EDWARDS PLATEAU VEGETATION
Plant Ecological Studies in Central Texas

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PREFACE

Because of its large size, topographic diversity, and southcentral position in North America, Texas has a flora of some 5,480 species (Correll and Johnston, 1970) in 10 natural regions (Gould, 1975a) and at least 77 major plant associations (Diamond et al., 1987). Central in the state's biogeographic pattern is the Edwards Plateau, a strongly dissected tableland, distinctly bordered on the east and south by the abrupt Balcones Escarpment. The steeply-rising Scarp and high Plateau feature an array of limestone and granite outcrops plus permanently watered canyons, dry mesas, and broad valleys that add to natural diversity.

In April, 1984, we met on the Plateau at Junction, Texas, for a symposium that addressed the region's vegetation patterns and dynamics of pattern development. O. W. (Bill) Van Auken organized this session, sponsored by the Southwestern Association of Naturalists. Each participant, whose original contribution follows, lives and works on the Edwards Plateau or Balcones Scarp. Our collective aim is to provide an introduction to the vegetational landscape, including representative photographs, specific research about the history of vegetation patterns, and quantitative information on current structure and succession.

We have arranged the symposium contributions in general to specific order over a "gradient" of woodland-forest to grassland studies. The introduction by David Riskind and David Diamond is followed by a historical appraisal of woody versus grassy vegetation by Del Weniger and a floristic geography of woody and endemic plants by Bonnie Amos and Chester Rowell, Jr. Then, chapters by Bill Van Auken and Fred Gehlbach describe woody vegetation structure, including community-types, and infer succession in different parts of the region. The role of fire in structuring a woodland-grassland mosaic is examined by Paul Fonteyn, Wade Stone, Malinda Yancy, John Baccus, and Nalini Nadkarni, while interspecific dynamics of both woodland and grassland are observed by Norma Fowler. Finally, a unique record of grassland succession is summarized by Fred Smeins and Leo Merrill. (See Fig. 1.)

All cited literature is grouped together in a separate section following the summary. After each citation we indicate by number which chapters and whether the preface and summary utilize that particular reference. Similarly, our selection of photographs is collected for ready access and comparison. At the end of each photo

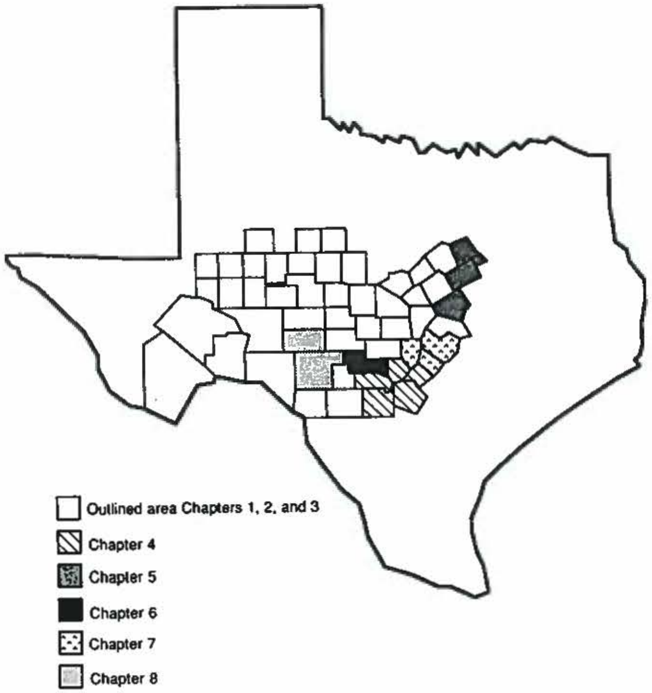

Fig. 1. Study areas, by chapter.

caption we indicate by chapter number those contributions that discuss details of the scene. Throughout the volume scientific nomenclature follows Correll and Johnston (1970) and Gould (1975b). Common names are also taken from these publications but with a few exceptions that we believe avoid confusion by being more descriptive of structure and relationship.

This volume is strictly an investigative effort, not a final synthesis. We are nearing the end of the necessary descriptive phase and only beginning controlled studies of vegetation dynamics. Our summary chapter provides a general view of the vegetational landscape but also makes the point that additional long-term studies are necessary. These will be particularly important because cultural changes are occurring at an increasing rate—the vegetation of the Edwards Plateau today is not the same as that described by William L. Bray 80 years ago. We dedicate this volume to Bray's memory, in view of his pioneering research.

Bonnie B. Amos
Frederick R. Gehlbach

1

AN INTRODUCTION TO ENVIRONMENTS AND VEGETATION

David H. Riskind and David D. Diamond

The Edwards Plateau of central and west-central Texas covers about 93,240 square kilometers, an area larger than the state of Louisiana (LBJ School of Public Affairs, 1978), and contains four distinct subregions (Fig. 1): (1) The eastern and southeastern portion, bordered by the Balcones Fault zone, is a highly dissected upthrown region with numerous high gradient streams in steep-sided canyons. This is the famous Texas Hill Country or Balcones Canyonlands. (2) North of the Colorado River along the northeast margin are the broad valleys and river scarps of the Lampasas Cut Plain. (3) The Llano Uplift or Central Mineral Region on the northeast is centered in Llano, Mason, and Burnet Counties and has a granitic substrate that is clearly distinguishable from the Cretaceous limestones of the rest of the Plateau. (4) The central and western portions of the Plateau, comprising about half of its area, are moderately dissected, with extensive flat to gently sloping stream divides and rounded hills.

PHYSIOGRAPHY AND TOPOGRAPHY

In broad context, the whole area is a southern extension of the Great Plains of North America (Great Plains Physiographic Province; Hunt, 1974). To the south and southeast the Plateau is separated from the lower-lying West Gulf Coastal Plain (South Texas Plains) by the Balcones Fault zone, where elevations on the down-thrust side of the Balcones Escarpment drop sharply to less than 190 m (Fig. 2). To the north the Plateau grades gradually into the Rolling Plains, to the northwest into the southern High Plains (south sandy plains), and to the east into the Blackland Prairie. To the west the region is separated from the Stockton Plateau by the Pecos-Devil's River divide. The Stockton Plateau is geologically similar to and has been considered by some as part of the Edwards Plateau (Gould, 1975a). However, it is usually grouped with the more arid Trans-Pecos region (Tharp, 1939; LBJ School of Public Affairs, 1978; U.S. Fish and Wildlife Serv., 1979).

Hill (1892) was the first to recognize the Edwards Plateau as a distinct physiographic province, but its definition has varied. Tharp (1939) described the vegetation of Texas and included the Grande Prairie to the north and Hill Country to the south and southeast as part of the Plateau but excluded the Llano Uplift and the flatter, central and northwestern portions. Dice (1943) provided a map of biotic provinces of North America, based primarily on faunal distributions, and included the Plateau with the Rolling Plains in his Commanchian Biotic Province. This treatment was later modified by Blair (1950), who treated the Plateau as his Balconian Province. Gould (1975a) included the Llano Uplift and Stockton Plateau west of the Pecos River but not the Lampasas Cut Plain in still another definition of the Edwards Plateau. Godfrey et al. (1973) used a similar definition but excluded the Llano Uplift. Kuchler (1964), in a widely recognized treatment of the potential natural vegetation of the United States, described the Lampasas Cut Plain and eastern half of the Plateau as juniper-oak savanna, the Llano Uplift as mesquite-oak savanna, and the northwestern portion as mesquite or mesquite-buffalograss savanna. The LBJ School of Public Affairs (1978) published a map of the natural regions of Texas, which was essentially the same as one adopted by the U.S. Fish and Wildlife Service (1979) and both excluded the Llano Uplift but included the Lampasas Cut Plain as part of the Edwards Plateau (Fig. 1).

Elevations of the Edwards Plateau generally increase from the southern and eastern margins toward the northwest. Austin and San Antonio on the south are at 167 m and 213 m, respectively, while Junction near the center of the Plateau is at 521 m, and Big Lake on the northwest is at 734 m. The topography is most rugged in the Balcones Canyonlands region, where stream valleys are often 100 m lower than adjacent ridges. For example, hills rising above the Frio River 130 km west of San Antonio are at 524 m, while the adjacent valley is at 372 m. Steep topography also occurs in the Llano Uplift region, where nearly barren granite outcrops tower above adjacent flats. An example is Enchanted Rock, 20 km north of Fredericksburg, which rises to 556 m or 130 m above the surrounding landscape.

The influence of faulting associated with the Balcones Escarpment is most pronounced along the southern and southeastern margins of the Plateau from Austin to San Antonio (Fig. 2). This Hill Country

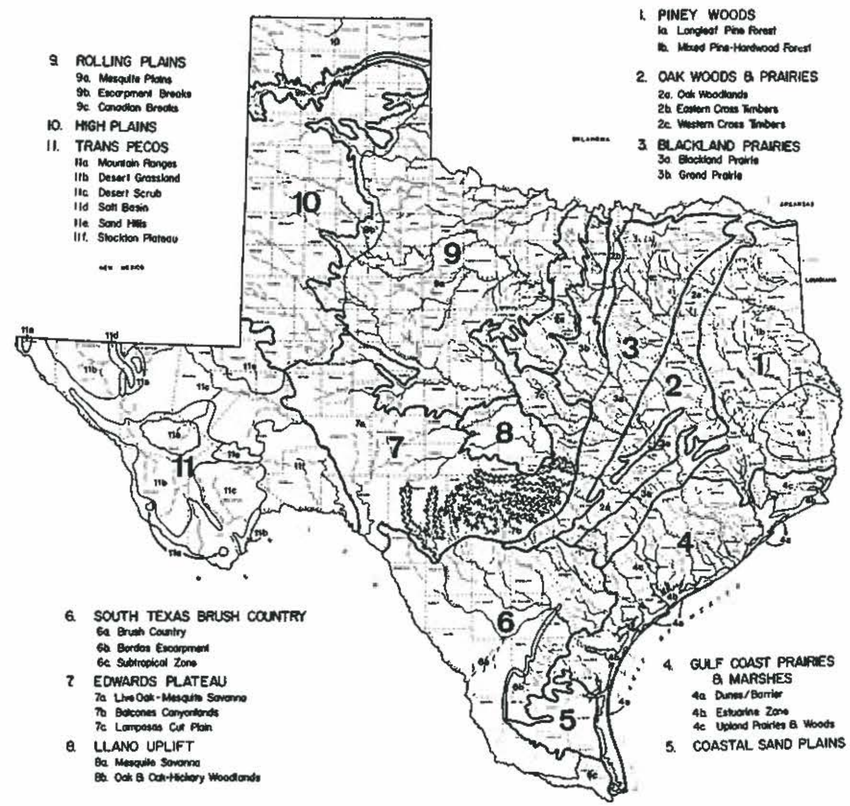

Fig. 1. The natural regions and subregions of Texas. The Edwards Plateau includes areas 7 and 8 (from *Preserving Texas' Natural Heritage*, LBJ School of Public Affairs, 1978).

is a highly dissected landscape with steep canyons, narrow divides, and high gradient streams that generally flow south or southeast to the Gulf of Mexico. They include, from west to east, the Neuces, Frio, Sabinal, Medina, Guadalupe, and Blanco Rivers. The Pedernales River flows eastward through the region, joining the Colorado just west of Austin. There are numerous springs in this area along the edge of the up-thrust portion of the Balcones Scarp, and they are important as water sources for cities situated along the Plateau boundary and West Gulf Coastal Plain (i.e., Del Rio, Uvalde, San Antonio, New Braunfels, San Marcos).

The granitic Llano Uplift is a basin with respect to the main body of the Plateau to the south and west, but it originated as an uplift, (Figs. 1, 2). Granite outcrops dot an otherwise rolling landscape, except near drainages such as the Llano, San Saba, and Colorado

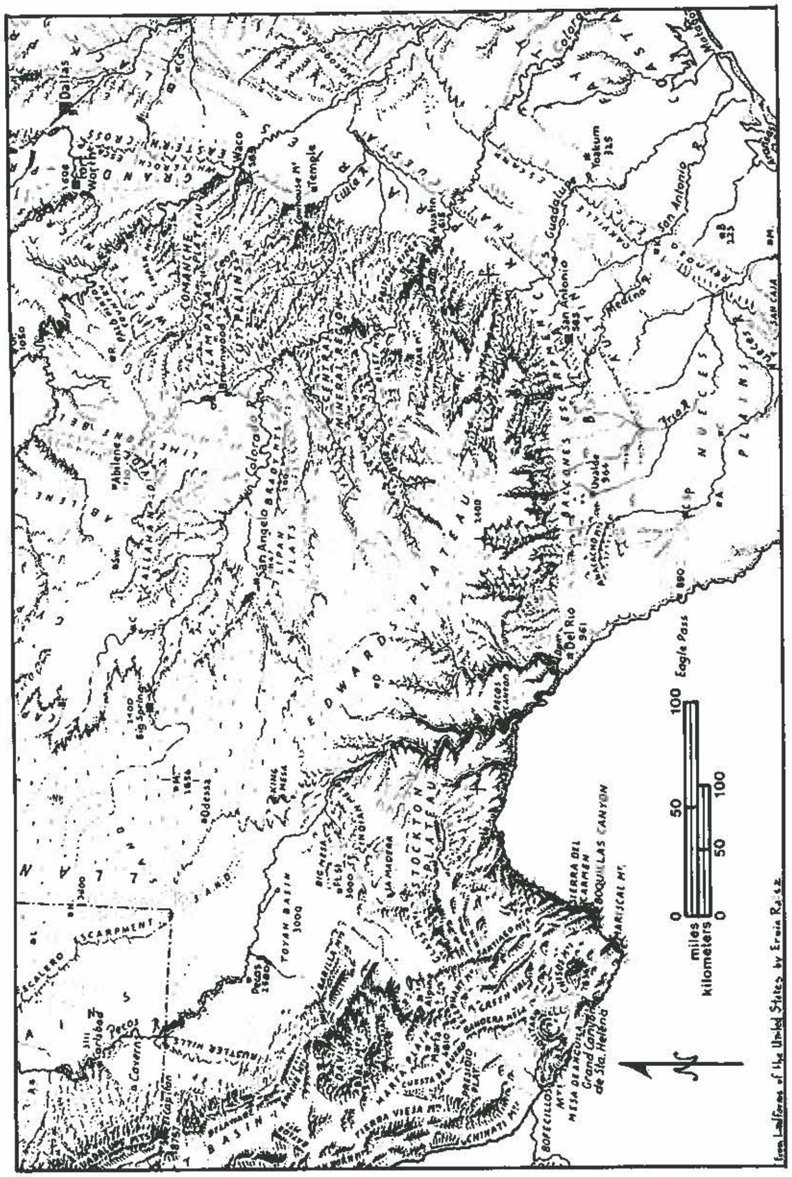

Fig. 2. The landforms of the Edwards Plateau region (from Raisz, 1957).

Rivers and their tributaries, where locally rough topography appears. The Lampasas Cut Plain on the northeast is generally less rugged. It consists of broad valleys and wide stream divides with some steep, high gradient canyons. The Lampasas and San Gabriel Rivers are the only major streams that bisect the area (Figs. 1, 2).

From the central Plateau to the north and northwest the topography is gently rolling with rounded hills, wide stream divides and few steep slopes. Much of the area could be described as a broad plain (Fig. 2). Several major streams cut east to west paths across this plain, including, from north to south, the Concho, San Saba, and Llano Rivers. These eventually join the Colorado, which flows southeast through the Llano Uplift and eventually to the Gulf of Mexico. The Devils River and its tributaries also bisect this plain in the southwest but flow south to join the Rio Grande.

GEOLOGY

Most of the Edwards Plateau is Cretaceous limestone rock. The less eroded central and western portions are generally dominated by limestone within the Edwards Formation, while southward and eastward Edwards limestone has largely been eroded, exposing older Cretaceous material, primarily within the Glen Rose and Georgetown Formations (Sellards et al., 1932). The Lampasas Cut Plain, which represents a more mature landscape than the main portion of the Plateau, is composed mostly of material within these groups, but more resistant Edwards limestone caps the mesas of the region. Both Glen Rose and Georgetown Formations are composed of several members with much variability. For example, stair-step topography is often caused by alternate exposures of resistant and recessive layers within the Glen Rose Formation. Patches of limestone, dolomite, chert, and marl may alternately outcrop at the surface within the same area.

The Llano Uplift is strikingly different from the remainder of the Edwards Plateau. It is an intrusive outcrop of Precambrian granitic material. Overlying this granite, where they have not been eroded away (around the perimeter, especially the northern border), are early Paleozoic sedimentary rocks including limestone, dolomite, sandstone, siltstone, and shale. The granitic material is composed variously of hornblende schist, graphite schist, quartz-feldspar gneiss, and quartz-plagioclase-microcline rock. In addition, local Cretaceous igneous outcrops are scattered throughout the southern and eastern portions of the Plateau.

SOILS

Variation in parent material and a generally hilly landscape have led to the development of many different soil types. Excluding the

Llano Uplift, upland soils have generally developed over limestone or caliche. They are usually shallow and rocky or gravelly on slopes and deep in broad valleys and on flats. Most are dark colored and calcareous, although pH is variable, depending on base saturation of the substrate plus the degree of soil profile development (Godfrey et al., 1973). Surface texture also varies from loamy to clayey, depending on substrate and profile development.

These upland soils are generally classified as Mollisols on flats and valleys (deeper soils) or Inceptisols on slopes (shallow soils). Many contain montmorillonitic clay and hence shrink and swell on wetting and drying and develop deep cracks in the dry months. Clayey Vertisols are also present, especially in the east, north, and northwest. Both Mollisols and Vertisols have surface layers that are high in organic matter, but various nutrients, especially nitrogen, may be limiting to plant growth. Inceptisols may also have a high organic matter content, although they are not generally as fertile, mature, or deep as Mollisols and Vertisols (Soil Survey Staff, 1975). Over less basic parent materials or non-calcareous secondary colluvium or alluvium (for example, on old stream terraces or in former shallow depressions), loamy Alfisols have developed. They are often less fertile than Mollisols or Vertisols, although plant-soil water relations may be good (Soil Survey Staff, 1975).

Soils of the Llano Uplift have generally developed from granitic materials or, around the margins of the region, from a variety of shale, limestone, dolomite, or siltstone substrates. Most have acid, loamy surface layers and are classified as Alfisols (Godfrey et al., 1973). Some deep, well-watered, sandy deposits are found around the base of major granite outcrops and in stream bottoms. These have poor soil profile development and are classified as Inceptisols.

CLIMATE

The Edwards Plateau becomes increasingly arid to the west and cooler to the north. Eastern and central portions are subtropical-subhumid, while the western one-fourth is subtropical-semiarid (Larkin and Bomar, 1983; Fig. 3). According to Thornthwaite (1948), these are dry subtropical and semiarid moisture regions respectively. The general decrease in moisture from the Gulf of Mexico, flowing northwest across the Plateau, is primarily responsible for this difference in moisture regime (Bomar, 1983).

Mean annual precipitation ranges from about 85 cm/yr on the eastern to 35 cm/yr on the western edge of the Plateau (Fig. 3; Bomar, 1983), with a concomitant increase in mean lake surface evaporation. July-August evaporation increases from 46 cm in the east to 57 cm in the west, while annual rates increase from 160 cm/yr to 206 cm/yr from east to west. July plus August precipitation

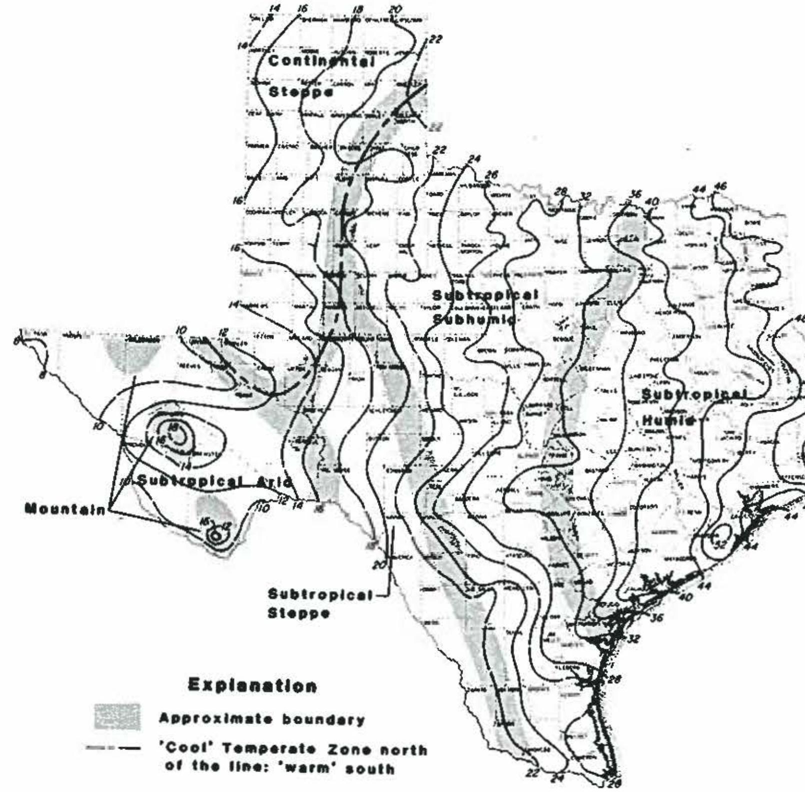

Fig. 3. Average annual precipitation (based on 1951-1980 data) and classification of climate for Texas.

also decreases from east to west, ranging from 13 cm to 9 cm (Larkin and Bomar, 1983), so there is a pronounced decrease in summer precipitation and an increase in summer evapotranspiration. In addition, periodic drought years, such as those in the mid-1950s and early 1980s, cause even more severe moisture stress on plants. For example, the flow of the Guadalupe River at New Braunfels was below average for 35 out of 36 months during the 1954 to 1956 period, some Hill Country streams dried up completely, and many wells declined to record-low levels (Bomar, 1983).

High intensity rainfall events are also characteristic of the Edwards Plateau. Torrential storms are most common in the Balcones Canyonlands along the southern and southwestern margins of the region (Baker, 1975; Bomar, 1983). Flooding and erosion caused by these storms are major impacts. For example, a major storm at Austin on the night of May 24, 1981, provided 25 cm of rain in a four hour period, causing catastrophic flooding and residential and commercial damage amounting to $40 million (Bomar, 1983). Another storm associated with a stalled, weak tropical depression (Amelia) dumped over 120 cm of precipitation on the Medina and Guadalupe River watersheds from August 1-4, 1978, causing disastrous flooding (Bomar, 1983).

The average frost-free period ranges from approximately 260 days in the south (early March through late November) to 230 days in the north (Larkin and Bomar 1983). July high and low temperatures average 35°C and 22°C, respectively, across the entire region, whereas mean January lows decrease northward, ranging from approximately 4°C to 0°C.

VEGETATION

Balcones Canyonlands (Tables 1, 2)

This region is dominated primarily by woodland and forest vegetation (*sensu* Driscoll et al., 1984). Grasslands are generally restricted to broad drainage divides and valleys plus the adjacent slopes. More qualitative and quantitative data on plant ecology are available for this region than elsewhere on the Plateau (Anderson, 1904; Palmer, 1920; Solcher, 1927; Culyer, 1931; Beuchner, 1944; Lynch, 1962, 1971; Van Auken et al., 1979, 1980, 1981; Ford and Van Auken, 1982; Bush and Van Auken, 1984, 1986; Fowler, 1986a; Van Auken and Bush, 1985; Fowler and Dunlap, 1986), but intra- and inter-regional variation in plant communities is still not well known. For example, north- and east-facing slopes are moister habitats than south- or west-facing slopes. Although concomitant changes in vegetation are obvious, only one study has dealt with variation due to exposure (Van Auken et al., 1981), and none have compared communities of similar habitat from east to west.

Mesic slopes of this region support deciduous woodlands or forests with Texas oak (*Quercus texana*), Plateau live oak (*Q. fusiformis*), Ashe juniper (*Juniperus ashei*), black cherry (*Prunus serotina*), and Texas ash (*Fraxinus texensis*) (Palmer, 1920; Solcher, 1927; Beuchner, 1944; Van Auken et al., 1981; Table 1). Cedar elm (*Ulmus crassifolia*), sugarberry (*Celtis laevigata*), netleaf hackberry (*Celtis reticulata*), and Arizona walnut (*Juglans major*) may also be present. In the central and western portions Lacey oak (*Quercus glaucoides*) is important, while scalybark oak (*Quercus sinuata*) is most important in the east. These vegetation-types often contain a distinct understory layer composed of yaupon (*Ilex vomitoria*), American beautyberry (*Callicarpa americana*), hoptree (*Ptelea trifoliata*), Mexican buckeye (*Ungnadia speciosa*), deciduous holly (*Ilex decidua*), and roughleaf dogwood (*Cornus drummondii*). Bigtooth maple (*Acer grandidentatum*), Carolina basswood (*Tilia caroliniana*), and ash (*Fraxinus* spp.)

are species with eastern affinities that are locally important on mesic slopes and floodplains; Texas madrone (*Arbutus xalapensis*) and Mexican pinyon (*Pinus cembroides*) are similar southwestern/Mexican species.

Table 1. Dominant trees and shrubs of floodplain forest and slope woodland of the Balcones Canyonlands and Lampasas Cut Plain; a generalized transect from wet (left) to dry (right) environments; species listed alphabetically.

Floodplain Forest	Deciduous Woodland	Evergreen Woodland
Acer negundo	*Fraxinus* spp.	*Berberis trifoliolata*
Carya illinoensis	*Juglans major*	*Diospyros texana*
Celtis laevigata	*Juniperus ashei*	*Juniperus ashei*
Quercus spp.	*Prunus serotina*	*Quercus fusiformis*
Salix nigra	*Quercus glaucoides*	*Q. sinuata*
Taxodium distichum	*Q. sinuata*	*Q. texana*
Ulmus americana	*Q. texana*	*Rhus* spp.
U. crassifolia	*Ulmus crassifolia*	*Sophora secundiflora*

Table 2. Dominants of major grassland-types of the Edwards Plateau; generalized transect from east (left) to west (right), a wet to dry environmental gradient; species listed alphabetically.

Tall Grassland	Mixed Grassland	Short Grassland
Andropogon gerardii	*Aristida* spp.	*Aristida* spp.
Bouteloua curtipendula	*Bothriochloa* spp.	*Bouteloua curtipendula*
Bothriochloa saccharoides	*Bouteloua curtipendula*	*B. gracilis*
Eriochloa sericea	*Bouteloua* spp.	*B. rigidiseta*
Juniperus ashei	*Buchloe dactyloides*	*Bouteloua* spp.
Muhlenbergia reverchonii	*Eriochloa sericea*	*Buchloe dactyloides*
Quercus fusiformis	*Hilaria belangeri*	*Erioneuron pilosum*
Q. sinuata	*Muhlenbergia* spp.	*Hilaria belangeri*
Schizachyrium scoparium	*Prosopis glandulosa*	*H. mutica*
Sorghastrum nutans	*Quercus* spp.	*Muhlenbergia* spp.
Stipa leucotricha	*Schizachyrium scoparium*	*Prosopis glandulosa*
Sporobolus asper	*Stipa leucotricha*	*Sporobolus cryptandrus*

Slope communities on dry southern and western exposures are primarily evergreen and dominated by Ashe juniper, often in nearly pure stands called cedar breaks. Plateau live oak, Texas persimmon (*Diospyros texana*), scalybark oak, evergreen sumac (*Rhus virens*), skunkbush sumac (*R. aromatica*), elbowbush (*Forestiera pubescens*), Texas oak, and Texas mountain laurel (*Sophora secundiflora*) may also be present (Beuchner, 1944; Blair, 1965; Van Auken et al., 1981).

Scrub oak (*Quercus pungens*) is important in the west. These xeric woodlands usually contain no understory woody layer and are less diverse in woody species than deciduous counterparts on north- and east-facing slopes.

West of the Frio river, slope communities take on a different aspect due to the increasingly arid climate. Woodlands, often dominated by Plateau live oak, become restricted to north and east (mesic) exposures. Xerophytic shrubs, small trees and succulents such as sumac (*Rhus* spp.), sotol (*Dasylirion texanum*), quajillo (*Acacia berlandieri*), *Acacia* spp., honey mesquite (*Prosopis glandulosa*), scalybark oak, scrub oak, Mohr's shin oak (*Quercus mohriana*), Texas persimmon, and cenizo (*Leucophyllum frutescens*) plus Ashe juniper form open shrublands on dry slopes over shallow soils (see Bray, 1905; Tharp, 1944; Webster, 1950; Flyr, 1966; Warnock, 1970; Smith and Butterwick, 1975a, 1975b).

Floodplains along perennial spring runs and rivers sometimes support bald cypress (*Taxodium distichum*) gallery forests with sycamore (*Platanus occidentalis*), black willow (*Salix nigra*), buttonbush (*Cephalanthus occidentalis*), and dwarf palmetto (*Sabal minor*) (Beuchner, 1944; Van Auken et al., 1979; Ford and Van Auken, 1982). This community is a western expression of eastern swamp communities, adapted to periodic flooding of great magnitude, which may be essential for its maintenance (see Gehlbach, 1981).

Smaller floodplains and higher terraces are usually dominated by some combination of elm (*Ulmus crassifolia* and *U. americana*), sugarberry, netleaf hackberry, ash, pecan (*Carya illinoensis*), and box elder (*Acer negundo*), although there is considerable east-to-west variation (Beuchner, 1944; Ford and Van Auken, 1982; Bush and Van Auken, 1984). Species such as pecan, scalybark oak, chinkapin oak (*Quercus muhlenbergia*), and Arizona walnut are more important in the east or on moister bottoms, while Plateau live oak, netleaf hackberry, and sugarberry generally increase to the west, on well-drained terraces, or on drier bottoms (see Bray, 1905; Beuchner, 1944; Ford and Van Auken, 1982). American beautyberry, deciduous holly, roughleaf dogwood, yaupon, and hoptree are often present in the understory. Sugarberry, netleaf hackberry, and cedar elm increase in disturbed floodplains. The lower Devils River on the far west is a mesic "island" with a riparian forest of Plateau live oak, pecan, and sycamore (Smith and Butterwick, 1975a; Gehlbach, 1981).

Most grasslands of the Balcones Canyonlands region have been heavily grazed by domestic livestock and subjected to various brush control techniques, hence they are patchy and dynamic. Variation due to soils and aspect is difficult to separate from that due to past disturbance (Dunlap, 1983; Fowler and Dunlap, 1986). Grasslands of the Blackland Prairie on the eastern boundary of the region are an extension of the True (tallgrass) Prairie (Diamond and Smeins, 1985). Allred (1956) considered the Plateau a southern extension of the Mixedgrass Prairie. Thus, well-watered, moderately grazed uplands of the region resemble tallgrass communities, but increasing aridity to the west or overgrazing creates midgrass and shortgrass communities (Smeins et al., 1976; Dunlap, 1983).

Little bluestem (*Schizachyrium scoparium*), Texas wintergrass (*Stipa leucotricha*), white tridens (*Tridens muticus*), Texas cupgrass (*Eriochloa sericea*), tall dropseed (*Sporobolus asper*), sideoats grama (*Bouteloua curtipendula*), seep muhly (*Muhlenbergia reverchonii*), and common curlymesquite (*Hilaria belangeri*) are among the dominants of moderately grazed areas (Dunlap, 1983; Smeins et al., 1976). Heavily grazed grasslands and drier soils contain more short grasses such as curlymesquite, threeawns (*Aristida* spp.), Texas grama (*Bouteloua rigidiseta*), red grama (*B. trifida*), hairy grama (*B. hirsuta*), hairy tridens (*Erioneuron pilosum*), and white tridens. Cedar sedge (*Carex planostachys*) is common in these grasslands. Old fields were extensively planted to the introduced K-R bluestem (*Bothriochloa ischaemum*) in the 1950s, and some areas are maintained as bermudagrass (*Cynodon dactylon*) or Johnsongrass (*Sorghum halepense*) hay fields and pastures.

Soil depth and texture are highly variable in most areas, and the grassland may be extremely heterogeneous (Smeins et al., 1976). An example of the interaction of grazing and soils is found in Fowler and Dunlap (1986), who concluded that flat uplands of the Hays-Travis-Blanco County area may support shortgrass communities, while slopes have more tall and midgrasses. This is due to a clayey and hence drier soil on flats and heavier grazing on ridges than on adjacent slopes.

Plateau live oak, scalybark oak, and other woody species are components of the grasslands, forming clumps or motts or occurring as scattered individuals (see Bray, 1905, 1906; Beuchner, 1944; Smeins, 1980). Steep scarps with shallow soil and drainages also support woody vegetation, including Ashe juniper, and these areas may have a park-like aspect (McMahan et al., 1984). On deep soils, live oak, Texas oak, cedar elm, post oak (*Quercus stellata*), and, especially on the east or in sandy soils, blackjack oak (*Q. marilandica*) may be scattered or form woodlands alternating with grasslands in both the uplands and broad stream valleys. Similar woodlands also inhabit well-drained stream terraces.

Although grasslands of the region may not have been devoid of Ashe juniper in pre-European settlement times, an increase in density of this species has been observed, creating cedar thickets in former grasslands (see Bray, 1905; Foster, 1917; Beuchner, 1944; Smeins, 1980). Mesquite is also a woody component of grasslands that has increased in density in many upland areas, and live oak, scalybark oak, and other woody species may cover more area now than in pre-European settlement times. Prickly pear (*Opuntia* spp.) is also a common component of disturbed grasslands here and in the other three regions.

Lampasas Cut Plain (Tables 1, 2)

Woody plant communities of the Lampasas Cut Plain intergrade with those of the Balcones Canyonlands, but because the general topography is flatter and there are fewer drainages, their character as a whole is more that of an open woodland (savanna, *sensu* Kuchler, 1964) than a closed woodland or forest (McMahan et al., 1984). Also, there are more northern elements and a larger extent of post oak-blackjack oak woodland, especially where the Cut Plain meets the Western Cross Timbers (Fig. 1). Southern elements such as Texas madrone, Lacey oak, and Mexican pinyon are absent, while scalybark oak and bur oak (*Quercus macrocarpa*) are more important. Ashe juniper forms cedar breaks on some limestone scarps, but perhaps not as frequently as in the Balcones Canyonlands (McMahan et al., 1984).

Although grasslands of the region are usually most closely related to Mixed Prairie (Allred, 1956; Dodd, 1968; Risser et al., 1981), grasslands to the north and east are considered extensions of the True or Tallgrass Prairie (Dyksterhuis, 1946; Diamond and Smeins, 1985). Tall, mid and shortgrasses such as little bluestem, Indiangrass (*Sorgastrum nutans*), big bluestem (*Andropogon gerardii*), silver bluestem (*B. saccharoides*), Texas wintergrass, tall dropseed, sideoats grama, and curlymesquite are present. Mesquite and Ashe juniper are common brush problems for ranchers and, as in other regions of the Plateau, the grasslands are patchy due to differential grazing, brush clearing, and past cultivation.

Llano Uplift

Woodland and savanna-like communities are characteristic of the granitic Llano Uplift, but the region is also dotted by granite outcrops that are nearly devoid of woody vegetation. These areas have been the subject of several studies on floristics and succession (Whitehouse, 1933; Butterwick, 1979; Walters, 1980; Walters and Wyatt, 1982). As on the adjacent limestone region, Plateau live oak is a major component, but Ashe juniper and Texas oak are nearly absent from the loamy or sandy, acid soils that predominate in the Llano region. Honey mesquite and white brush (*Aloysia gratissima*) are often dominants, especially on finer-textured soils and disturbed sites, and the mesquite-dominated community-type occupies large flats over loamy soils in the region (Tharp, 1939; McMahan et al., 1984). Other important species of typical upland woodlands include kidneywood (*Eysenhardtia texana*), *Acacia* spp., *Bumelia* spp., netleaf hackberry, Texas persimmon, lotebush (*Ziziphus obtusifolia*), prickly pear, *Condalia* spp., and cedar elm.

Plateau live oak-post oak and comparatively mesophytic oak-black hickory (*Carya texana*) woodlands and forests occupy deep, sandy soils derived from granite or Tertiary sandstone (Tharp, 1939; S.C.S., unpubl.). In protected locations adjacent to granite exposures, oak-hickory forests are close to oak-dominated communities with scattered, low-growing oaks and Mexican buckeye (Tharp, 1939; Butterwick, 1979). Additional important species of mesophytic woodlands include blackjack oak, pecan, white buckeye (*Aesculus arguta*), cedar elm, netleaf hackberry, and prickly ash (*Zanthoxylum* spp.).

Grasslands form a mosaic with woodlands in the region. As in other parts of the Plateau, cultural impact has created a patchy distribution of community-types. Grasslands in good condition over sandy soils are dominated by little bluestem with Indiangrass, switchgrass (*Panicum virgatum*), love grass (*Eragrostis* spp.), silver bluestem, green sprangletop (*Leptochola dubia*), threeawns, and fall witchgrass (*Leptoloma cognatum*) (Kuchler, 1964; McMahan et al., 1984). Threeawns, *Tridens* spp., gramas (*Bouteloua hirsuta*, *B. rigidiseta*), and sand dropseed (*Sporobolus cryptandrus*) increase under heavy grazing pressure. Purpletop (*Tridens flavus*) and Canada wildrye (*Elymus canadensis*) are common, shaded, understory species. Loamy soils usually support mesquite along with midgrasses including sideoats grama, California cottontop (*Digitaria californica*), silver bluestem, *Tridens* spp., bristlegrass (*Setaria* spp.), curlymesquite, gramas, buffalograss (*Buchloe dactyloides*) and threeawns.

Central and Western Plateau

Vegetation-types of this area grade into those of the western and northern Canyonlands. Semi-open grasslands, grassland-shrubland, or grassland-woodland mosaics are characteristic (McMahan et al., 1984). Curlymesquite is often dominant along with mid- and shortgrass species such as sideoats grama, little bluestem, cane bluestem (*Bothriochloa barbinodis*), silver bluestem, Texas wintergrass, Texas cupgrass, sand dropseed, bristlegrass, green spangletop, seep muhly, fall witchgrass, threeawns, and *Tridens* spp. (Valentine, 1960; Smeins et al., 1976; Table 2). Shortgrass species such as blue grama (*Bouteloua gracilis*), buffalograss, hairy tridens, threeawns, hairy grama, sand dropseed, and tobosa (*Hilaria mutica*) increase in importance to the west and northwest or on overgrazed range (Thomas and Young, 1954). Black grama (*Bouteloua eriopoda*), sand dropseed, bush muhly (*Muhlenbergia porteri*), and other shortgrasses inhabit shallow, rocky soils in the west, where woody elements common in the Trans-Pecos form open shrublands (see

Bray, 1905; Webster, 1950; Warnock, 1970). Several introduced grasses have been used in range plantings; for example, K-R bluestem is a common and persistent exotic.

The woody component of these grassland communities changes from predominantly oak or juniper in the east to mesquite in the west and northwest (McMahan et al., 1984). Plateau live oak, scalybark oak, and scrub oak are often scattered or form dense motts within midgrass grasslands (Smeins et al., 1976; McMahan et al., 1984). Ashe juniper sometimes forms cedar breaks on the uplands, especially over naturally shallow or eroded soils. Other common woody species include elbowbush, netleaf privet (*Forestiera reticulata*), agarita (*Berberis trifoliolata*), redbud (*Cercis canadensis*), netleaf hackberry, kidneywood, sumac, Texas persimmon, *Condalia* spp., and *Bumelia* spp.

West of the upper Devils River the environment becomes increasingly arid. On flat, heavy-textured soils, shrubby mesquite is often scattered in shortgrass communities dominated by tobosa, buffalograss, and gramas (Thomas and Young, 1954; Kuchler, 1964; McMahan et al., 1984). Redberry juniper (*Juniperus pinchotii*) becomes a more common component of the vegetation, although Ashe juniper dominates shrublands over steep, shallow soils as in the rest of the Plateau (Webster, 1950). Other woody components include lotebush, *Acacia* spp., kidneywood, *Condalia* spp., prickly ash, *Bumelia* spp., and elbowbush (Smeins et al., 1976; McMahan et al., 1984).

Much land in the region has been cleared of woody species, often several times, by various mechanical and chemical means, and the woody and herbaceous components are highly variable resulting in a patchy landscape. In the east, Ashe juniper and honey mesquite occur in various densities and age classes in disturbed communities, while in the west, dry-adapted shrubs such as lotebush and *Acacia* spp. are more important over shallow soils (Webster, 1950).

Floodplain and slope communities are depauperate in the central and western Plateau. Eastward the slopes are generally dominated by evergreen and deciduous woodlands similar to those of the Canyonlands region, while to the west, mesquite, mesquite-juniper, or mixed shrublands occur. In the far west, succulents such as lechuguilla (*Agave lecheguilla*), *Yucca* spp., and sotol plus xerophytic shrubs such as scrub oak, *Acacia* spp., and cenizo occur along with semi-desert grassland species such as chino grama (*Bouteloua breviseta*) and black grama (Webster, 1950; Warnock, 1970). Floodplains are generally codominated by cedar elm, Plateau live oak, netleaf hackberry, or sugarberry. Mesquite and mixed shrubs inhabit shallow drainages, while sycamore, *Salix* spp., little walnut (*Juglans microcarpa*), and *Baccharis* spp. grow in flood-scoured streambeds.

SUMMARY

The Edwards Plateau is a vast region with diverse climate, geology, landforms, and soils. At least four subdivisions can be recognized based on these abiotic variables: 1) the Balcones Canyonlands (Hill Country); 2) the Lampasas Cut Plain; 3) the Llano Uplift or Central Mineral Region; and 4) the central and western Plateau (Fig. 1). The climate becomes more arid and the land less dissected to the west, and there is a shift from more woodland and forest vegetation to a grassland-woodland or grassland-shrubland mosaic (see Bray, 1906; Johnson, 1931; Tharp, 1939). A recent map of the current vegetation of Texas based on LANDSAT data (McMahan et al., 1984) and a map of potential natural vegetation by Kuchler (1964) confirm the differences among these regions. A highly generalized summary of vegetation-types would include: deciduous forests or woodlands on floodplains and mesic slopes; evergreen woodlands on xeric slopes and scattered in upland grasslands; evergreen and deciduous shrublands on dry slopes in the west and on disturbed uplands; and an east-to-west (mesic-to-xeric) tallgrass-to-shortgrass gradient of grasslands on uplands and in broad valleys (Tables 1, 2). Uplands often appear savanna- or park-like because of scattered clumps or individuals of woody species.

The demise of free-roaming bison, introduction of intensive, year-round grazing by domestic livestock, and change in fire regime have led to a widespread increase in woody species and loss of grassland across the Plateau (Bray, 1904; Foster, 1917; Smeins, 1980). Plateau live oak and honey mesquite are generally viewed as natural components of upland tallgrass and shortgrass communities, respectively, but these species have increased in abundance, and Ashe juniper has invaded many overgrazed grasslands since European settlement. Almost all grasslands are in some stage of secondary succession related to overgrazing, brush clearing, or past cultivation. Thus, the contemporary landscape is a mosaic of vegetation-types related to variation in abiotic factors and differences in cultural impacts.

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