of this deep-sand scrub oak forest suggested a low level of biodiversity and, perhaps, by extension incomplete ecosystem function and maturity. Madritch and Hunter (2002) studied nutrient fluxes in tree litter relative to phenotypic diversity in a turkey oak (*Quercus laevis*)-dominated sandhills community which had comparatively low species diversity. They concluded that high species diversity might not be as important to ecosystem function as was diversity at various levels, including intraspecific variation, relative to natural diversity at those levels (Madritch and Hunter 2002).

Turkey oak is a scrubby species that is often associated with sand post oak on sandy soils (Berg and Hamrick 1994; Espeleta and Donovan 2002, 2004, 2009; Schafale and Weakley 1990). It seemed reasonable that principles regarding ecosystem functions of a turkey oak-dominated forest might apply also to a sand post oak-dominated scrub forest. Madritch and Hunter (2002) proposed that intraspecific diversity was more important in a community composed of a low number of species (such as scrub oak-dominated forests) than in relatively species-rich forests. Hiers et al. (2014) specified that clones of sand post oak provided habitat heterogeneity on poor sites of longleaf pine-oak forests. Considerable genotypic and phenotypic variation was to be assumed in the scrub oak forest community of the West Cross Timbers which had numerous and obviously distinct trees of sand post oak, almost all having multiple trunks. In addition, this same form of variation could be expected with the clonal, many-stemmed saw greenbrier, the dominant shrub of the Cross Timbers deep-sand dwarf forest. Simpler natural communities comprised of a few species can have considerable biodiversity and stability so as to perform as fully functional ecosystems.

Factors determining development of Cross Timbers scrub oak forest. We considered the most likely major factors responsible for development of pygmy or scrub forests on deep-sand sites in the Western Cross Timbers. Possible factors included fire, grazing, local disturbance, and soil.

Fire as a factor. Fire has long been considered to be an important factor in development and maintenance of Cross Timbers vegetation, especially of the savanna form. This was shown in early personal accounts like that by Irving (1835) and through reviews by Hoagland et al. (1999) and Francaviglia (2000). Savanna physiogonomy was alluded to in some range site descriptions for the Patilo soil series (Soil Conservation Service 1980) and for similar soils and the Deep Sand Savanna range site in Oklahoma (Soil Conservation Service 1960, 1966, 1979) where oaks were of lower density and less cover (i.e. more widely spaced) and with relatively well-developed herbaceous understories. Such Cross Timbers savanna communities that may have existed to considerable degree as fire-maintained or, at least, fire-influenced communities were in contrast to vegetation of deep-sand habitats (and in absence of recent fire) in which large shrubs to small trees along with saw greenbrier developed into scrub forests with closed canopies and soil surfaces covered with oak leaves.

Stambaugh et al. (2011) hypothesized that absence of fire contributed to increased tree density and canopy closure in a relict post oak-sand post oak woodland in the transition between the Post Oak and Blackland Prairie vegetational areas. Stambaugh et al. (2011) reported a sparse cover of herbaceous species in an old-growth relict stand of post and sand post oak in northern Texas. These two factors are interrelated as, for instance, when overgrazing eliminates herbage that is the source of fuel. Continued overgrazing and underburning creates a cycle of ever increasing tree canopy and on-going reduction of any herbaceous layers. Anderson and Brown (1986) reported varying responses to fire in closed canopy oak-hickory forest, blackjack oak savanna, and forest-prairie edge plant communities in which sand lovegrass and little bluestem were major grasses. Fire is interrelated with overgrazing which reduces fuel. Anderson and Brown (1986) reported that when there was adequate accumulation of fuel, fire had destabilizing impacts on forests resulting in savannas and forests with more open canopies. Yet, fire did not result in secondary succession or apparent changes in species composition. In some instances, there were greater numbers of young tree shoots (seedling and sapling) following fire. Response of grass to fire was not reported by Anderson and Brown (1986) though they implied that fire stabilized grasslands dominated by species such as little bluestem and sand lovegrass. Overall, fire has had an array of impacts on oak and oak-hickory forests in the greater Cross Timbers Region.

Peet (2006) listed several associations of fire-maintained longleaf pine (*Pinus palustris*) ecosystems in which sand post oak was a major component. Glitzenstein et al. (1995) found that sand post oak was a major fire-adapted species in sandhills longleaf pine types. Based on studies in north-central Florida, Cavender-Bares et al. (2004) placed each of 17 oak species in one of five groups of fire return intervals. Sand post oak was included in the group of three oak species with the greatest fire frequency (Cavender-Bares et al. 2004). Greenberg and Simons (1999) analyzed fire effects on old-growth oaks in the sandhill oak-pine ecosystem of peninsular Florida and found that oaks of several species, including sand post oak, were important components of this "fire type" forest community. Sometimes topkill of sandhill oaks, particularly smaller plants, occurred depending on fire intensity, season, etc., but such trees or shrubs resprouted. Likewise, most adult oaks were "fire-resistant" with over 80% of sand post oaks having fire scars at some locations (Greenberg and Simons 1999). Hiers et al. (2014) explained that the prolifically resprouting sand post oak developed a "clonal dome" that afforded fire protection and prevented topkilling of shoots inside asexual clumps. Sand post oak was reported as living to ages of over 200 years on fire-maintained forests (Greenberg and Simons 1999) and up to 300 years on regularly burned forests in Florida (Knight 2004; Varner and Pederson 2004). In reporting these ages, Hiers et al. (2014) emphasized that such longevity and persistence with frequent fire indicated that sand post oak was a pyrophytic species.

It could be expected that sand post oak would have a similar response to fire in the sandyland Cross Timbers scrub forest where most oak shoots were adult size and fine fuels were limited almost exclusively to shoots of saw greenbrier. Studies have shown consistently that sand post oak is a fire-adapted species. Kreye et al. (2013) designated it as a pyrophytic oak. Fire adaptations of sand post oak include vigorous resprouting and even protection against topkill of shoots by development of clonal clumps (Hiers et al. 2014). In some of the earliest writing concerning fire in the Cross Timbers, Gregg (1844) described the adaptation of post and blackjack oaks to annual burning. Sand post oak might be even better adapted to fire. (Hiers et al. 2104) reported that sand post oak burned as intensely as post oak.

The rhizomatous or, according to some authors, stoloniferous habit of sand post oak was found to be a growth form and a means of asexual reproduction of this species that takes place irrespective of disturbances like fire, felling, or land-clearing (Townsend 2005). The formation of large rhizomes among boles of sand post oak on the current study locations was consistent with the finding of Townsend (2005) because there was no record, landowner memory, or conclusive fire scar evidence that the scrub oak forests in the current study had undergone fire during the lifetimes of existing sand post or blackjack oak boles. In the scrub forests of the present study, fire - alone or in concert with other variables - cannot be ruled out as a factor in initiation or maintenance of sand post oak populations present at seedling and early clonal shoot stage (or both) prior to existing records or that bore no fire scars. Given absence of recorded pre-history of fire it is possible that catastrophic fire (mega-fires) could reset vegetation of these deep sand sites.

Sand post oak also reproduces sexually, with acorns being dispersed by animal vectors up to distances of tens of meters (Berg and Hamrick 1994). These workers determined that clumps of the highly clonal sand post oak could consist of more than one genetic individual, but that most shoots in clusters of sand post oak were clonal units (Berg and Hamrick 1994). After remarking that burning in the Cross Timbers scorched lower branches of trees, Washington Irving (1835: 220) described scrub oaks "some not above a foot high, yet bearing abundance of small acorns." Such frontier observations suggested that frequent burning of Cross Timbers vegetation by Indians did not prevent acorn production even on the smallest oaks. We noted acorn production on both tracts of scrub forest that we sampled as well as on other observed forest stands in the Western Cross Timbers, and this was over multiple years.

Given the strongly rhizomatous nature of sand post oak (with or without disturbance), its re-sprouting feature, the lack of fine fuels in closed canopy scrub forest dominated by this species, and production of acorns it was unlikely that absence of fire was a major factor in determining this plant community. There was empirical evidence for this conclusion based on incidence of land-clearing and wild fire on two areas of sand post oak-dominated forest adjoining the two forest tracts we sampled.

A portion of the larger tract of dwarf forest sampled in the current study had been mechanically cleared (combination of sawing and bulldozing) for a power line corridor immediately prior to sampling of the intact portion. The following year almost all of the sand post and blackjack oaks, nearly all of which had been adult trees, had re-sprouted from stumps and/or rhizomes. This indicated that even if fire did top kill adult trees (an unlikely event due to limited availability of fine, flammable fuels for initial ignition) these same plants would have resprouted.

Part of the other tract of sand post oak scrub forest in the present study had a lightening-ignited wild fire in August during Severe Drought (Palmer Index). Less than 0.25 ha burned before it was extinguished by fire suppression crews. Fire-suppression activity severely disturbed the soil surface so that this small area was not representative of either natural or prescribed fire. Nonetheless, it was observed that 15 months after the hot fire (during prolonged drought) none of the sand post or blackjack oak shoots that ranged from sapling up to adult trees had any apparent damage from the fire. All shoots of saw greenbrier had been top-killed, but this species had resprouted profusely resulting in greater apparent foliar cover in the understory of the burned than in the adjoining unburned and sampled part of this forest tract.

These observations were consistent with statements that fire results in increases of woody plants on the Deep Sand Savannah range site of southern Oklahoma (Soil Conservation Service 1960, 1966) which was similar to the deep-sand scrub forest site in the Western Cross Timbers. Kreye et al. (2013) classified post oak and sand post oak as pyrophytes and explained that these flammable pyrophytic species were being replaced by fire-sensitive mesophytic species as a result of fire exclusion in much of the southeastern forest region. Hiers et al. (2014) reached the same conclusion describing sand post oak as an old-growth component in frequently burned upland forests.

Tyrl et al. (2008) stated that control of saw greenbrier was difficult unless it was burned frequently because this species has large food-storing lignotubers. Frequency of fire needed for control of saw greenbrier was not given, but it was remarked that even with periodic burning or mowing saw greenbrier became more shrub-like (Tyrl et al. 2008). Gucker (2011) concluded that this species was tolerant of periodic fire due to its ability to resprout from rhizomes when top-killed. Gucker (2011) also concluded that saw greenbrier was not dependent on fire for maintenance or reproduction. Saw greenbrier is a member of fire-tolerant communities that develop with periodic fire, yet also of other plant communities developing with low fire frequency (Gucker 2011).

Saw greenbrier exhibited little difference in cover following a summer fire that burned through vegetation on the eastern margin of the Eastern Cross Timbers in south-central Oklahoma (Adams et al. 1982). Hutcheson et al. (1989) reported that following a winter fire in the Texas Edwards Plateau, saw greenbrier had by July of that year already developed greater dominance and shoot frequency than before prescribed burning. In southeastern North America, saw greenbrier is an abundant member of various forms of pine forests, especially those of longleaf pine (*Pinus palustris*), a climax forest type that can only persist with periodic fire (Beckett and Golden 1982; Gilliam and Christensen 1986).

It seemed unlikely that this scrub forest vegetation would accumulate quantities of fuel sufficient for fire frequency or intensity adequate to have other than minimal impact on cover of saw greenbrier, especially given its tremendous capacity to store food in subterranean organs. Release of nutrients from burnt vegetation could benefit growth of new shoots. Hutcheson et al. (1989) and Gucker (2011) showed that fire resulted in increased cover and density of saw greenbrier.

Successional status of saw greenbrier has not been established. Status of saw greenbrier in vegetation development is perhaps as variable as this widespread species itself. Tyrl et al. (2008) wrote that saw greenbrier was a species of mid to late succession though it formed densest thickets following recent disturbance (e.g., old fields). Gucker (2011) concluded that saw greenbrier was a facultative seral species citing several studies in which saw greenbrier had increased with disturbance. On bottomland forests in the Texas Blackland Prairie, Nixon (1975) studied secondary plant succession on gravel quarries of different ages subsequent to abandonment. Overall (across successional stages), Nixon (1975) found that saw greenbrier was the most important liana species though it declined with advancing age of the sere (time since quarry abandonment) until it was second in importance to poison ivy (*Toxicodendron radicans*) on oldest quarries. Saw greenbrier was also the shrub species with the second-highest importance value on unquarried forests (Nixon 1975). Saw greenbrier defied a simple successional status across north-central Texas. This was consistent with it being a common species in various plant communities and habitats in this general area (Diggs et al. 1999).

Nixon (1975) emphasized that Dyksterhuis (1948) had recognized a *Quercus-Smilax* community as one of four major topographic or edaphic climax communities of the Western Cross Timbers. In his classification, Dyksterhuis (1948) unequivocally indicated that saw greenbrier was a dominant climax species, though certainly there were implied limits to cover of saw greenbrier beyond which this species exceeded that of the climax vegetation. Nonetheless, Dyksterhuis (1948: 333) specified that “dense thickets of saw greenbrier” commonly found on “deep sands” were representative of some Western Cross Timbers vegetation that existed in frontier times. These conclusions were consistent with our interpretation that the deep-sand dwarf forest type comprised climax vegetation of a Sand Post Oak-Saw Greenbrier habitat type based on the widely used Daubenmire (1966) method of community inventory.

Sand post and blackjack oaks on the eight tracts of scrub oak forest we observed were almost all adult trees. Tree heights and trunk diameters of several trees were noticeably greater for oaks growing on the two tracts on which we conducted vegetational analyses. Nonetheless, oak trees were of similar size and morphology on the eight tracts, all of which had developed on some combination of the general Nimrod-Arenosa-Patilo soil mapping unit (Soil Conservation Service 1973, 1977b). If there had been recurrent fires on the tracts of the present study, trees might have been immature (sub-adult age classes) and of corresponding smaller sizes (depending on frequency of fire). In such cases, fire would have retarded tree development or progression to life-cycle maturity. In such hypothetical circumstances, fire would have overridden the genetic potential of oak growth on the deep-sand habitat. Such arrested tree development would have been in concert with other climatic variables such as precipitation and ambient temperature. For that matter, fire is an atmospheric or climatic variable.

Retardation of tree development by recurrent fire would have changed age-size structure, though not necessarily species composition, of the vegetation. Assuming (for sake of argument) that fuel was adequate for top-killing of adult and younger oaks, fire could have changed forest structure and physiogonomy, though not likely species composition. Even under this extreme (and unlikely) condition, there might have been no reduction in number of trees at a genotypic level yet an increase in number of clonal oak shoots (as well as of saw greenbrier shoots like that described above).

Unless there was annual or very frequent fire, some of these clonal oak sprouts would continue to grow and produce increasingly greater foliar cover so that in a few to several growing seasons crowns of juvenile trees would probably have formed a closed canopy, though of immature rather than adult oaks. This was the condition described by Gregg (1844) for post oak and blackjack oak in the Cross Timbers due to annual burning. A closed canopy of oak regrowth would be closer to the soil surface which might be even less conducive to development of herbaceous species like the climax grasses. Such a phenomenon has been documented with regrowth of various woody species in this region (Hamilton et al. 1981).

A more fundamental consideration is flammability of this scrub oak type. While saw greenbrier shoots readily burn, fuel of these shoots is apparently inadequate to generate fires intense enough to cause much lasting damage to this woody vine, let alone to adults or even saplings of the two oak species. Francaviglia (2000) concluded that even fires set by Native Americans died out for lack of fuel in certain parts of the Cross Timbers. Such conditions might form the sand post oak-saw greenbrier community, especially at the most advanced stage with a sporadic herbaceous understory and approximately 80% of the soil surface covered by a densely packed layer of partly decomposed oak leaves (i.e. low-flammability leaf mulch). Obviously herbaceous material growing in natural openings would burn readily, but fuel in the oak-greenbrier vegetation surrounding these openings might not be adequate to carry fire to the grass-dominated herbage. Besides, these local microsites already supported climax grasses without recent fire. The one plant species that most likely would have been eliminated or, at least, reduced by frequent fire in the scrub forest was Ashe juniper, a nonsprouting conifer (Diggs et al. 1999).

It was concluded that scrub forests dominated by sand post oak in the Western Cross Timbers could not be interpreted as a fire community type or pyric climax. Neither, however, should these plant communities be seen as vegetation existing due to absence of periodic fire given the demonstrated ability of the dominant species to survive or even thrive with recurrent fire. Rather, fire is a largely irrelevant factor in influencing species composition of what we regarded as the potential natural vegetation. The possible role of fire in retarding tree growth and preventing development of sand post and blackjack oaks to their mature size in some stands cannot be ruled out (periodic fire could result in stands of sub-adult trees), but evidence in this study and reports from previous observations and investigations led to the conclusion that fire does not play a defining role in development of this scrub oak-saw greenbrier forest community.

Grazing and browsing as a factor. The possible role of defoliation by animals in determining at, least, influencing vegetation of this sand post oak-dominated forest was considered. Conceivably, heavy grazing and browsing by ungulates, especially grass-preferring cattle (Holechek et al. 2004), could have been a factor - though not necessarily a sole-determining factor -in species composition of the grazable-browsable understory of this scrub forest. This possibility was considered given the obviously heavy defoliation, high degree of use of the dominant grasses.

Ultimately, heavy defoliation as a variable responsible for the sparse, sporadic herbaceous cover was ruled out because the major herbaceous species, especially the perennial grasses, in the understory of the scrub forests were the same species that were reported (Soil Conservation Service 1973, 1977a, 1977b, 1978, 1979) to be the climax herbaceous species for this range site (named variously as Deep Sand, Deep Sandy, or Sandy for the Nimrod and Patilo soil series). Little bluestem and sand lovegrass, the native tall- and mid-grass species, respectively, with most cover and greatest density on the two forest tracts we sampled, were interpreted as the two major potential grass species for this range site (Soil Conservation Service 1973, 1977a, 1977b, 1978, 1979). White-haired panic, the grass species with greatest cover on our sampled tracts, was not named in these reports, but it was included under the name of Scribner panicgrass, the general common name in these soil surveys for all the rosette-forming *Panicum* species.

Little bluestem was recognized as the dominant climax herbaceous species of the Cross Timbers (Shiflet 1994). Little bluestem and sand lovegrass are readily eaten by cattle and generally categorized as decreaser or even ice cream species (Leithead et al. 1976; Tyrl et al. 2008), meaning they are some of the first species to decline under overgrazing (i.e. they are most sensitive to heavy or, especially, excessive defoliation by animals (Soil Conservation Service 1967; Stoddard et al. 1975). Dyksterhuis (1948) emphasized that sand lovegrass was a species that was virtually absent under overgrazing in the Western Cross Timbers. Sand lovegrass was named as the principal decreaser on the Deep Sandy range site in Erath County, Texas (Soil Conservation Service 1973).

The fact that white-haired panic, little bluestem, and sand lovegrass remained the principal grasses (though limited in their cover and density) on heavily grazed sand post oak-saw greenbrier scrub oak forests indicated that grazing was not solely responsible for the limited herbaceous layer in this range plant community. The Deep Sandy range site description for Erath County, Texas (Soil Conservation Service 1973) explained that typically “small post oak trees” [i.e. sand post oak] shade 60% to 90% of the soil surface and restrict grass growth. Our findings were consistent with this conclusion.

Furthermore, when vegetation was sampled at peak standing crop (in early autumn) there were none of the naturalized, cool-season, Eurasian, annual grasses and forbs that are widespread throughout this region and that invade overgrazed range and domestic pasture often to point of dominance. Remarkably, none of these exotic herbaceous species (at any stage of growth or decomposition) were found in any of the sand post oak-saw greenbrier stands that were observed.

In summary, there was no evidence that grazing by livestock or wildlife had changed species composition of the understory of this deep-sand range plant community. The potential for greater numbers of grass plants, increased grass cover, and higher vigor of dominant grasses under lighter utilization cannot be ruled out given these commonly observed responses of high-successional species to lighter degree of use (Stoddard et al. 1975; Butler et al. 2003; Holechek et al. 2004). Heavier degree of use did not, however, result in elimination of climax grasses, increased numbers and cover of invasive annual species, or partial replacement of native species by exotic grasses or forbs, which is the usual pattern of range degradation (plant community retrogression) on these range sites (Soil Conservation Service 1973, 1977a, 1977b, 1978, 1979, 1980).

Local disturbance as a factor. Another possible cause of limited herbaceous understory and, with exception of scattered openings, development of a closed canopy forest was competition between expansive root systems of established trees and smaller herbaceous plants, perhaps in conjunction with mulching and alleopathic impacts as reported by McPherson and Thompson (1972) with post oak and blackjack oak leaves in the Cross Timbers of northern Oklahoma. The tree leaf layer on the soil surface of the sand post oak-dominated forest undoubtedly had a mulching influence, but it was not determined if this was responsible for the limited herbaceous cover. Nor was it known if oak leaf cover (and possible alleopathic affects) acted in concert with shade, potential root competition, etc. to restrict cover and density of herbaceous species. Alternatively, it was not known if this leaf mulch functioned to conserve soil moisture so as to benefit the few plants of herbaceous species.

Gaps in vegetation, especially those in forests, have been the focus of some recent vegetation studies as summarized by Keddy (2007). Patch dynamics (Pickett and White 1985) is concerned with more or less local disturbances in established (usually high-seral or climax) vegetation. Windthrow, lightning strike, ice breakage, spot fires, disease, and local zootic disturbances ranging from insects to rodents have been considered as variables in vegetation dynamics or plant disturbance ecology (Johnson and Miyanishki 2007). No basis for such spatially restricted factors or processes was found explaining the occurrence of scrub oak-greenbrier forests in the Western Cross Timbers or for natural openings (canopy gaps) in this vegetation. Even if future studies in this pygmy forest revealed allelopathic and mulching effects of oak leaves such interactions would be manifest, to large degree, through the soil component of this dwarf forest ecosystem.

Soil: an edaphic climax. The key distinguishing features of the Cross Timbers scrub forest community were its deep-sand habitat, dominance by sand post oak, and high shoot density of saw greenbrier. The earliest ecological studies of the Cross Timbers such as that by Tharp (1939) recognized that this mosaic of natural vegetation was primarily attributable to soils, especially sandy soils such as the Trinity sands of the Western Cross Timbers (Braun 1950; Sellards et al. 1932). Dyksterhuis (1948:334) stated definitively: "The very existence of the Cross Timbers is largely traceable to certain geologic units from which the sandy soils are derived." The greater moisture availability of Cross Timbers soils is so much more favorable than that of surrounding soils in this drought-prone region that the Cross Timbers was used as a textbook example of post-climax vegetation, a natural plant community with composition and structure characteristic of vegetation that develops under wetter, more moderate climates than climatic conditions leading to development of the regional climax (Weaver and Clements 1938). These older climax theories did not directly address soil microbiota (Jensenet al. 1986; Coleman and Crossley 1996; Lakshmannan et al. 2014). The soil microbiome could influence soil chemistry, especially pH (Pinton et al. 2007; Fierer 2017; McPherson et al. 2018).

The sandyland or deep sand aspect of the Patilo-Nimrod-Arenosa soil unit that underlaid the sand post oak-dominated scrub forest differs from the general sandy soil characteristic of the Cross Timbers. The soils of the scrub forest have both greater depth of profile and higher proportion of sand than most other Western Cross Timbers soils (Soil Survey Staff 2018). Given the traditional explanation for development of Cross Timbers vegetation (especially of trees being dominant and defining components) attributable to more mesic edaphic habitats (Braun 1950; Dyksterhuis 1948; Francaviglia 2000), our initial hypothesis for forests dominated by sand post oak was that deeper sand was even more mesic. The reverse condition proved to be the case. Rooting depth of sand Postoak was not determined so as to know if roots extended to any surface aquifers.

The Patilo, Nimrod, and Arenosa soils that comprised the composite mapping unit of the sand post oak scrub forest were shown to have physical and chemical properties different from those of neighboring Cross Timbers soils (Soil Survey Staff 2018). While no physical limitations were recorded for these three soil series, each was shown to demonstrate redoximorphic features that indicated waterlogged states and possible anaerobic conditions, but other soils in this area also have seasonal water tables and do not have sand post oak. This absence of molecular oxygen limits root development, especially when such anaerobic environments coincide with rapid root elongation and respiration (Pezeshki 1991).

Depths of redoximorphic features of these soils were related to the landscape positions on which the soils form (Ruhe 1975). Nimrod is typically found on broad upland summit landscape positions. Patilo is found on moderately steep shoulder and backslope portions of the landscape. Arenosa typically occurs on more strongly sloping backslope portions of the landscape (https://soilseries.sc.egov.usda.gov/OSD_Docs/P/PATILO.html). The relief of these landscape positions impacts water movement through the soils and leaves a legacy in the morphology of the soils (Ruhe 1975). This could be related to current and/or past climates.

Timing of anaerobic condition occurrence was not measured, but it can be assumed it followed precipitation events. Precipitation events occur predominantly in spring and autumn. The soils differed in depths to the redoximorphic features with Nimrod showing the shallowest depths (102 cm), followed by Patilo (127 cm) at an intermediate depth, and Arenosa with the greatest depth of 165 cm (Soil Survey Staff 2018).

The Arenosa soil is poorly developed consisting of a thin A horizon over several C horizons. This is likely do to the steeper landscape position where erosion exceeds soil development. Lateral translocation of soil weathering products are probably more pronounced than vertical translocation as evidenced by a distinct lack of subsurface accumulation of soil weathering products. Arenosa soil is not devoid of vertical movement, however, and shows a markedly lower reactivity at greater depth (pH 4.5 to 5) than Nimrod or Patilo (pH 5.1 to 5.5). This is likely due to a relatively higher fulvic acid fraction (derived from vegetative humus) moving through the Arenosa profile (Soil Survey Staff 2018). Fulvic acids are very efficient at chelating and translocating mineral weathering products, probably out of the solum into the unconsolidated parent material below (Brady and Weil 2008; Greenland and Hayes 1978; Joffe 1949). Fulvic acids enhance growth of shoots and roots as well as stimulate root initiation and elongation (Chen and Avaid 1990). Thus, limited root development due to anaerobic conditions resulting from waterlogged conditions of these deep-sand soils (Pezeshki 1991) could conceivably be partially offset by role of fulvic acids in stimulating roots. Given these conditions, it was unlikely that periodic waterlogged soils hindered growth of sand post oak.

Arenosa soil has less than 5% weatherable minerals in the solum (Soil Survey Staff 2018). Consequently, the ability to hold nutrients in the Arenosa is lower than either the Patilo or Nimrod. Cation exchange capacity of Arenosa, Patilo, and Nimrod series was 1 to 4, 1 to 25, and 7 to 15 centemoles of charge per kg, respectively. By comparison, cation exchange capacity of five associated, sometimes contiguous, soil series was: 1 to 20, 1 to 25, 2 to 20, 2 to 25, and 2 to 30 centemoles of charge per kg for Selden, Windthorst, Duffau, Demona, and Chaney soils, respectively (Soil Survey Staff 2018).

With the conspicuous exception of the lowest cation exchange capacity values for the Arenosa and the highest low end of cation exchange capacity for the Nimrod soil, fertility did not appear to vary substantively between soils of the scrub forest and those of associated soils which did not support sand post oak-dominated forest communities. Certainly there was not enough difference in fertility between soils of the scrub forest and those of more typical West Cross Timbers vegetation to explain the contrast of a closed canopy scrub forest that was comprised almost exclusively of sand post oak with more open woodland or savanna vegetation devoid of sand post oak and populated by post and blackjack oaks.

The subsoil accumulation of soil weathering products such as secondary phylliosilicate clay along with oxides and oxihydroxides of metals in the Nimrod and Patilo is the source of nutrient-holding capacity (Soil Survey Staff 2018). These subsoil accumulations also impact the soil's available water-holding capacity, the water status between field capacity and permanent wilting point (Soil Science Society of America 2001).

Available water-holding capacity of Nimrod, Patilo, and Arenosa were shown to vary, depending upon exact texture and soil compaction (or bulk density), from 11.4 to18.5, 9.7 to 16.3, and 4.8 to 10.4 cm of available water-holding capacity, respectively (Soil Survey Staff 2018). These values compared to available water-holding capacities of the following associated soil series: Chaney, 15.7 to 21.1; Windthorst, 15.7 to 22.9; 15.7 to 22.9; Demona, 16.3 to 22.1; Duffau, 16.5 to 27.4; and Selden, 26.9 to 41.7 cm of available soil water, respectively (Soil Survey Staff 2018). Available water-holding capacities of the three soils of sand post oak-dominated scrub forests were considerably lower than those of five associated Cross Timbers soils. This phenomenon was most pronounced for the Arenosa series. Droughty (xeric) conditions of the three scrub forest soil series likely produced a harsher habitat that had a major influence on colonization and establishment of sand post oak, which again, is a species restricted to deep sands (Diggs et al. 1999; Nixon and Muller 1997). It is likely that this xeric, edaphic habitat gave a competitive advantage to sand post oak relative to post and blackjack oak on this Deep Sand range site resulting in a forest stand comprised almost exclusively of sand post oak.

The complex relationship between retention of water in soil and its subsequent absorption by roots (Black 1968) would be quite similar among the related species of sand post, post, and blackjack oaks. Perhaps sand post oak had a competitive advantage in water absorption on beds of deep sand. Regardless of effectiveness of soil water uptake by sand post oak, this species via natural selection was better adapted to the more limited soil moisture conditions (and, secondly, to lower soil fertility) of the three deep-sand soils of the dwarf forest ecosystem.

Rates of water infiltration into mineral portions of sola of sandy soils were likely influenced by their O horizons as well as the mulching feature of the oak leaf layer present on soil surfaces. It could be assumed that leaf litter on soil surfaces reduced evaporation of soil water (i.e. a mulching affect). Although details of the soil-water-plant complex were not studied, it was determined that lower quantity of available soil water was the operative phenomenon which permitted establishment and persistence of sand post oak. Deep sandbeds of the three soils of the dwarf forest had less water available for plant growth in their profiles. The lower water-holding capacities of these West Cross Timbers soils (in spite of their considerable depths) limited tree domination of this scrub forest to a single species, sand post oak. Likewise, sand post oak was restricted to a habitat characterized by xeric or droughty (and comparatively infertile) soils. Said another way, it was only on these extremely water-limited soils that sand post oak could outcompete post oak and blackjack oak, co-dominant trees of the Cross Timbers.

Numerous workers (Diggs et al. 1999; Gleason and Cronquist 1991; Muller 1951; Tucker and Muller 1958) specified that sand post oak was restricted to soils comprised of deep sand. Linex (2014:276) was the only reference we found that specifically stated this edaphic habitat was "too droughty for many other trees to survive." Linex (2014) provided no data or sources as basis for his empirical conclusion, but it was supported by the current assessment that was based on quantitative findings, field observations, and published characteristics of these sandbed soils (Soil Survey Staff 2018).

With limited water-holding capacity (low quantities of available soil water) and low to moderate buffering capacity of cationic nutrients, plants would need larger root systems, larger roots relative to shoot biomass and crown cover, or perhaps some sort of endomycorrhizal association in order to explore a greater volume of soil to meet their mineral and water demands (i.e. greater surface areas of roots would be needed on drier, less fertile soils to obtain plant nutrients). Individual plants of comparatively small or diminutive size and plant species that grow to smaller size at maturity might be adaptations to harsh soil environments that explained domination of sandbed soils by the shrublike sand post oak. Soil, specifically soil water, is the principal environmental variable responsible for development of a dwarf forest with a single dominant tree species. The sand post oak-dominated scrub forest is the potential natural vegetation for this forest site in the West Cross Timbers. It constitutes a sand post oak cover or dominance type that is an edaphic climax.

Current quantitative findings of this dwarf forest corroborated qualitative descriptions of the natural vegetation as defined for the Deep Sand or Deep Sandy range site (Soil Conservation Service 1973, 1977a, 1977b, 1978, 1980). Site descriptions and our inventory consistently showed that for this deep-sand habitat the native plant community was scrub forest dominated by sand post oak with saw greenbrier comprising the major shrub component and with a sporadic, poorly developed herbaceous layer that was limited primarily to natural forest openings on mounds or hummocks.

Unlike sand post oak, saw greenbrier is not restricted to sandy environments and instead is widely distributed and adapted to diverse environments, including a variety of soil and light conditions (Gleason and Cronquist 1991; McGregor et al. 1986; Tyrl et al. 2008). Likewise, blackjack oak is adapted to a number of habitats though these are generally on sites of comparatively low production potential (Burns and Honkala 1990; Correll and Johnston 1979; McGregor et al. 1986; Sargent 1933). None of the herbaceous species growing on the scrub forest are limited to deep-sand environments even though sand lovegrass is more abundant on sandy soils (Diggs et al. 1999; Shaw 2012). The widespread Texas bullnettle is generally more common in sandy soils, especially partially wooded areas, but it is also abundant on disturbed locales such as abandoned fields (Diggs et al. 1999).

Sand post oak was the only plant species of this forest community that is restricted to deep-sand soils. Presence of sand post oak was the defining feature of this dwarf forest and its edaphically determined environment. This feature is elaborated on below in discussion of affinities of this sandyland forest with other deep-sand forest communities.

In final analysis, it was concluded that the sand post oak-saw greenbrier forest was the potential natural vegetation and that this vegetation was an edaphic climax. Sand post oak-saw greenbrier was a subtype, a deep-sand variant, of the *Quercus-Smilax* type of Dyksterhuis (1948) who, in his seminal ecological survey, did not offer details for specific forms of the general climax types he described.

This woody plant-dominated vegetation was not a brush invasion or a disturbance climax, but instead the natural vegetation to which disturbed plant communities would ultimately return. Some range site descriptions for Deep Sand range sites in the Western Cross Timbers implied that sandyland vegetation dominated by scrub oak and associated woody species was degraded savanna or grassland converted into a brush field by disturbances like overgrazing (Soil Conservation Service 1966, 1990b). These implications were inconsistent with this agency's description of potential vegetation for these soils, especially the Patilo (https://soilseries.sc.egov.usda.gov/OSD_Docs/P/PATILO.html).

Such conclusions also ignored initial reports by this same agency (Bushnell 1923; Smith et al. 1917) as well as descriptions by pioneers. For example, in a journal entry of 1843 (when fires still frequently burned through the pre-European vegetation), an Army captain described some Cross Timbers vegetation as consisting "of dwarfish looking scrub oaks, whose branches extending down and interlacing render it almost impenetrable" (quoted by Foreman 1947:68).

A perspective of the sand post oak-saw greenbrier vegetation as a degraded savanna converted to brush by human disturbance was inconsistent with findings from the present study as well as historic descriptions. Instead, these dense, closed-canopy dwarf oak forests on deep-sand habitats are the potential natural plant community as shown in other site descriptions (Soil Conservation Service 1973, 1977a, 1977b, 1978, 1980), journal entries by early explorers, cursory surveys like that of Dyksterhuis (1948), and the preliminary classification by Elliott (2013).

The natural vegetation for the Deep Sandy range site in Erath County, Texas was described by the Soil Conservation Service (1973) as producing "mostly post oak trees with little grass." One of the most apt descriptions of this climax dwarf forest was in the original soil survey of Erath County Texas (Bushnell et al. 1923:393): "This land was originally heavily forested with blackjack oak and some post oak, with a tangled undergrowth of vines and bushes…" This description was for the original and general Nimrod soil series including the deep-sand phase which is now recognized as the separate Patilo series. Hence, the emphasis on blackjack oak was for a less restricted soil. Furthermore, this was when sand post oak was regarded as being restricted much farther to the east (Small 1933) and before it was recognized as occurring in the Cross Timbers region (Francaviglia 2000; Muller 1951). Instead, sand post oak was commonly included as a variety or scrub form of the broader, generic post oak as, for example, in Sargent (1933) and Fernald (1950). In the early soil survey of Eastland County, Texas, this deep-sand vegetation was described as "a growth of scrub oak, shin oak, brush, and grasses" (Smith et al. 1917:24). Gregg (1844:361) described "a very diminutive dwarf oak" in the Cross Timbers that was called "shin-oak" by hunters.

No scientific name was applied to "shin oak" in the Cross Timbers literature including range site descriptions by the leading federal conservation agency in this area as, for instance, a reference to "shin oak" in Shackelford County, Texas (Soil Conservation Service 1990b) was found. It is possible that "shin oak" as applied in early accounts and some current technical applications was a general term for any low-growing oak and did not refer to any species (i.e. did not correspond to a specific epithet). In this usage "shin oak" could have referred to younger or resprout shoots of post, sand post, or blackjack oaks as these were the only *Quercus* species common on sandy soils in the Western Cross Timbers. Residents in this area apply "shin oak" to scrubby oaks of any *Quercus* species.

It is also probable that "shin oak" was used as a species-specific common name for sand post oak. Although they did not use scientific names, accomplished frontier authors like Irving (1835) and Gregg (1844) distinguished between post oak and blackjack oak as well as their habitats. It followed that early authors such as Gregg (1844) regarded "shin oak" as a distinct species rather than a general term for any small or immature oaks. Richardson (1963:140) used accepted common names for several native plants of the Cross Timbers and referred to "masts of the post oak, blackjack and shinnery."

In categorizing and describing natural vegetation of Oklahoma, Hoagland (2000) did not recognize a dwarf or scrub forest dominated by sand post oak, but plant communities of the sand post oak-blackjack oak-saw greenbrier type occur on deep-sand habitats in the East Cross Timbers in south-central Oklahoma. We observed several tracts of such forest vegetation in Love County, Oklahoma where black hickory (*Carya texana*) was present as an apparent associate tree species such that this East Cross Timbers scrub forest corresponded to the Cross Timbers sandyland oak vegetation described briefly by Elliott (2013). Black hickory has not been reported in the drier West Cross Timbers (Turner et al. 2003). White-haired panic and eastern prickly-pear were common to both the East and West Cross Timbers forms of scrub oak forest. Exact data on land area in this East Cross Timbers form of scrub oak-saw greenbrier forest is not available, but this forest community covers considerable area as, for example, in Love County, Oklahoma (W. R. Sanders, district conservationist, Natural Resources Conservation Service, personal communication).

The East Cross Timbers scrub oak-saw greenbrier forest was especially well-developed on the Eufaula soil series which is currently classified as, Siliceous, thermic, Psammentic Paleustalfs. Eufaula soil is associated with the Arenosa series, Thermic, uncoated Ustic Quartzipsamments, and is similar to the Patilo series currently classified as Loamy, siliceous, semiactive, thermic Grossarenic Paleustalfs (Soil Conservation Service 1990a; Soil Survey Staff 2018). The Eufaula series has an available water holding capacity ranging from 9.3 to 12.5 cm, cation exchange capacity varying from 2 to 8 centermoles of charge per kg, and a pH of 5.1 (Soil Survey Staff 2018). This compares to an available water-holding capacity ranging from 4.8 to 10.4 cm, cation exchange capacity of 1 to 4 centermoles of charge per kg, and a pH of 4.5 to 5 for the Arenosa series (Soil Survey Staff 2018). Eufaula soil obviously has low water-holding capacity along with low nutrient concentrations and poor nutrient retention due to high leaching rates. The Eufaula series consist of xeric, relatively infertile soils, a nearly ideal edaphic habitat for sand post oak that is restricted to deep-sand environments (Correll and Johnston 1979; Diggs et al. 1999; Gleason and Cronquist 1991; Muller 1951; Tucker and Muller 1958).

Apparently the Eufaula series (at least in part) was previously included in and mapped as a more general Nimrod series that extended into the Cross Timbers of central Oklahoma (Hoagland et al. 1999: Figure 14.1), as in Okfuskee County (Agricultural Research Administration 1952) where Nimrod was replaced by the Eufaula series (Natural Resources Conservation Service 2007). Natural vegetation of Eufaula fine sand was described as "thickets of dwarf oak" used as "woods pasture" even though there was limited cover of tall and mid grasses beneath oak canopies (Soil Conservation Service 1966:15, 84).

Natural Resource Conservation Service official series descriptions explained that Patilo, Nimrod, and Arenosa soils formed in sandbeds, sands, and sandy loams to sandy clay loams, respectively, that were apparently reworked by wind (https://soilseries.sc.egov.usda.gov/OSD_Docs/P/PATILO.html) whereas, Eufaula soil formed in sand sediments reworked by stream action (https://soilseries.sc.egov.usda.gov/OSD_Docs/E/EUFAULA.html). Nimrod, Patilo, and Arenosa result in concave/convex land surfaces (Soil Conservation Service 1966, 1973) seen as hummocky or mounded microtopography. Official descriptions of Patilo, Nimrod, and Arenosa recognized the potential natural vegetation as a scrub forest of post oak and blackjack oaks with greenbrier plus an herbaceous component of perennial and annual forbs and grasses, including little bluestem. The official description for natural vegetation of the Eufaula series was post and blackjack oaks with an herbaceous understory of tall grass species.

The pygmy forest dominated by blackjack oaks in Missouri (Reich and Hinckley 1980) developed on the Bolivar soil series, fine-loamy mixed, thermic ultic hapludalfs. The Patilo and Nimrod soils of the sand post oak forest we evaluated, the Eufaula soil of the Red River Valley on which sand post oak forests develop, and the Bolivar soil of the scrub blackjack oak are Alfisols. The Arenosa series of our study forests was an Entisol.

Development of similar scrub forests dominated by post oak, sand post oak, and blackjack oak as the potential natural vegetation took place on soils that developed from deposits of deep sand. Edaphic and micro-topographic features were comparatively consistent among dwarf forests communities. Likewise, brief and strictly qualitative descriptions of potential natural vegetation for these soils, especially those in official series descriptions by Natural Resources Conservation Service (available online at https://soilseriessc.egov.usda.gov/OSD_Docs/_/series name html) were consistent with our quantitative report. These descriptions and the study by Reich and Hinckley (1980) corroborated our overall observations that a scrub oak-saw greenbrier community that developed on deep-sand habitats in the Western Cross Timbers constituted a unique edaphic climax.

In the earliest description of Oklahoma vegetation Bruner (1931) included in his chaparral communities dense stands of sand post oak and dwarf plants of blackjack oak that established rapidly in cleared areas and on some grasslands. Bruner (1931) presented his seminal description of native vegetation in the hierarchy of the then-dominant Clementsian monoclimax theory (Clements 1916; Weaver and Clements 1938) such that his chaparral communities comprised *associes*, vegetation that was pre- or post-climax to climatic climax. By contrast, in polyclimax theory (Tansley 1935) or climax pattern theory (Whittaker 1953) many of the chaparral communities described by Bruner (1931) were edaphic or topographic climaxes that would correspond to associations, climatic climaxes in monoclimax theory.

Range and ecological site descriptions such as those used in conjunction with soil series and published in soil surveys, as for the general Cross Timbers region (Soil Conservation Service 1966, 1973, 1977a, 1977b, 1978, 1980), are, in effect, vegetational units historically viewed from polyclimax or climax pattern perspectives (Butler et al. 2003; Dyksterhuis 1949; Soil Conservation Service 1967, 1976). Interpretation of scrub or dwarf oak forests as climax or potential natural vegetation is consistent with historic and current soil and vegetation mapping units that were based on the smaller spatial (and shorter temporal) scales of polyclimax or climax pattern perspectives (Tansley 1935; Whittaker 1953) More recently, state-and-transition models of vegetation development (Briske et al. 2005; Laurenroth and Laycock 1989), along with traditional theories of climax vegetation, were incorporated into current ecological site descriptions of natural vegetation (Butler et al. 2003). Interpretation of dwarf forests that develop on deep sand in the Western Cross Timbers as the potential natural vegetation determined primarily by soil features (an edaphic climax) is in line with all of these successional-climax models. The sand post oak-dominated dwarf forest exists as the potential natural vegetation in the Cross Timbers by the same fundamental phenomenon that determines development of other pygmy forests. Dwarf forests of oak species in the Ozarks Plateau (Reich and Hinckley 1980) and the California Coast Range (McBride and Stone 1976) and of stunted conifers in coastal California (Jenny et al. 1969; Westman 1975) and lava flows in the southwest Basin and Range are all products of unique and generally low-fertility soils. These soils may sometimes (often for brief periods) hold more water than surrounding habitats, but the forests of dwarfish trees that develop on these soils establish and persist as the natural vegetation as a consequence of edaphic environments that are ecologically distinct from those which support neighboring plant communities. Apparently post oak is incapable of competing with sand post oak. These pygmy or dwarf forests are edaphic climaxes.

Soil and plant relations. Cross Timbers vegetation has traditionally been interpreted as having developed and persisted due to edaphic environments characterized by water-holding clays overlaid by sands that permit rapid infiltration of precipitation (Braun 1950; Dyksterhuis 1948; Tharp 1952). This traditional view did not take into account soil pH or soil microbiota. Together, these soil layers make for habitats more mesic than would otherwise exist in this subhumid area (Francaviglia 2000; Hoagland et al. 1999). This general Cross Timbers phenomenon of greater soil water availability is, however, less pronounced for the deeper sands such as that of the Arenosa or Patilo soil series (known in earlier works as Nimrod fine sand, deep phase).

In the early soil survey of Erath County, Texas (Bushnell et al. 1923) soil scientists explained how most rainfall was quickly absorbed by the porous deep sand which was underlaid by an "impervious clay subsoil." The result was that the Nimrod fine sand, deep phase (currently the Patilo series) stayed wet (and cold) late in the spring resulting in scrub oak forests. (Waterlogged soil profiles and consequent anaerobic soil conditions of the Cross Timbers scrub forest were discussed above.) The first soil survey of Eastland County, Texas (Smith et al. 1917) described this deep phase of Nimrod soil in virgin condition as having a surface layer of fine sand extending to depths of one to two meters with a densely structured clay layer beneath. Scrub oaks, cactus, and miscellaneous grasses constituted the natural plant community of this deep, loose soil known locally as "blow sand" (Smith et al. 1917). From the onset of soil and vegetation descriptions like those of Smith et al. (1917) and Bushnell et al. (1923), it was recognized that edaphic features played a major role in the relatively greater tree canopy cover of this scrub forest. The dwarf forest developed in contrast to the savanna physiogonomy that was more typical of the Western Cross Timbers vegetation (Dyksterhuis 1949, 1957).

Features of this deep sand-clay soil permitted establishment and dominance of the vegetation by sand post oak. Whether this was due to less water-holding capacity, lower water availability, periodically waterlogged soils, poor soil fertility, ease of shoot and root growth-development, or other factors was not known. The importance of porous sandy soil was obvious regardless of whatever edaphic features were responsible. Tucker and Muller (1958) and Linex (2014) explained that the distribution of sand post oak was determined by beds of deep sand, an environmental feature to which this dwarf species is an "obligate inhabitant" and on which it develops into "pure stands" (Muller 1951). Restriction of sand post oak to sandy soils has been reported consistently in standard treatments whether this taxon was treated as a variety of post oak as by Sargent (1933) or as a separate species (Diggs et al. 1999; Gleason and Cronquist 1991).

Deep sand was the key feature traditionally used to distinguish the habitat of sand post from post oak, this latter of which has a much greater species range and broader ecological niche including adaptation to shallow, rocky soils (Diggs et al. 1999; Tyrl et al. 2008). Even though sand post oak is limited in its edaphic adaptation, Sargent (1933) specified that it was the most common and widely distributed of what he interpreted as varieties of post oak, although post oak (which he treated as *Q. minor*) was the major oak of the Texas Cross Timbers (Sargent 1933).

On seven of the eight forest tracts observed in the present study, plant communities dominated by sand post oak were conterminous with Cross Timbers vegetation that developed on less sandy soils and in which post oak was a major species. On the boundaries between these two West Cross Timbers communities, we found trees with morphological features characteristic of sand post oak yet that were considerably larger than typical sand post oak growing on deep sand. It was conceivable that these were hybrids of *Quercus margarettiae* X *Q. stellata* as described by Muller (1952), Correll and Johnston (1979), and Diggs et al. (1999). If such was the case, this was further evidence of the strict affinity of sand post oak (whether a distinct species or variety of post oak) for sandbeds.

Ecophysiological phenomena which restrict sand post oak to deep-sand sites have received limited investigation. Some plausible factors for this restriction were suggested by a few studies and reviews. Donovan et al. (2000) evaluated distribution of turkey oak, bluejack oak (*Q. incana*), and sand post oak along gradients of soil water and mineral nutrients on a longleaf pine-scrub oak forest in the sandhills of South Carolina. Sand post oak had the lowest overall water-use efficiency, the most negative midday water potential, highest stomatal conductance, and lowest instantaneous water use efficiency (Donovan et al. 2000). These workers suggested that poor stomatal response to drought in sand post oak could result in rapid depletion of available water to its roots.

Another investigation in the pine-oak forest of the South Carolina sandhills (Espeleta et al. 2004) involved evaluation of hydraulic lift (redistribution of soil water from dry to wet and from deep to shallow soil) among major species. Longleaf pine, turkey oak, bluejack oak, and pineland threeawn (*Aristida stricta*) exhibited hydraulic lift whereas sand post oak and little bluestem did not. Espeleta et al. (2004) reported that the former four species were dominant in xeric sandhill environments while the latter two species were rarely found in the xeric habitats. The different capacities of species to redistribute soil water from deep to shallow soil layers affected water balance of sandhills vegetation and, presumably, reflected species distributions along gradients of soil variables, especially soil moisture.

Lack of hydraulic lift in sand post oak and little bluestem was thought to be due, first, to death of fine roots in dry surface soil thereby resulting in loss of soil-root interaction and, secondly, in case of little bluestem, shallower roots that did not extend to deeper, more moist soil. In a companion study, at the same location as that of Espeleta et al. (2004), West et al. (2004) concluded that the typical pattern of species distribution was of turkey oak being dominant on deep sands whereas mixtures of turkey, bluejack, and sand post oaks developed on soils of intermediate depth while blackjack oak was dominant on the shallowest soils.

In a study of root demography, Espeleta and Donovan (2002) reported parallel results for blackjack oak and concluded that it was a mesic (versus xeric and subxeric) species in sandhills sites. There was greater death and turnover of fine roots in blackjack oak. Espeleta et al. (2009) conducted a further study of tree root demography at this location and found that sand post oak, which grew on subxeric sites, had higher fine-root production yet also higher root mortality and turnover rates with shorter root life span than was the case for turkey and bluejack oaks, species that grew on drier sites. In a partially compensatory or equilibration response, sand post oak exhibited some production of fine roots during the leafless, dormant season when the other deciduous oak species did not (Espeleta et al. 2009).

Espeleta et al. (2009) concluded that fine-root demography of turkey and bluejack oaks (members of *Erythrobalanus*, the red oak subgenus) was characteristic of the “low-resource syndrome” whereas demography of fine roots in sand post oak (*Leucobalanus*, white oak subgenus) was characteristic of "high resource syndrome" species. The higher turnover-death rate of blackjack oak (Espeleta and Donovan 2002) would place this member of the red oak subgenus with sand post oak as a "high resource" species. In the southeastern Coastal Plain, both oak species of the West Cross Timbers deep-sand scrub forest had more vulnerable fine roots and grew on the less xeric sites.

West et al. (2003) studied root demographics of pineland threeawn and little bluestem at the same location as that of Espeleta et al. (2004) and Espeleta et al. (2009). These two native perennial grasses had root turnover and longevity features that were consistent with those of hydraulic lift found by Espeleta et al. (2004). Roots of little bluestem had pronouncedly shorter life spans because little bluestem underwent winter dormancy in contrast to pineland threeawn which did not undergo seasonal dormancy.

Sand post oak was reported by Cavender-Bares and Holbrook (2001) to grow on habitats with the lowest soil moisture (volume water/volume of soil) of 17 oak species although there appeared to be little or no difference between sand post and turkey oak. Abrams (1990) reviewed drought adaptations in various oak species (of which sand post oak was not one) and concluded that post and blackjack oaks were well-adapted to xeric sites in the central plains and southeastern regions of North America. Sand post oak is better adapted to dry environments than are post and blackjack oaks (Espeleta and Donovan 2002; Espeleta et al. 2004, 2009).

In essence, these various investigations suggested that sand post oak, the dominant tree species, and little bluestem, one of two major warm-season grasses, in deep-sand scrub forests of the West Cross Timbers are comparatively mesic species (perhaps even drought avoiders). Sand post oak is, however, more tolerant of drought than some native tree species such as post oak and blackjack oak (Espeleta et al. 2009). Likewise, little bluestem, the dominant grass of the Texas Cross Timbers (Shiflet 1994), was not excluded from this deep-sand habitat. Nonetheless, the Nimrod-Arenosa-Patilo soil complex comprised a comparatively harsh habitat with relatively low water-holding capacity and low soil fertility as compared to soils of other upland sites within the West Cross Timbers.

Soil-plant adaptation and variation. Depauperate or dwarf forms of plant species growing on harsh, infertile habitats have historically posed problems for plant systematists. Under such environmental situations it cannot be determined conclusively whether (how much) morphological differences are genetic or phenotypic variations in response to growing conditions and, hence, whether or not morphologically different plants represent distinct taxa (Stuessy 2009). Woody species of pygmy or scrub forests that develop on podzol, podzolic, and deep-sand soils reflect this conundrum.

In the pygmy forest of northern California (Jenny et al. 1969; Westman 1975), there were four parapatric subspecies of *Pinus contorta* that corresponded to different edaphic environments along a chronosequence of podzolic soils (Aitken and Libby 1994; Eckert et al. 2012) thereby constituting edaphic subspecies. Mendocino or pygmy cypress (*Cupressus pigmaea* = a subspecies or variety of *C. goveniana*) was another dwarf or scrub conifer in this pygmy forest that was a contested taxon. Two genetic races (varieties) of sand pine (*Pinus clausa*) were recognized as occurring on scrub forests that developed on infertile, sandy soils in Florida (Christensen 2000).

Similar genetic and taxonomic phenomena (with accompanying ecological implications) apparently exist for sand post oak, a dwarf taxon closely related to post oak, that is restricted to deep sands (Diggs et al. 1999; Muller 1951). Sand post oak has most frequently been designated as a distinct species, with three variations of spelling for the specific epithet: *Q. margarett*a = *Q. margarettae* = *Q. margarettiae* (Diggs et al. 1999; Muller 1951; Nixon and Muller 1997). Other authors (Burns and Honkala 1990; McGregor et al. 1986) treated sand post oak as a taxonomic variety of post oak (*Q. stellata* var. *margaretta*). Muller (1951:52) explained that in the Western Cross Timbers, there was a "heterogeneous assemblage of intermediates between *Q. margaretta* and *Q. stellate.*" In addition, there were populations that have been interpreted as *Q. drummondii*, but these are not stable and have such sporadic distribution that they were treated as a nothospecies, *Q. x drummondii* (Nixon and Muller 1997).

Cavender-Bares et al. (2004) evaluated commonly shared phenotypic traits and the phylogenetic clustering of 17 *Quercus* species along gradients of soil variables. They found that although *Q. margarettiae* and *Q. stellata* were the species most closely related to each other, their current biological distributions did not overlap along a soil moisture gradient.

Regardless of hierarchial rank, sand post oak was distinguished from the more common and more typical post oak in all floras and field guides. Sand post oak has been separated from post oak based on restriction of the former to deep sands of podzol soils, whereas the latter is adapted to a wide range of soils (Diggs et al. 1999; Muller 1952).

Blackjack oak apparently does not have a similar array of confusing taxonomic forms, but it does form numerous hybrids with other oak species (Muller 1952; Nixon and Muller 1997). Blackjack oak has a much wider adaptation to different habitats than does sand post oak which is restricted to deep sands (Diggs et al. 1999; Nixon and Muller 1997).

White-haired panic, the native grass and the herbaceous species with greatest cover in these dwarf forest tracts, apparently has a pattern or condition of genetic, morphological, and taxonomic variation that is similar to that of sand post oak and dwarf conifer species found on harsh, infertile soils. Taxonomic interpretation of white-haired panic has varied among agrostological authorities (Diggs et al. 1999; Freckman and Lelong 2003; Gould 1975; Shaw 2012; Silveus 1933) at levels of genus, species, subspecies, and variety. White-haired panic was designated by numerous scientific names including *Panicum acuminatum* var. *villosum*, *P. villosissimum*, *P. lanuginosum* in part, *P. ovale* var. *villosissimum*, *Dichanthelium villosum*, *D. acuminatum* var. *villosum*, and *D. lanuginosum* var. *villosissimum.* Intergradation and hybridization among subspecies and varieties is widespread within the *Panicum* or *Dichanthelium* taxon resulting in morphological diversity and taxonomic difficulty (Freckman and Lelong 2003; Gould and Clark 1978; Shaw 2012). Lelong (1984) described eight taxonomic varieties within the polymorphic *Panicum acuminatum* complex which he described as the "most troublesome" species in the *Panicum* genus. Even with such varietal diversity in *P. acuminatum*, Lelong (1984) departed from the treatment by Gould and Clark (1978) and interpreted *P. acuminatum* var. *villosum* as a variety of the morphologically similar *P. ovale* (= *P. ovale var. villosum*) which had been recognized by Hitchcock and Chase (1950) at the species level as *P. villosissimum* as was *P. ovale* which Gould and Clark (1978) recognized as *Dichanthelium ovale*. For this taxon in the Cross Timbers of Texas, Diggs et al. (1999) used *P. acuminatum* var. *villosum* while Shaw (2012) gave *D. ovale* var. *villiosissimum*.

The widely distributed and morphologically variable saw greenbrier (Fernald 1950; Gleason and Cronquist 1991) shares with sand post oak and hairy rosette panicgrass diverse taxonomic treatments by various workers (Diggs et al. 1999; Fernald 1950). This variation is seen as an array of varieties rather than as species or subspecies. Unlike sand post oak, saw greenbrier (and most species of the West Cross Timbers scrub forest) grows on a diverse range of habitats.

Little bluestem and sand lovegrass, dominant warm-season grasses of this forest understory, are also adapted to various habitats and are not restricted to deep-sand environments. Little bluestem is widely recognized as the dominant climax plant of the Texas Cross Timbers (Shiflet 1994). Sand lovegrass is commonly found to be the most locally abundant grass species in relict tracts of Western Cross Timbers vegetation, especially on its preferred habitats of sandy grasslands and open forests (Gould 1975; Shaw 2012; Tyrl et al. 2008), but sand lovegrass is clearly not restricted to deep-sand sites to the degree found in sand post oak.

Sand post oak is the only major species of the "sandrough" vegetation that is confined to the distinctive deep-sand habitat of the dwarf forest that it dominates. Sand post oak is both the dominant and the defining species of scrub forests that develop on deep-sand sites in the West Cross Timbers.

In addition to its edaphic habitat, sand post oak has been distinguished by numerous morphological features of leaves, twigs, fruit, etc. (Diggs et al. 1999; Muller 1951; Nixon and Muller 1997). The clonal feature of sand post oak, characterized by large, often pronounced horizontal trunks that develop both above and below the soil surface, is another prominent characteristic that distinguishes sand post oak from the similar and closely related post oak. Development of horizontal shoots was recognized by Sargent (1933) in his designation, *Q. stellata* var. *margarettiae* form *stolonifer*. This characteristic was also recognized for *Q. margaretta* by Muller (1951) who applied the vernacular name, runner oak. Gleason and Cronquist (1991:85) described sand post oak as "spreading underground and becoming colonial (forming colonies)." Berg and Hamrick (1994) found as many as 30 shoots in clumps of sand post oak. They concluded that although sand post oak reproduced both sexually and asexually, most shoots in clusters were ramets of the same genetic individual there being a 71% probability that boles less than a meter apart were clonal shoots (Berg and Hamrick 1994).

Modular growth form was largely responsible for the high density of sand post oak shoots that characterized its dwarf tree morphology along with the internal structure and physiogonomy of a pygmy forest. This growth form might provide for competitive advantages like capturing more sunlight and soil nutrients. The scrub forest type contrasted dramatically with the more open structure of Cross Timbers savanna or woodland communities dominated by post oak and blackjack oak.

Like sand post oak, saw greenbrier is highly clonal. It produces abundant numbers of circular, knotlike, woody modules at intervals along rhizomes which are morphologically similar to aboveground vertical shoots. Under the canopy of sand post oak aboveground shoots (both as individuals and in groups) of saw greenbrier grew into the crowns of oak trees. Fewer numbers of saw greenbrier shoots were found in the natural openings that existed on the slightly higher mounds within this dwarf forest.

Saw greenbrier is common throughout the Cross Timbers where it grows in association with other woody vines such as poison ivy, trumpet creeper (*Campsis radicans*), Virginia creeper (*Parthenocissus quinquefolia*), and mustang grape (Diggs et al. 1999; Dyksterhuis 1948). This relationship between saw greenbrier and other lianas was especially prominent in mesic habitats like bottomland forests (Nixon et al. 1990, 1991; Rosiere et al. 2013). The distinctive aspect of saw greenbrier in sandyland oak scrub was its extremely high density of shoots. The combination of high density of saw greenbrier shoots with frequent clumps of sand post oak boles typically formed a nearly impenetrable barrier to humans as well as beef cattle and white-tailed deer. Both ruminant species traversed throughout stands of "sandtangle" forest and fed primarily in natural openings and along established trails or paths. Francaviglia (2000) noted that while most of the Cross Timbers was a savanna with a parklike physiogonomy, there were sizable portions of this ecotonal vegetation with a tangled understory so dense in woody species, especially vines, that human travel had been deterred. Gregg (1844:361) wrote that in parts of the Cross Timbers "[t]he underwood is so matted in many places with grape-vines, green-briars, etc., as to form almost impenetrable 'roughs'…" The first Erath County, Texas soil survey (Bushnell et al. 1923:393) described this "heavily forested" oak community as having "a tangled undergrowth of vines and bushes."

In fact, much of the pre-European Cross Timbers appears not to have been a fire-maintained savanna or open woodland as often described in later ecological treatments. From careful rereading of early accounts of travel through the Cross Timbers it seems that vegetation of the earliest frontier-era Cross Timbers was far from a consistent savanna structure. After study of records kept by General Randolph B. Marcy while traveling through the Cross Timbers in 1849, especially in conjunction with the classic account of Gregg (1844), Hollon (1955:63) concluded that much of the Cross Timbers was "dense thorny brush" that "provided an effective barrier to commerce" and that was "the dread of every traveler." Irving (1835:144, 186) gave similar descriptions of arduous journeys through various forms of Cross Timbers vegetation including those dominated by post and blackjack oaks that varied from "oak barrens" on "quicksand" (loose sand) to "forests of cast iron" on land that had been frequently burned over by Indians. Kendall (1845:118, 119) described his troublesome travels through and "escape from" the Texas Cross Timbers with such descriptions as a "toilsome journey," "dreaded passage," "toilsome and tedious passage." This was in pre-settlement vegetation that frequently consisted of "small gnarled post oaks and black jacks" with "an almost impenetrable undergrowth of brier and other thorny bushes" which in some places was "impenetrable even by mules" (Kendall 1845:110,115).

Dyksterhuis (1948) reviewed accounts such as these and concluded that while much of the Western Cross Timbers permitted of wagon movement during the early freighting period there was also vegetation characterized as "dense woods" that developed on Nimrod sands extending into parts of Oklahoma (Dyksterhuis 1948:333). Restricted movement of humans and ungulates through the barrier-forming vegetational structure of the scrub oak forest (a result of multiple-shoot sand post oaks and dense saw greenbrier) that we described in this study was consistent with earliest descriptions of difficult passage through portions of the Cross Timbers. Presence of thorn-bearing shrubs like chittamwood, lime prickly ash, and devil's tongue pricklypear along with saw greenbrier corroborated descriptions of dense thorny brush recorded in the earliest accounts of travel through the Cross Timbers.

Other woody vines that are common in the West Cross Timbers were absent in the sand post oak-saw greenbrier forest with the exception of mustang grape that grew along outer margins and infrequently in openings of this dwarf oak forest. This was in marked contrast to the occurrence of several liana species growing with saw greenbrier in other Cross Timbers plant communities such as in bottomland forests (Nixon et al. 1990, 1991; Rosiere et al. 2013). Also in contrast to other Cross Timbers vegetation was infrequent occurrence (near absence) of non-oak tree species and presence of fewer shrub species in this deep sand forest. For example, Drummond's or rough-leaf dogwood (*Cornus drummondii*) is a widespread shrub throughout the Cross Timbers (Diggs et al. 1999), but it was limited to the perimeter and missing from the interior of sandyland dwarf oak forests that we characterized.

Domination, sometimes exclusively so, of the shrub or smaller woody plant component by saw greenbrier with its dense, curtain-like growth of prickle-armed, hard shoots was a key feature of this woody plant community. If the habitat type classification system of Daubenmire (1966), which is used by conservation agencies like the US Forest Service, was applied to this natural plant community it would clearly be the *Quercus margarettiae-Smilax bona-nox* habitat type.

Eastern prickly-pear was a distinguishing woody species of the sand post oak-saw greenbrier community. Although this succulent, which is the only cactus species in such non-woodland communities as interior tallgrass prairies and glades, was a minor species from cover and density perspectives, it proved to be an important indicator species. Eastern prickly-pear was listed as a component in the understory of a pygmy blackjack oak forest that developed on a sandstone bluff in the Ozark Plateau (Reich and Hinckley 1980). It was also a member of native pine-oak communities on sandhill habitats in Virginia (Fleming and Patterson 2012), North Carolina (Schafale and Weakley 1990; Schafale 2012), and Louisiana (Louisiana Natural Heritage Program 2009). In our observations, eastern prickly-pear was more commonly found in sand post oak scrub forest than in other plant communities of the Western Cross Timbers where such species as *O. engelmannii*, *O. phaeacantha*, *O. macrorhiza*, and *O. leptocaulis* predominate yet which were absent from the dwarf oak forest community. Furthermore, eastern prickly-pear was associated more with this Cross Timbers scrub forest (as it is with forests of sandy habitats along the Atlantic and Gulf Coasts) than with other natural communities of the West Cross Timbers.

White-haired panic was another diagnostic species though perhaps less so than the more highly reported eastern prickly-pear. Gould (1975), Hignight et al. (1988), and Shaw (2012) recognized from nine to 12 species of white-haired panic (either as *Panicum* subgenus *Dichanthelium* or genus *Dichanthelium*) for the Cross Timbers Region in Texas. Problems of nomenclature remain within this group of $C_{3,}$ cool-season, panicoid grasses yet presence of hairy rosette panicgrass as the major herbaceous species of this West Cross Timbers dwarf forest served as an indicator of its deep-sand habitat and the distinctiveness of this native plant community. We also noted that hairy rosette panicgrass was the apparent herbaceous dominant in East Cross Timbers scrub forests that developed on deep-sand soil in south-central Oklahoma.

Affinity with other natural communities. The sand post oak-saw greenbrier plant community appeared to be unique and limited to the Cross Timbers yet to have a botanical affinity with various natural plant communities that develop on sandyland environments of the Coastal Plain and Piedmont physiographic provinces. We found no descriptions or even titles of sand post oak-dominated vegetation, but similar natural communities on deep-sand sites in which sand post oak was an important component have been categorized and described in the literature. For example, a pine-scrub oak sandhill and a xeric sandhill scrub community were described for North Carolina (Schafale 2012; Schafale and Weakley 1990). In these two sandhill communities, sand post oak was a frequent, important member of the understory beneath an open canopy of longleaf pine. The herbaceous layer in these two communities (Schafale and Weakley 1990) was dominated by *Aristida stricta*, but little bluestem was common and spurge bullnettle (*Cnidoscolus stimulosus*) was a counterpart species to Texas bullnettle that grew on the Cross Timbers sand post oak-dominated dwarf forests. *Smilax* species were not reported for the two North Carolina communities (Schafale 2012; Schafale and Weakley 1990), and these communities were characterized by more species of oaks and dominated by a conifer. Devil's tongue pricklypear was found on the two sandhill plant communities as well as the sand post oak-saw greenbrier plant community. The edaphic environment of the North Carolina communities was typically deep sand to loamy sand and included some soil series classified as Paleudults (Schafale and Weakley 1990). These were similar to the Paleustalfs of the sand post oak-dominated scrub forests of the West Cross Timbers. Christensen (2000) summarized community composition and structure, including presence of sand post oak, of subxeric longleaf pine woodlands in the southeastern coastal plain.

Two pine and scrub oak sandhills woodland communities and one fluvial terrace woodland community in which sand post oak was a component were listed for Virginia (Fleming and Patterson 2012). In these brief descriptions, no greenbrier species were listed, but eastern prickly-pear and spurge bullnettle were given. These two species again showed similarity and affinity of natural woody vegetation that develops on soils of deep sands and undulating microtopography.

Such descriptions of natural plant communities along with various flora extending from eastern North America (Fernald 1950; Gleason and Cronquist 1991; Weakley et al. 2012) across to the Great Plains (McGregor et al. 1986) showed that sand post oak is limited to sandy soils, and primarily in the Coastal Plains and Piedmont physiographic provinces with the most westward and interior extension of its species range being the Western Cross Timbers. Fenneman (1931) regarded the Western Cross Timbers as being the western edge of the Comanche Plateau of the Great Plains physiographic province, but Fenneman (1938) also included the Western Cross Timbers as a subdivision of the Coastal Plain physiographic province.

Treatments in the definitive works on North American physiography (Fenneman 1931, 1938) and comparisons of the sand post oak-saw greenbrier community with natural vegetation in southeastern North America indicated the close geologic association of the Cross Timbers with the physiographic provinces of Atlantic and Gulf Coasts, and hence the botanical affiliation of the natural vegetation of these vast regions.

This relatedness was clear from the presence of little bluestem, bullnettle, and devil’s tongue pricklypear in all of the above sandyland natural communities as well as in the sand post oak-saw greenbrier scrub forest in the Western Cross Timbers. Blackjack oak was reported for all sandhill communities except those in Virginia.

Interestingly, sand post oak was a dominant species of natural vegetation only at the margin of its biological range in the West Cross Timbers. Also interesting was the fact that greenbrier was not a major species of the natural communities described for any of the other deep-sand or sandhill environments even though there are numerous *Smilax* species throughout the Coastal Plains and Piedmont provinces. Saw greenbrier is native to an area extending from Massachusetts through Maryland to Texas and north to Kansas and Missouri where it has various varieties and commonly forms dense thickets (Diggs et al. 1999; Tyrl et al. 2008; Weakley et al. 2012). As was the case for sand post oak, saw greenbrier was a dominant woody species at the more western (and less mesic) margin of its biological range.

The sand post oak-saw greenbrier climax vegetation shares an obvious floristic affinity with other natural plant communities of deep-sand habitats. It is also a distinctively different native community and one whose dominants achieve dominance only at the interior- and westernmost extensions of their species ranges. This West Cross Timbers scrub forest was designated as the Sand Post Oak-Saw Greenbrier habitat type following the method of Daubenmire (1966). It was also shown that this forest community was a variant of the Cross Timbers rangeland cover type described by the Society for Range

Management (Shiflet 1994) and proposed it as the Sand Post Oak forest cover type for recognition by the Society of American Foresters as in descriptions by Eyre (1954, 1980). This natural vegetation would be designated as Cross Timbers: Sandyland Dwarf (Scrub) Oak Forest in the Ecological Systems Classification and Mapping Project for Texas vegetation types compiled by Elliott (2013). Using the method of Diamond et al. (1987) and as applied to Texas this natural vegetation would be *Quercus margarettiae*- (*Q. marlandica, Opuntia humilis*) / *Smilax bona-nox* Scrub Forest with the translated name of Sand Post Oak – (Blackjack Oak, Devil's tongue pricklypear) / saw greenbrier Scrub Forest to appear in NatureServe Explorer (Natureserve 2014).

CONCLUSIONS

In summary, the closed-canopy scrub forest dominated by sand post oak and saw greenbrier is the climax or potential natural vegetation on some deep-sand sites in the Western Cross Timbers. This forest community was designated as a *Quercus margarettiae-Smilax bona-nox* habitat type. Although the agricultural productivity of this native vegetation is extremely low, it could be emphasized that the uniqueness and comparatively small acreage remaining of this natural vegetation warrants its conservation.

The uniqueness of the dwarf oak forest that develops on deep sand in the West Cross Timbers adds to the diversity, distinctiveness, and historic chronicle of the Cross Timbers Region. Land acquisition by conservation organizations for the purpose of preserving, to the extent possible, representative natural communities of the Western Cross Timbers should include examples of the sand post oak-saw greenbrier scrub forest. This natural vegetation is an integral part of the Cross Timbers landscape mosaic. Although this pygmy forest is a climax community of the patchwork of natural vegetation that comprises the Cross Timbers, the sand post oak scrub forest has been largely ignored or received brief mention in vegetational investigations, including classic ecological surveys and summary descriptions.

Ironically, the combination of scrub physiogonomy, species composition, and community structure of this deep-sand dwarf forest encapsulates the nature of the Cross Timbers as a large ecotone between forest and grassland. The sparsely dispersed, tangled, and nearly impenetrable patches of sandyland dwarf forest have also been less readily available for commercial purposes than the more accessible surrounding prairies, savannas, and open woodlands. At the same time, it appears that a higher proportion of this Cross Timbers scrub forest has been more drastically altered than has vegetation of larger, more widespread Cross Timbers communities.

With availability of powerful land-clearing machinery much of this scrub forest was converted into cropland during the 1960s and 1970s. At the end of World War I, Smith et al. (1917) estimated that although 80% to 90% of the Nimrod soil in Eastland County, Texas was being farmed, only 5% of the deep phase of Nimrod fine sand (presently mapped as the Patilo series) was under cultivation. The deep phase continued to support "a growth of scrub oak, shin oak, brush, cacti, and various grasses" (Smith et al. 1917:24). Thereafter, much of the remaining sand post oak forests were converted to peanut fields, pecan (*Carya illinoinensis*) orchards, home sites, and pasture, especially of introduced forage grasses.

For example, in the 1960s-1970s intensive management era, sizable acreages of these "sandrough" forests were cleared and seeded to the introduced species, weeping lovegrass. This was largely through cost-sharing incentives paid through the Great Plains Conservation Program administered by the Soil Conservation Service. Much, if not most, of this weeping lovegrass died out (perhaps due to poor adaptation to the harsh edaphic environment, pasture mismanagement, or a combination of these conditions). Currently, many of these old fields seeded to weeping lovegrass remain in a degraded state with sparse cover of exotic annual grasses such as Japanese chess (*Bromus japonicus*) and rescuegrass (*Bromus catharticus*). At the same time, removal of natural vegetation, including sand post oak-dominated scrub forest, has influenced local environments by increasing wind currents and decreasing areas of shade due to loss of taller, denser plant growth (i.e. a reduction in moderation of local climate).

A half century after many of these sand post oak forests had been converted to short-lived weeping lovegrass pasture members of the Natural Resources Conservation Service, the agency that previously sponsored these type conversions, recognized the questionable value of such practice. Linex (2014:276) concluded that disturbance to sand post oak forests should be approached with caution due to "… the difficulty of getting other desirable vegetation to survive the droughty conditions" under which this natural plant community developed.

Given the relatively small area remaining in sand post oak-dominated scrub forests, it would seem more appropriate that public conservation agencies explain the nature of this natural vegetation to private land owners, including its value for wildlife, shelter for livestock, and aesthetics. This would be especially the situation for privately owned land used for fee hunting and where wildlife production is accorded the same tax allowance as that for other agricultural uses. It might be a greater good for stockmen, sportsmen, and society in general if government agencies would refrain from using tax monies to remove sand post oak vegetation and losing a uniquely distinctive part of the West Cross Timbers. Native dwarf forests in several US states have been described in the peer-reviewed literature, become of interest to the general public, and preserved by being incorporated in state and national park systems. Perhaps it is time that Texas began to appreciate the deep-sand pygmy forest that is part of its natural heritage.

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