

Grassland Ecosystems of the Llano Estacado

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Abstract: The Llano Estacado, or Southern High Plains, has been a grassland throughout the Quaternary. The character of this grassland has varied through time, alternating between open, parkland, and savannah as the climate has changed. Different lines of evidence are used to reconstruct the climatic regimes and ecosystems, consisting of sediments and soils, vertebrate and invertebrate remains, phytolith and macrobotanical remains, isotope data, and radiocarbon ages. Binding or key indicator species throughout the late Pleistocene and Holocene are bison, pronghorn antelope, and prairie dog. Depending on time period, hackberry, cottonwood, sumac, honey mesquite, and Texas walnut are among the native trees and shrubs growing in the valleys and around upland basins. The middle Pleistocene is characterized as a sagebrush grassland whereas that of the late Pleistocene is a cool-climate pooid-panicoid dominated grassland. Focusing on the Holocene, this dynamic period experiences climatic changes, the early rise of the short-grass ecosystem, and modulations to that ecosystem.

The Llano Estacado and Distribution of Localities

The last synthesis of the Quaternary vegetation of the Llano Estacado, based on pollen data, was more than 40 years ago (Wendorf 1961). A hallmark of this seminal study was its multidisciplinary research effort to examine the paleoecology. Since then, research has generated several lines of evidence leading to an increased database from an expanded number of localities representative of the major geomorphic landforms across the region. Refinements in pollen processing and greater understanding of post-depositional processes have led to increased interpretive ability that calls into question the validity of the earlier pollen diagrams and interpretation. Other lines of evidence, generally concordant with each other, are not in agreement with the earlier pollen record and regional interpretation. This current synthesis, then, is an update based on an expanded record that presents a different perspective on the past vegetation and ecosystems of the Llano Estacado.

The Llano Estacado, or Southern High Plains, is a flat, expansive plateau in northwestern Texas and eastern New Mexico covering 130,000 km² (fig. 1). Part of the High Plains, a subdivision of the Great Plains province (Fenneman 1931; Hunt 1967; Holliday and others 2002), the Llano Estacado is in the southern portion of the province. Escarpments define the region along the north, west, and east sides. The northern escarpment overlooks the Canadian River Valley that separates the Southern High Plains from the rest of the High Plains section. The Pecos River Valley section is to the west and southwest and includes the Mescalero Plains along with the Monahans Dunes and Mescalero Dunes that abut the southwestern escarpment. Bordering the eastern escarpment is the Osage Plains of the Central Lowland province. To the south, the region merges with the Edwards Plateau without an obvious break. Superimposed over, but not coincident with all

of the High Plains, is the short-grass ecosystem or short-grass steppe (Lauenroth and Milchunas 1992).

The Southern High Plains (Llano Estacado) of today has a continental climate. The region experiences a large temperature range that is not influenced by the ocean or other large bodies of water (Johnson 1991). Rainfall occurs throughout the year, but highs are in the spring and fall as a result of frontal lifting of warm moist air. Summer droughts are common due to high pressure that dominates the region during this time. Summer rains, then, occur mainly through intense thunderstorms that depend on daytime heating and the weakening of the high pressure cell. Winter snowfall is minimal, but extended periods of below freezing are normal (Barry 1983; Haragan 1983:67; Bomar 1995:10). The Southern High Plains is dry and classified as semi-arid. It grades into the deserts of the Trans Pecos and southeastern New Mexico, the Rocky Mountain foothills of northeastern New Mexico, and the savannahs of the southern Central Lowlands (Osage Plains).

The modern vegetation of the Llano Estacado is a short-grass prairie dominated by blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyloides*) with patches of honey mesquite (*Prosopis glandulosa*). Historically, how one viewed and used this vast landscape was a matter of cultural perspective. In 1839, an Anglo trader and explorer returning to the East from Santa Fe described the Llano Estacado as “an open plain...which was one of the most monotonous I have ever seen, there being not a break, not a valley, nor even a shrub to obstruct the view. The only thing which served to turn us from a direct course pursued by the compass, was the innumerable ponds which bespeckled the plain, and which kept us at least well supplied with water” (Gregg 1954:252). Despite that acknowledgement of water, he also noted the Llano Estacado as “that immense desert region,” “dry and lifeless” and “sterile” (Gregg 1954:357, 362). In the 1850s, government-backed Anglo explorers reported that the area was “the Zahara of North America” (Marcy 1850:42) with “no inducements to

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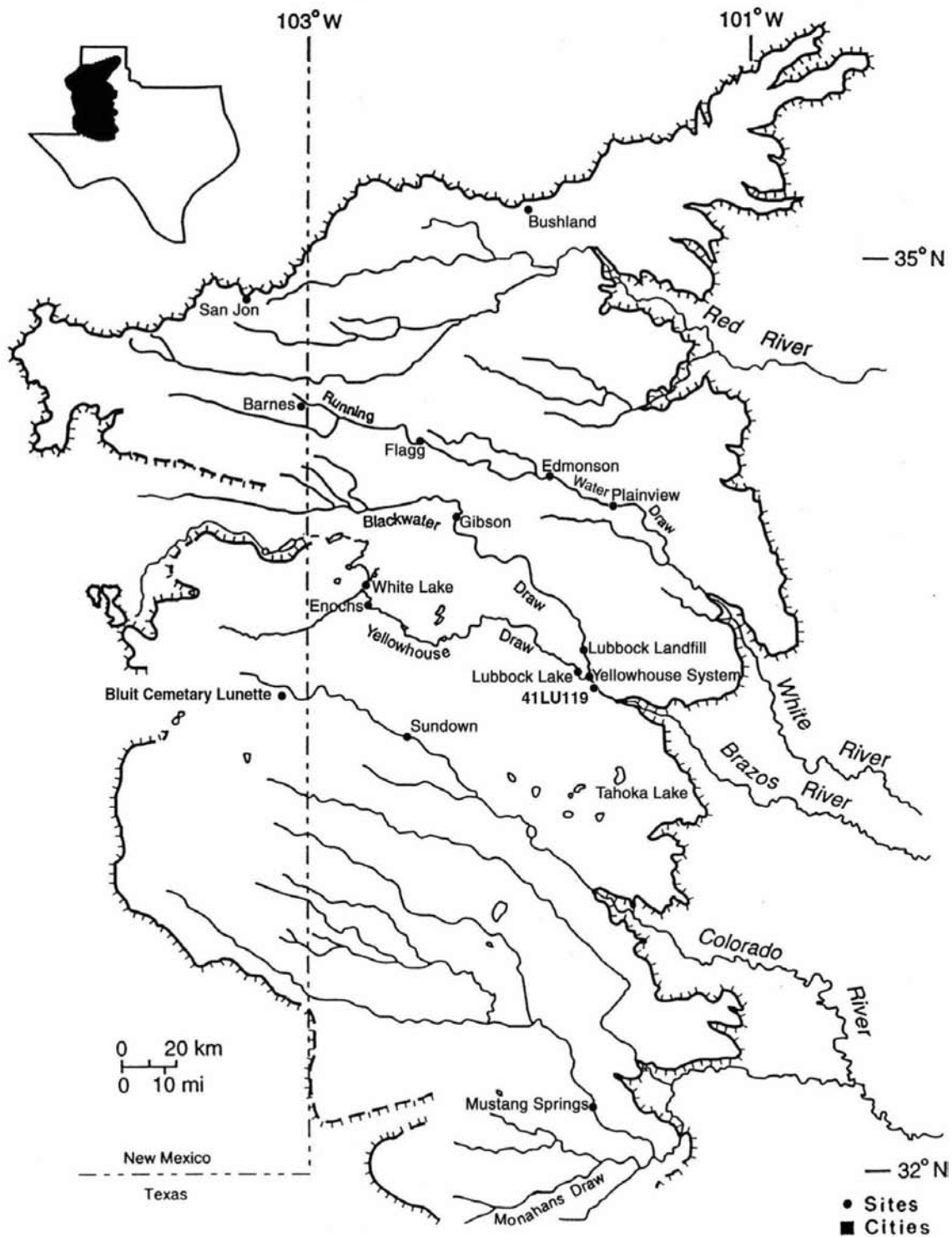


Figure 1. Localities on the Llano Estacado yielding paleovegetation data (direct evidence).

cultivation” (Pope 1855:9). Yet, 20 years later in the 1870s, the Pastores (Hispanic shepherders from New Mexico and the first non-indigenous settlers of the region) saw the territory as a vast, well-watered grassland ideal for expansion first through transhumance and then through year-round sedentary village pastoralism (Hicks and Johnson 2000). They called the western escarpment *La ceja de Dios* or “God’s eyebrow”

(Cabeza De Baca 1954). This appellation imparted a much different sentiment from that of the Anglo statements.

A synthesis of the development of the late Quaternary grassland ecosystems of the Llano Estacado from the Last Glacial Maximum (LGM) to historic times is based on the data from more than 20 localities across the region (table 1; fig. 1). These localities occur in the principal landforms (valleys, lake basins,

Table 1—Localities on the Llano Estacado yielding paleovegetation data (direct evidence).

Locality	Geomorphic setting	Stratum/sge	Evidence	Reference
Bluitt Cemetery Lunette	lunette	LGM	phytoliths	Fredlund and others 2003
Bushland Playa	upland playa	LGM	phytoliths, pollen	Fredlund and others 2003
White Lake	salina	LGM	phytoliths	Fredlund and others 2003
San Jon	upland playa	stratum 1	phytoliths	Fredlund and others 2003
		stratum 2	phytoliths	Fredlund and others 2003,
		8,000 B.P.	phytoliths, charcoal	Fredlund and others 2003,
				Johnson unpublished data
Barnes Playa	upland playa	stratum 1	phytoliths	Fredlund and others 2003
		stratum 2	phytoliths	Fredlund and others 2003
		8,000 B.P.	phytoliths	Fredlund and others 2003
Lubbock Lake Landmark	valley	stratum 1	phytoliths, seeds, preserved wood,	Fredlund and others 2003, Thompson 1987, Robinson 1982
		stratum 2	phytoliths, pollen, impressions, seeds	Fredlund and others 2003, Hall 1995, Thompson 1987, Robinson 1982
		8,000 B.P.	phytoliths	Fredlund, unpublished data
		stratum 3	seeds	Thompson 1987
		stratum 4	seeds	Thompson 1987
		stratum 5	seeds, charcoal	Thompson 1987, Johnson unpublished data
Yellowhouse system ^a	valley	stratum 1	seeds, charcoal	Johnson unpublished data
		stratum 2	phytoliths, seeds, charcoal	Johnson unpublished data
		stratum 3	phytoliths, seeds, charcoal	Johnson unpublished data
		stratum 4	phytoliths, seeds, charcoal	Johnson unpublished data
		stratum 5	phytoliths, seeds, charcoal	Johnson unpublished data
Mustang Springs	valley	stratum 1	phytoliths	Bozarth 1995
		stratum 2	phytoliths	Bozarth 1995
		stratum 4	phytoliths	Bozarth 1995
		stratum 5	phytoliths	Bozarth 1995
Plainview	valley	stratum 2	pollen	Hall 1995
Edmonson	valley	8,000 B.P.	phytoliths	Bozarth 1995
Gibson	valley	stratum 3	phytoliths	Bozarth 1995
Enochs	valley	stratum 3	phytoliths	Bozarth 1995
Lubbock Landfill	valley	stratum 4	phytoliths	Bozarth 1995
Sundown	valley	stratum 4	phytoliths	Bozarth 1995
Flagg	valley	stratum 5	phytoliths	Bozarth 1995
41LU119	uplands	stratum 5	seeds	Johnson unpublished data
Tahoka Lake	salina	stratum 5	seeds, charcoal	Johnson unpublished data

^aRepresents a compilation of more than 10 localities within a 20 km stretch of the Yellowhouse system.

dunes). Some localities are stratified, providing a record for several time periods in one place, whereas others represent only a single time period. Some provide multiple lines of evidence for past plant communities whereas others produced only one. Taken together, these localities cover the region and the late Quaternary using multiple lines of evidence to view these changing ecosystems.

The Llano Estacado has been a grassland since Miocene-Pliocene times (Fox and Koch 2003). Despite previous

interpretations of a boreal forest during latest Pleistocene times (Hafsten 1961; Wendorf 1961, 1970, 1975; Oldfield and Schoenwetter 1975), the Llano Estacado throughout the Quaternary has been a grassland (Holliday 1987). Interpretations based on pollen data have proven to be untenable (Holliday 1987; Holliday and others 1985; Hall and Valastro 1995). As the climate changed, the character of the Llano Estacado grassland has varied through time, alternating between open, parkland, and savannah, with isolated to small stands of deciduous trees.

Lines of Evidence

The synthesis is based on both direct and indirect lines of evidence that form the basis for interpretation. Direct evidence is composed of the vestiges of plants themselves represented by phytoliths, pollen, or macrobotanical specimens. Phytoliths are hydrated silica-bodies produced by grasses and certain other monocotyledon and dicotyledon families as well as some spore-producing families (Piperno 1988). The phytolith record generally is well-preserved on a regional basis (Bozarth 1995; Fredlund 2002; Fredlund and others 2003) and is thought to indicate what was growing in the local environs.

Based primarily on phytoliths, three major grass subfamilies have been identified in the record. Pooid grasses are C_3 plants that are short-day grasses, having limited available sunshine for growing and flowering. They generally prefer cool to cold climates with a sufficient moisture regime during the growing season. Limiting factors are available moisture and temperature. Panicoid grasses are composed of both C_3 and C_4 plants that are long-day grasses, having maximum available sunshine. They generally prefer moist, humid tropic to subtropic conditions. They have the same limiting factors as pooid grasses. Chloridoid grasses are C_4 plants that are long-day grasses. They generally prefer warm, dry climates.

The pollen record for the Southern High Plains is generally considered unreliable due to the lack of duplication or notably dissimilar nature of pollen diagrams within the same locality, very low counts, grain corrosion, and other preservation problems (Bryant and Schoenwetter 1987; Hall 1981; Hall and Valastro 1995). The few dependable records are included in the synthesis. Because of the ease of wind transport and dispersal, pollen records may be a mix of the local environs, regional vegetation, and extraregional plants.

Macrobotanical remains consist of seeds, charcoal, preserved wood, and preserved impressions (fig. 2). Carbonized seeds and charcoal are the most pervasive of the four types, having been recovered from throughout the late Quaternary stratigraphy. Preserved wood and impressions are rare and, to date, have been found only in late Pleistocene fluvial (wood) and early Holocene lacustrine (impressions) environments.

Indirect evidence providing proxy data on vegetation communities includes sediments and soils, radiocarbon and stable-carbon isotope data, and vertebrate records. The regional sediments and soils reflect the influence of climate, environmental factors, and biota (Buol and others 1973; Birkland 1999; Holliday 2004). Well over 325 radiocarbon dates are available that provide a solid chronology. Many of these are assays from organic-rich sediments that also provide $\delta^{13}C$ values as a result of routine measurement along with radiocarbon dating. This isotopic value reflects the C_3 and C_4 plant biomass. A positive correlation exists between $\delta^{13}C$ and the proportions of C_3 and C_4 biomass and $\delta^{13}C$ values (Cerling 1984; Bowen 1991; Nordt 2001). The C_3 plants have a lighter isotopic composition. This group is comprised of cool season grasses, most aquatic plants, and trees. The C_4 plants have a heavier isotopic composition and are composed of primarily warm season grasses. Each per mil change represents a shift

of about 7 percent in the ratio of C_3 to C_4 biomass (Bowen 1991).

Although less than half the available radiocarbon dates with $\delta^{13}C$ values have been analyzed, an initial pattern has emerged that indicates both a shift from lighter (C_3 plants) to heavier (C_4 plants) isotopic composition and a time-transgressive nature of the shift across the Southern High Plains from

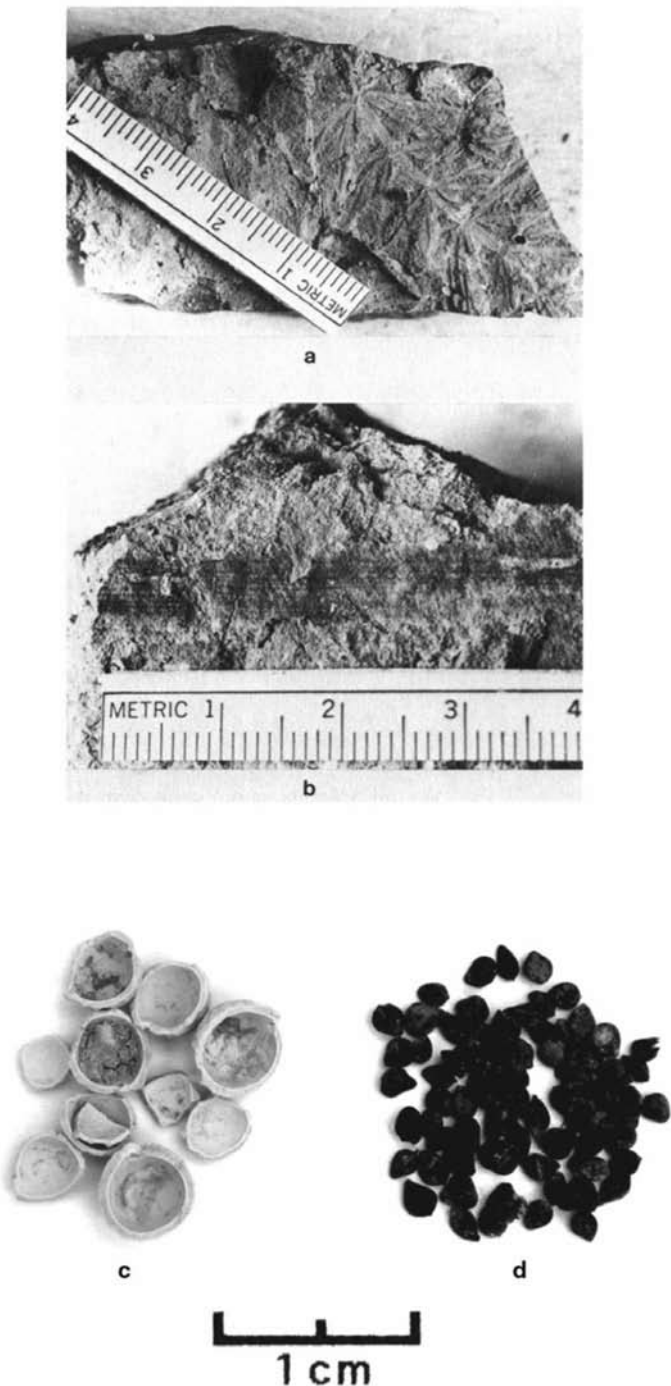


Figure 2. Macrobotanical evidence from localities on the Llano Estacado: a) preserved impression of musk-grass (*Chara*); b) preserved impression of horsetail (*Equisetum*); c) fossil net-leaf hackberry (*Celtis reticulata*) seeds; and d) fossil bulrush (*Scirpus*) seeds.

ca. 8,800 to 8,200 B.P. (Holliday 1995a). This difference in timing could reflect localized conditions or be an artifact of sampling.

The best and longest record (Lubbock Lake Landmark; Holliday 1995a:57) covers the Holocene and indicates both change and stability. Lighter isotopic values dominate from ca. 10,000 to 8,200 B.P. An abrupt shift from lighter to heavier isotopic composition occurs ca. 8,200 B.P., with ca. 28 percent C_4 grasses in the earliest Holocene. The C_4 grasses dominate throughout the middle Holocene between 7,000 to 4,500 B.P., with ca. 79 percent C_4 grasses. That pattern holds for most of the late Holocene between 4,500 to 500 B.P., with ca. 79 percent C_4 grasses. Around 500 B.P., a shift to lighter composition (C_3 plants) occurs, with only ca. 19 percent C_4 grasses. This high frequency of C_3 plants (ca. 81 percent) most likely reflects the aquatic plants of the extensive marsh at this time in the valley floor. Based on this record, grasses indicative of cooler conditions dominate the valleys of the Llano Estacado in the earliest Holocene and were replaced by grasses of warmer conditions by the end of the early Holocene. These warm season grasses continue throughout the middle and late Holocene.

Stable-carbon isotope data from lunettes on the uplands of the central Llano Estacado provide a regional perspective with a lengthier and compatible but incomplete record that indicates broad trends (Holliday 1997:63-64, 66). From 25,000 to 15,000 B.P., a gradual shift toward lighter isotope values indicates an increase in cooler, temperate-climate plants. Between 15,000 and 13,000 B.P., both lighter and heavier values occur, with a shift to heavier values from 13,000 to 10,000 B.P. A shift back to lighter values occurs from 10,000 to 8,000 B.P., with a shift at 8,000 B.P. back to heavier values that is maintained throughout the rest of the Holocene. The shift to post-LGM warmer conditions is most dramatic from 13,000 to 10,000 B.P., with a second shift to warmer conditions around 8,000 B.P.

Major physiographic features and indicator plants and animals bind the grasslands together over the vast Great Plains (Coupland 1992). The regional late Quaternary vertebrate record is known, and is particularly extensive for the late Pleistocene and early Holocene (Johnson 1986, 1987). A number of forms are environmentally sensitive or characteristic of certain ecosystems or vegetation communities. The vertebrate binding or key indicator species for grasslands are bison, pronghorn antelope, and prairie dog. These species are common on the Llano Estacado throughout the late Quaternary.

Framework

The Ogallala Formation and the Blackwater Draw Formation are the principal units responsible for the flat, almost featureless, constructional surface of the Llano Estacado. The upper Ogallala Formation (Miocene-Pliocene), the principle geologic bedrock of the Llano Estacado, was a stable land surface for hundreds of thousands of years, resulting in a well-developed soil. The ca. 2 m thick highly

resistant calcrete at the top of the Ogallala Formation is a remnant of that soil. This pedogenic calcrete unit primarily is responsible for the configuration and size of the Llano Estacado, the prominent escarpments around its margin, and contributes to the topographic flatness.

The landforms and Quaternary soils and sediments form the framework for examining the past ecosystems of the region. The Blackwater Draw Formation (Pleistocene) was formed by deposition of episodic, thick, and widespread aeolian sediments laid down starting sometime in the early Pleistocene up to about 50,000 years ago (Holliday 1989a; Reeves 1976). Originating in the Pecos River Valley, these sediments draped the region and blanketed all underlying units and geomorphic features (including the drainage system and basins). The sediments were altered by soil formation under dry and warm conditions. This deposit and its associated soils represent the major surficial deposit of the Llano Estacado.

Landforms

Modern geomorphic features have cut into or through, or rest upon the Blackwater Draw Formation. The surface of the Llano Estacado has been modified by three geomorphic forms. Two of these, basins and dunes, occur on the uplands.

About 25,000 small lake basins (locally known as playas) and 40 saline depressions (locally known as salinas) cover the landscape, occurring primarily on the High Plains surface (Sabin and Holliday 1995). Playas are inset into the Blackwater Draw Formation and formed primarily through erosional processes. They usually are freshwater sources. Most playas began forming in the late Pleistocene. Some basins were filled completely and no longer have a surface expression. Salinas are large, irregularly shaped basins probably formed through dissolution and collapse into the Ogallala Formation. They appear to be subsidence basins where long-term infiltration of ground water has caused point-source dissolution of the Permian salts (Reeves 1991). Although freshwater springs are associated with some salinas, the basins contain salt deposits and lake waters are brackish (Wood and others 2002).

Dune fields and lunettes rest on the Blackwater Draw Formation throughout the Llano Estacado. Extensive dune fields occur in three areas on the western side of the Southern High Plains. They are coincident with three major reentrant valleys on the western escarpment that acted as ramps or channels for sediments blowing off the Pecos River Valley in an incursion onto the Llano Estacado. Elsewhere along the western edge, large dune fields built up against the escarpment.

Lunettes are lee side dunes formed on the downwind side of drying playa and salina lake basins. Not all playas have lunettes, but of those that do, the lunettes generally are on the east and southeast side of the playa basin. Lunettes along playas form a single dune ridge. Those around the larger salinas typically occur as three dune ridges (Holliday 1997; Rich and others 1999).

The northwest-southeast trending now-dry river valleys (locally known as draws) are tributaries of the Red, Brazos,

and Colorado rivers that flow through the Osage Plains and into the Gulf of Mexico or the Mississippi River. Generally, these valleys have cut through the Blackwater Draw Formation to the Ogallala Formation except where the drainages have intercepted late Pliocene (Blanco Formation) or Pleistocene lake sediments. Final down cutting that resulted in the modern drainage system began sometime after 20,000 years with aggrading and infilling of the valleys starting around 12,000 years ago (Holliday 1995a).

Numerous springs, active since at least the late Pleistocene (Holliday 1995a, 1995b), flowed in various reaches of the valleys prior to the 1930s, with both ponds and free-flowing water available (Brune 1981). These springs were not distributed throughout the draws but rather were concentrated and confined to certain reaches of the valley system where the aquifer had been breached by valley downcutting. Today, the valleys generally are dry due to the dropping water table, and the playas and salinas contain the only naturally impounded, although generally seasonal, surface water for the region.

Quaternary Stratigraphy

Soil characteristics provide information on the vegetation community or ecosystem under which they developed. A boreal forest imparts distinctive pedologic characteristics to the soils, all of which are absent in the buried and surficial soils of the Southern High Plains (Holliday 1987, 1989a). The Blackwater Draw Formation is the aeolian mantle that covers the Southern High Plains and forms the surficial sediment. It contains several buried soils, the oldest of which was buried ca. 1.5 million years ago. Sedimentation ceased around 50,000 years ago and the regional surface began developing (Holliday 1989a). All buried soils virtually are identical to surface soils. What this means is that the late Quaternary vegetation represents that of most of the Quaternary. At no time during the Quaternary were boreal forests or coniferous woodlands present on the Llano Estacado. Rather, the region has been dominated by grassland, albeit varying in grass composition.

The late Quaternary stratigraphic record for the Southern High Plains is contained in the three landforms, although primarily in the valley system. Generally, late Holocene aeolian sediments over Blackwater Draw Formation occur in the upland areas between playas, salinas, and dune fields. Dune formation is a Holocene feature. Deposition of sand sheets began in the early Holocene, with episodic development in the middle and late Holocene (Holliday 1995b, 2001a; Muhs and Holliday 2001).

Few playas or salinas are stratified. Salinas contain discontinuous stratigraphic records. Early and middle Pleistocene playas occur below some of the recent playas (Gustavson and others 1995; Holliday and others 1996). Playas can contain thick (average 3 to 5 m) fills of lake mud and some aeolian sediments that span the late Pleistocene and Holocene and provide a lengthy record of shifting waters in the basin through time (Hill and others 1995; Holliday and others 1996). Lunettes, a late Pleistocene to Holocene feature, are stratified and

typically contain buried soils indicative of episodic accretion (Holliday 1997). Lunettes around salinas occur in three bands representing different time periods (late Pleistocene, middle Holocene, late Holocene) and wind directions (Holliday 1997; Sabin and Holliday 1995).

Valley fills provide the most extensive regional record (Holliday 1995a). The valley fill stratigraphy is composed of five major stratigraphic units within which a number of buried soils are contained. Subunits are defined within the major units as well as facies. Although the five major units are well-represented throughout the valley system, no one location contains the entire record of units, subunits, and facies. The most complete record is at Lubbock Lake (Holliday 1985; Holliday and Allen 1987) in Yellowhouse Draw. Although local subunit and facies designations have been maintained, they are correlated with the regional terminology (table 1). Although some boundaries regionally are time-transgressive (Holliday 1995a), Lubbock Lake's geochronology provides a general framework in which to view the hydrologic and landscape changes through time.

The lowest stratum of valley fill is stratum 1 consisting of a basal sand and gravel unit (substratum 1A), cross-bedded sand (substratum 1B), and locally, an overlying clay drape (substratum 1C). Stratum 1 is interpreted as a meandering stream deposit with point bar sediments and overbank deposits. Deposition of stratum 1 generally ended about 11,000 B.P., although in some reaches flowing water continued as late as 10,000 years ago. The climate was cool and humid (maritime conditions) with enhanced rainfall in the winter (Johnson 1987, 1991).

Stratum 2 is primarily a lacustrine and marsh deposit found along the valley axis. Substratum 2A contains beds of pure diatomite that represent periods of standing water with interbedded peaty muds indicating marshy conditions. Substratum 2B overlies 2A and contains a homogeneous layer of organic-rich silt and clay representing a slowly aggrading marsh. A sandy shore facies is found in a narrow zone along the valley margin while a sandy, aeolian facies with some slopewash and interbedded marsh sediments is found along the outer valley margin. Deposition of stratum 2 began about 11,000 B.P. and the 2A-2B transition occurred about 10,000 B.P. Aggradation of 2B ceased about 8,500 B.P. and the Firstview Soil formed on a stable surface from about 8,500 to 6,400 B.P. Elsewhere in the valley system, the Firstview Soil was buried earlier than at Lubbock Lake (Holliday 1995a) and at one locality, stratum 2 started accumulating as early as 11,300 B.P. (Holliday 1995a:13). The climate was warming with a shift in rainfall pattern. Rainfall levels and a lower evaporation rate led to more effective moisture reflective of continuing wet conditions (Johnson 1987). Nevertheless, the first signs of Holocene drought (less available moisture) occurred during the period 10,900 to 10,200 B.P. (Holliday 2000).

Stratum 3 lies conformably on top of stratum 2 and is composed of a moderately calcareous, sandy aeolian deposit along the western valley margin and a highly calcareous, silty lacustrine unit found along the valley axis. Stratum 3 represents an alkaline lake or marsh along the valley floor with considerable aeolian additions along the valley margin. Stratum 3

deposition and formation of the Yellowhouse Soil occurred between about 6,400 to as late as 5,000 B.P. Elsewhere in the valley system, stratum 3 deposition occurred perhaps as early as 10,000 B.P. and internal buried A-horizons locally occur within stratum 3 (Holliday 1995a). Stratum 3 denotes a time of increasing temperatures, decreasing rainfall, and lower humidity (Johnson 1987).

Stratum 4 is composed of alluvial and marsh deposits found only along the valley axis (4A), and a sandy aeolian deposit that blankets the valley (4B) with a clayey marsh facies (4m) found along the valley axis. The Lubbock Lake Soil formed in substratum 4B under well-drained conditions and is well-developed with prominent A and B horizons and often multiple calcic horizons. Deposition of 4A occurred between 5,500 and 5,000 B.P. and 4B between 5,000 and 4,500 B.P. The Lubbock Lake Soil began forming around 4,500 to around 1,000 B.P. when it locally was covered by stratum 5. Elsewhere in the valley system, stratum 4 is buried as early as 3,900 B.P. (Holliday 1995a). Where not buried by stratum 5 sediments, soil formation continues today. Stratum 4 represents the culmination of the warming trend, with increasingly hot, dry, and dusty conditions known as the Altithermal (Holliday 1989b). The climate is very xeric. By 4,500 B.P., the modern continental climate emerges with a return to cooler and mesic conditions (Johnson 1987; Holliday 1989b).

Stratum 5, the uppermost stratum, is represented by marsh deposits and upslope, valley margin facies composed of layers of aeolian sand and slopewash sand and gravel, burying stratum 4. Buried soils occur locally. Deposition of lower 5 began around 750 to 600 B.P. and continued to about 450 B.P. when a soil began to form locally. Deposition of upper 5 began about 300 B.P. A weakly developed soil began to form locally about 100 B.P. and is exposed locally at the surface today. Elsewhere in the valley system, deposition of stratum 5 valley margin sands begins as early as 3,900 B.P. and valley axis marsh muds by 3,200 B.P. (Holliday 1995a). By 2,000 B.P., an episodic drought cycle begins that continues today as part of the modern climatic pattern. The intensity and frequency of droughts varies through time, alternating between more mesic and less mesic conditions (Johnson 1987; Holliday 1995a).

The Record

The various localities across the Southern High Plains (fig. 1) provide a composite of the floral and faunal communities from the Last Glacial Maximum (LGM) to the latest Holocene. That composite is segmented by time and stratigraphy, with any one time period represented by three to six localities. Each locality, as well as stratigraphic units within a locality, varies in terms of the type of direct and indirect evidence available (table 2). The data come from two primary sources—those that are published (Bozart 1995; Hall 1995; Hall and Valastro 1995; Holliday 1995a; Johnson 1986, 1987b; Thompson 1987) and those that are unpublished. Unpublished data either have been presented at professional meetings (Fredlund 2002; Fredlund and others 2003) or are those of

Table 2—Correlation of valley fill stratigraphic terminology for the Lubbock Lake Landmark with the regional stratigraphy.

Lubbock Lake stratigraphy ^a	Regional stratigraphy ^b
stratum 5	stratum 5
substratum 5B	stratum 5s2 and 5gs
substratum 5Bm	stratum 5m
substratum 5A	stratum 5s1 and 5g1
substratum 5Am	stratum 5m
substratum 5m	stratum 5m
stratum 4	stratum 4
substratum 4B (upper/A-horizon)	stratum 4s
substratum 4B	stratum 4s
substratum 4A	stratum 4m
substratum 4m	stratum 4m
stratum 3	stratum 3
substratum 3c (upper/A-horizon)	stratum 3c
substratum 3c	stratum 3c
substratum 3m	stratum 3m
substratum 3e	stratum 3s
stratum 2	stratum 2
substratum 2s	stratum 2s
2s local bed c	stratum 2s
2s local bed b	stratum 2s
2s local bed a	stratum 2s
substratum 2e	stratum 2s
substratum 2B (upper/A-horizon)	stratum 2m
substratum 2B	stratum 2m
2B cienega	stratum 2m
substratum 2A	stratum 2d
2A local bed 5	stratum 2d
2A local bed 4	stratum 2d
2A local bed 3	stratum 2d
2A local bed 2	stratum 2d
2A local bed 1	stratum 2d
stratum 1	stratum 1
substratum 1C	stratum 1
substratum 1B	stratum 1
substratum 1A	stratum 1

^aBased on Holliday (1985), Holliday and Allen (1987), and field notes on file at the Museum of Texas Tech University.

^bBased on Holliday (1995a).

the author's. Nevertheless, the overall record is robust with a clear dominance of grasslands and grassland vertebrate forms throughout.

The late Quaternary period is subdivided into late Pleistocene and Holocene epochs. Discussion of the late Pleistocene begins with the LGM, ca. 20,000 to 18,000 B.P., and continues through post-glacial time to the Pleistocene-Holocene boundary at 11,000 B.P. Climatic changes and large-scale extinctions occurring at the end of the Pleistocene and around 11,000 B.P. mark the biotic and ecosystemic end of Wisconsinian conditions on the Southern High Plains. This time period is used as the boundary between the Pleistocene and Holocene rather than the geologic convention of using an arbitrary 10,000 B.P. as the boundary (Hageman 1972; Holliday 2001b).

Late Pleistocene Background

The LGM is represented by three localities dating from 21,865 to 17,710 B.P. (table 1) that are associated with playas or salinas on the uplands. Data indicate a grassland composed of sagebrush (*Artemisia*), grasses (Poaceae), ragweed (*Ambrosia*), daisy-sunflower-aster family (Asteraceae), Chenopods (chenopods and amaranth), and juniper (*Juniperus*). A rare component of the flora consists of hackberry (*Celtis*), Liguliflorae (herbs such as wild lettuce [*Lactuca*]), wild buckwheat (*Eriogonum*), carrot or parsley family (Apiaceae), greasewood (*Sarcobatus*; a chenopod shrub), amaranth family (Amaranthaceae), evening primrose family (Onagraceae), yucca (*Yucca*), cactus family (Cactaceae), and bluebell-lobelia family (Campanulaceae). Aquatic plants indicative of wet ground to open water are the sedge family (Cyperaceae), ditch grass (*Ruppia*; submersed vegetation in alkaline lakes), common cattail (*Typha latifolia*; emergent vegetation), and colonies of the freshwater algae (*Botryococcus* and *Pediastrum*). Ditch grass is known only from White Lake, reflecting the brackish waters of that salina.

Little is known of the fauna at this time. The presence of mammoth (*Mammuthus* spp.), ancient horse (*Equus* spp.), and ancient bison (*Bison antiquus*) (Evans and Meade, 1945) is indicative of grasslands. The records denote a sagebrush grassland with high amounts of composites. This grassland is an herbaceous prairie community under an equitable, cooler, and humid climate with no modern analog (Hall and Valastro 1995:244).

Late Pleistocene stratum 1 times are represented by five localities dating from 12,500 to 11,000 B.P. (table 1) that are associated with upland playas and the valley system. Pooid grasses, including needlegrass or wintergrass (*Stipa*; cool-moist season), dominate with a very low component of panicoid grasses and chloridoid grasses. Almost no C_4 grasses are present and sagebrush is absent. Other floral elements reflecting the valley system are seepweed (*Suaeda*), gromwell (*Lithospermum*), devil's claw (*Proboscidea louisianica*), and net-leaf hackberry (*Celtis reticulata*). Aquatic plants indicative of wet ground to open water are bulrush (*Scirpus*; emergent vegetation) and spikerush (*Eleocharis*; emergent vegetation).

A highly diverse herd herbivore fauna, indicative of grasslands, is complimented by an equally diverse carnivore guild (table 3). The larger carnivores are dependent upon these herbivores and preyed upon and scavenged their carcasses (Matheus 1995, 2003; Matheus and others 2003). Other grassland forms are as varied (table 3). The tiger salamander and meadow vole, in particular, reflect the riparian habitat along the streams. Sedge beds, reflected in the macrobotanical remains, are the preferred habitat of meadow voles (Findley and others 1975; Thompson 1965). Equally of note is the prairie dog town community (prairie dog, ground squirrels, grasshopper mouse, burrowing owl, western hognose, and ground snakes) reflected in these smaller grassland forms and some of the town's predators (rattlesnake, turkey vulture, ferruginous hawk).

Table 3—Late Pleistocene (stratum 1) grassland fauna of the Llano Estacado.

Taxon	Common name
<u>Herd herbivores</u>	
<i>Mammuthus columbi</i>	Columbian mammoth
<i>Bison antiquus</i>	ancient bison
<i>Equus mexicanus</i>	large, stout-legged horse
<i>Equus francisci</i>	small, stilt-legged horse
<i>Camelops hesternus</i>	yesterday's camel
<i>Capromeryx</i> spp.	extinct, 4-pronged antelope
<i>Hemiauchenia macrocephala</i>	large-headed llama
<i>Odocoileus virginianus</i>	white-tailed deer
<i>Antilocapra americana</i>	pronghorn antelope
<i>Platygonus compressus</i>	flat-headed peccary
<u>Carnivore guild</u>	
<i>Arctodus simus</i>	short-faced bear
<i>Smilodon fatalis</i>	saber-toothed cat
<i>Canis dirus</i>	dire wolf
<i>Canis lupus</i>	gray wolf
<i>Canis latrans</i>	coyote
<i>Vulpes velox</i>	swift fox
<i>Urocyon cinereoargenteus</i>	gray fox
<u>Other grassland forms</u>	
<i>Ambystoma tigrinum</i>	tiger salamander
<i>Scaphiopus</i> spp.	spade-foot toad
<i>Bufo cognatus</i>	Plains toad
<i>Kinosternon flavescens</i>	yellow mud turtle
<i>Elaphe guttata</i>	corn snake
<i>Gyalopion canum</i>	western hook-nosed snake
<i>Heterodon nasicus</i>	western hognose snake
<i>Lampropeltis triangulum</i>	common king snake
<i>Sonora semiannulata</i>	ground snake
<i>Thamnophis</i> cf. <i>sirtalis</i>	common garter snake
<i>Tropidoclonion lineatum</i>	lined snake
<i>Crotalus atrox</i>	western diamondback rattlesnake
<i>Carthartes aura</i>	turkey vulture
<i>Buteo regalis</i>	ferruginous hawk
<i>Athene</i> cf. <i>cunicularia</i>	burrowing owl
cf. <i>Pooecetes gramineus</i>	vesper sparrow
<i>Holmesina septentrionalis</i>	giant pampathere
<i>Glossotherium</i> (= <i>Paramylodon</i>) <i>harlani</i>	Harlan's ground sloth
<i>Lepus californicus</i>	black-tailed jack rabbit
<i>Spermophilus richardsonii</i>	Richardson's ground squirrel
<i>Spermophilus tridecemlineatus</i>	13-lined ground squirrel
<i>Spermophilus mexicanus</i>	Mexican ground squirrel
<i>Cynomys ludovicianus</i>	black-tailed prairie dog
<i>Geomys bursarius</i>	Plains pocket gopher
<i>Reithrodontomys montanus</i>	Plains harvest mouse
<i>Onychomys leucogaster</i>	Northern grasshopper mouse
<i>Neotoma micropus</i>	Southern Plains woodrat
<i>Microtus pennsylvanicus</i>	meadow vole
<i>Microtus ochrogaster</i>	prairie vole

These prairie dog towns existed within an overall dominant pooid grass prairie that was a parkland. Isolated hackberry trees to small groves grew along the streams in the valley system, continuing the presence of this native tree from the LGM. A lower mean annual temperature than today, cooler summers and warmer winters that lacked extended freezing conditions, more effective moisture, lower evaporation rate, and enhanced winter precipitation indicated an equitable, humid, and

maritime-like climate that lacked seasonal extremes (Johnson 1991). Nevertheless, a major environmental shift at 11,000 B.P. is represented in the draws by an abrupt hydrologic change from flowing to standing water, and on the uplands, by the onset of regional dune construction that heralds the Holocene.

Holocene Dynamics

Early Holocene stratum 2 times are represented by five localities dating from 10,800 to 8,200 B.P. (table 1) that are associated with upland playas and the valley system. While still dominant, pooid grasses, including needlegrass or winter-grass, are steadily decreasing. Chloridoid grasses show a continuing rise with a low but steady component of panicoid grasses including the short-grass threeawn (*Aristida*; warm season). Other floral elements reflecting the valley system are goosefoot (*Chenopodium*), buffalo bur (*Solanum rostratum*), guarra (*Guara*), devil's claw, ragweed, the daisy-sunflower-aster family, Liguliflorae, mustards (Brassicaceae), and the evening primrose family. A variety of emergent and submersed vegetation indicative of wet ground to open water include cattail, sedge (*Cyperus*), bulrush, spikerush, horsetail (*Equisetum*), musk-grass (*Chara*), and colonies of the fresh-water algae (*Botryococcus*).

Native trees in the valley are net-leaf hackberry, sumac (*Rhus*), and cottonwood (cf. *Populus*), with juniper (cf. *Juniperus*) and piñon-pine (cf. *Pinus edulis*) along the High Plains escarpment. The latter three are from pollen of questionable reliability (Hall 1995), but plausible. Juniper and an occasional piñon-pine grow along the western High Plains escarpment today and occasional cottonwoods grow in the lower reaches of the valley system. Sumac, like hackberry, is a shrub to small tree. Isolated, disjunct populations of littleleaf sumac (*R. microphylla*) occur today on the Llano Estacado, with a similarly isolated population of prairie sumac (*R. lanceolata*) just to the north of the region (Petrides and Petrides 1992:134, 137).

The diversity of herd herbivores, along with the carnivore guild, decreased considerably (table 4) due to the changes occurring around 11,000 B.P. and the collapse of the Pleistocene food web (Matheus and others 2003). Ancient bison became the dominant herd herbivore. Although some reduction in diversity occurred with the smaller grassland forms, variety was still maintained with some new taxa appearing (table 4). Both plant and animal forms indicated sedge beds around the marshy edges of the ponded waters in the valleys and later with the aggrading marshes, along with submersed vegetation in the ponds. A prairie dog town community continued along with the badger as its predators.

These prairie dog towns existed within an overall mixed grassland with an increase in C_4 grasses without sagebrush. The setting was that of a savanna. Low numbers of hackberry, sumac, and possibly cottonwood trees grew along the valley margins in the valley system. Equitable climatic conditions gave way to the onset of winters with at least occasional

Table 4—Early Holocene (stratum 2) grassland fauna of the Llano Estacado.

Taxon	Common name
<u>Herd herbivores</u>	
<i>Bison antiquus</i>	ancient bison
<i>Capromeryx</i> spp.	extinct 4-pronged antelope
<i>Odocoileus</i> spp.	deer
<i>Antilocapra americana</i>	pronghorn antelope
<u>Carnivore-guild</u>	
<i>Canis lupus</i>	gray wolf
<i>Canis latrans</i>	coyote
<i>Taxidea taxus</i>	badger
<u>Other grassland forms</u>	
<i>Ambystoma tigrinum</i>	tiger salamander
<i>Kinosternon flavescens</i>	yellow mud turtle
<i>Terrapene ornata</i>	western box turtle
<i>Phrynosoma cornutum</i>	Texas horned lizard
<i>Eumeces obsoletus</i>	Great Plains skink
<i>Coluber constrictor</i>	racer
<i>Sonora semiannulata</i>	ground snake
<i>Thamnophis</i> cf. <i>sirtalis</i>	common garter snake
<i>Tropidoclonion lineatum</i>	lined snake
<i>Circus cyaneus</i>	harrier
cf. <i>Eremophila alpestris</i>	horned lark
<i>Mimus polyglottis</i>	mockingbird
<i>Tympanuchus cupido</i>	prairie chicken
<i>Notiosorex crawfordi</i>	desert shrew
<i>Lepus californicus</i>	black-tailed jack rabbit
<i>Spermophilus tridecimlineatus</i>	13-lined ground squirrel
<i>Spermophilus mexicanus</i>	Mexican ground squirrel
<i>Cynomys ludovicianus</i>	black-tailed prairie dog
<i>Geomys bursarius</i>	Plains pocket gopher
<i>Chaetodipus hispidus</i>	hispid pocket mouse
<i>Dipodomys ordii</i>	Ord's kangaroo rat
<i>Reithrodontomys montanus</i>	Plains harvest mouse
<i>Onychomys leucogaster</i>	Northern grasshopper mouse
<i>Sigmodon hispidus</i>	cotton rat
<i>Neotoma</i> cf. <i>micropus</i>	Southern Plains woodrat
<i>Microtus pennsylvanicus</i>	meadow vole
<i>Microtus ochrogaster</i>	prairie vole

periods of freezing temperatures. Summers were warming and occasional droughts (less effective moisture) occurred (Holliday 2000). While conditions still were humid, rainfall pattern was shifting with an eventual decrease in rainfall, and mean annual temperature was rising (Johnson 1986, 1987b).

By around 8,000 B.P., the dynamics between climate, vegetation, and fauna were such that the character of the landscape is changing. Chloridoid grasses are dominant, most likely produced by a grama-buffalograss (*Bouteloua-Büchloe*) prairie. A low level of pooid and panicoid grasses that included short-grass threeawn continues. Based on phytolith data, the short-grass ecosystem emerges around 8,000 to 8,200 B.P., with modulations in that ecosystem into modern times (Fredlund and others 2003). The phytolith and stable-carbon isotope data, then, are in general agreement.

In tandem with this change but somewhat later, modern bison (*Bison bison*) emerged, not as a replacement species, but as the transformation of the ancient form into the modern form due to the plasticity of the bison genome (Lewis 2003;

Lewis and others 2001). Bison underwent a rapid decrease in body size during the period post-8,000 B.P. and before 6,500 B.P., most likely with fully modern bison emerging by 7,000 B.P. This decrease in size appeared correlated with the rise and spread of the short-grass ecosystem and the greater productivity, but less nutritive value of C_4 grasses.

Early middle Holocene stratum 3 times are represented by four localities dating from 7,000 to 5,500 B.P. (table 1) that are associated with the valley system. Chloridoid grasses, most likely produced by a grama-buffalograss prairie, are dominant, but some pooid and panicoid grasses continue. Wet ground to open water plants include emergent bulrush, submerged musk-grass, and the water lily family (Nymphaea). The native trees net-leaf hackberry and sumac persist.

In comparison to the faunal diversity in late Pleistocene to early Holocene times, the known Middle Holocene faunas in general are depauperate. Herd herbivores are modern bison and pronghorn antelope (*Antilocapra americana*), with the carnivore guild represented by gray wolf (*Canis lupus*) and coyote (*Canis latrans*). Other grassland forms include tiger salamander (*Ambystoma tigrinum*), Couchi's spadefoot toad (*Scaphiopus couchi*), yellow mud turtle (*Kinosternon flavescens*), western box turtle (*Terrapene ornata*), Texas horned lizard (*Phrynosoma cornutum*), bull snake (*Pituophis melanoleucus*), black-tailed jackrabbit (*Lepus californicus*), black-tailed prairie dog (*Cynomys ludovicianus*), Plains pocket gopher (*Geomys bursarius*), yellow-faced pocket gopher (*Cratogeomys castanops*), and cotton rat (*Sigmodon hispidus*). Despite the reduction in diversity, elements occur indicating the continuance of a prairie dog town community.

This prairie dog town community, as well as the other animals, represents basically a modern fauna adapted to an open short-grass prairie with some brushland. The occasional hackberry and sumac may have been more like shrubs than trees at this time. Warming and drying conditions occur, with a decrease in available moisture and humidity levels, greater seasonality, and aeolian sedimentation accumulation that indicates the beginning of a reduction in vegetation cover.

Middle and early Late Holocene stratum 4 times are represented by five localities that date from 5,500 to 2,000 B.P. (table 1) and are associated with the valley system. Chloridoid grasses increase in frequency and dominance throughout this time, most likely produced by a grama-buffalograss prairie. Some pooid grasses persist, including needlegrass or wintergrass, and panicoid grasses, including the short-grass threeawn.

In lower stratum 4, dating to the middle Holocene (5,500 to 4,500 B.P.), other floral elements are pigweed (*Amaranthus*), knotweed (*Polygonum*), buffalo bur, and the spurge family (Euphorbiaceae). Wet ground to open water plants include emergent bulrush and the water lily family. Native trees are net-leaf hackberry and honey mesquite.

Modern bison dominate the grassland fauna at this time as the herd herbivore. The carnivore guild is represented only by the coyote. Other grassland forms include long-nosed snake (*Rhinocheilus lecontei*), black-tailed prairie dog, yellow-faced pocket gopher, Ord's kangaroo rat (*Dipodomys ordii*), cotton rat, and white-throated woodrat (*Neotoma albigula*).

The grassland fauna was adapted to dry to desert conditions. Conditions had been warming since the early Holocene and this period is the height of the Altithermal (Holliday 1989b, 1995a, 1995b), a climatic episode of greatly reduced precipitation and available water, increased temperatures, and blowing dust. The setting most likely was a desert grassland with an occasional hackberry or mesquite shrub. Prairie dog towns persisted, although most likely reduced in size and scope. The short grass, herbaceous prairie dominated within a dry landscape of reduced vegetation.

In upper stratum 4, dating to the early part of the late Holocene (4,500 to 2,000 B.P.), floral elements in the short-grass prairie are buffalo bur and the spurge family. Net-leaf hackberry and honey mesquite are the native trees.

Herd herbivores are modern bison and pronghorn antelope, with the carnivore guild represented by gray wolf and coyote. Other grassland forms include tiger salamander, western box turtle, Texas horned lizard, 13-lined ground squirrel (*Spermophilus tridecemlineatus*), black-tailed prairie dog, and Plains pocket gopher.

By 4,500 B.P., the climate ameliorated, the landscape stabilized, and mesic and cooler conditions returned. Landscape stability heralded the establishment of basically modern conditions. Only the open prairie was reflected in the fauna and prairie dog towns existed in a short-grass, herbaceous prairie under essentially a continental climate.

Late Holocene stratum 5 times are represented by five localities dating from 2,000 to 200 B.P. (table 1) that are associated with both an upland salina and the valley system. Chloridoid grasses, most likely produced by grama-buffalograss prairies, continue to dominate. A low frequency of pooid grasses persist, including needlegrass or wintergrass, and panicoid grasses, including the short-grass threeawn. Crown grass (*Paspalum*; C_4 warm-season grass) joins the grass roster. Other floral elements are devil's claw, prickly poppy (*Argemone*), and buffalo bur. Only emergent bulrush represents wet ground to open water plants. Native trees are net-leaf hackberry, honey mesquite, and Texas walnut (*Juglans microcarpa*), another small tree to shrub. Isolated populations of the Texas walnut occur today on the Llano Estacado in the lower reaches of the canyons (Petrides and Petrides 1992:124; Cox and Leslie 1995).

The late Holocene fauna was more diverse than the middle Holocene fauna. The mainstay herd herbivores were modern bison and pronghorn antelope. The carnivore guild expanded to include gray wolf, coyote, badger (*Taxidea taxus*), and striped skunk (*Mephitis mephitis*). Other grassland forms were tiger salamander, Plains toad, yellow mud turtle, western box turtle, Texas horned lizard, ground snake (*Sonora semianulata*), checkered garter snake (*Thamnophis* cf. *marcianus*), western diamondback rattlesnake (*Crotalus atrox*), hawks (*Buteo* spp.), Say's phoebe (cf. *Sayornis saya*), northern mockingbird (*Mimus polyglottis*), Audubon cottontail (*Sylvilagus audubonii*), black-tailed jackrabbit, 13-lined ground squirrel, hispid pocket mouse (*Chaetodipus* cf. *hispidus*), black-tailed prairie dog, Plains pocket gopher, and cotton rat. A prairie dog town community continued, along with hawk and badger as its predators.

This prairie dog town community existed within a short-grass, herbaceous prairie in a savanna setting of occasional deciduous trees in the valley and mesquite along the upland lake basins. Despite the greater availability of moisture and less arid conditions than those of the middle Holocene, a cyclical drought pattern began around 2,000 B.P. that continues today. Periods of some aridity occurred through increased temperatures and decreased effective moisture. The droughts appeared not to have been severe enough to alter either the faunal community or the short-grass prairie significantly. Surface erosion from periodic denuding of the vegetation led to deposition and altered landscapes (Holliday 2001a; Muhs and Holliday 2001).

Summary Statement

Throughout the Quaternary, the Llano Estacado has always been a grassland, albeit the character of this grassland has changed through time. During the late Quaternary, it remains an herbaceous grassland. By the LGM, the region is a grassland steppe that was a sagebrush grassland in a cool-dry climate. During the latest Pleistocene (stratum 1), the grassland is a tall grass prairie in a cool-humid climate with a parkland setting in the valleys. By the beginning of the early Holocene (stratum 2), the grassland is a mixed prairie experiencing an increasing rise in C_4 grasses in a warming, less humid, and more seasonal climate with a savanna setting in the valleys. The emergence of the short-grass ecosystem occurs between 8,200 to 8,000 B.P. and is the dominant vegetation throughout the rest of the Holocene. Middle to late Holocene (strata 3 to 5) grasslands are short-grass prairies within a fluctuating climate that affected the ecosystem from a mesic to xerix to mesic grassland setting with a continued savanna setting in the valleys.

Various trees are native to the Llano Estacado, and most are deciduous. All but one of the deciduous trees can occur in a small tree to shrub form, making them more flexible in response to changing climatic conditions. Occurring primarily in the valley system, an occasional hackberry and mesquite were on the uplands around the lake basins depending on the period. Net-leaf hackberry is the most consistent tree, having persisted in the region since the LGM. Conifers are restricted to juniper and the occasional piñon-pine that grew along the western escarpment, primarily in the late Pleistocene and earliest Holocene. Today, junipers are thick along the western escarpment with again the occasional piñon-pine.

Key transformations take place that appear to involve climate and vegetation response. An early Holocene warming trend with greater seasonality and probable decrease in winter precipitation is coupled with a shift from the tall grass prairie to the mixed grass prairie. By 8,000 B.P., humid conditions have declined with a probable shift in rainfall pattern and increasing seasonality leading to less effective moisture than preceding periods. This situation is coupled with the rise of the short-grass ecosystem that maintains dominance through an increasingly arid period. Heat and drought tolerance are key characteristics of the short-grass prairie that maintained

this dominance then, and throughout the rest of the Holocene. The emergence of the continental climate around 4,500 B.P. provides more mesic but still semi-arid conditions and that climatic regime is modernized by the modification of a cyclical drought pattern starting around 2,000 B.P.

Bison, pronghorn antelope, and prairie dog are the binding grassland species. The transformation of ancient bison into modern bison appears to be in response to the rise of the short-grass ecosystem and its greater productivity but less nutritional value. The rapid size change reflects both a coping mechanism with the changing grassland composition and the flexibility of the bison genome. Pronghorn antelope browse on forbs and other herbaceous vegetation. Their presence throughout the late Quaternary underscores the continuance of the herbaceous aspect regardless of the character of the grassland. Prairie dogs also are adaptable and resilient, with a continuing prairie dog town community throughout, regardless of the character of the grassland.

The various lines of evidence are for the most part concordant and provide a solid foundation for examining the late Quaternary ecosystems of the region. Phytolith and macrobotanical remains have proven more informative and reliable than pollen. These lines of evidence are more reflective of local conditions and generally not influenced by extraregional factors. Explorations are on-going to expand the record and fill in the details. Of specific interest are the expansion of the upland record, an increased knowledge of the herbaceous nature of the grassland through time, and the relationship between prairie dog town communities (and, in particular, the prairie dog) and the health and status of a grassland.

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