Away from the railroad, the Big Bend – sometimes called the Bloody Bend – is a hardy country, that is, one in which, through lack of water, civilization finds it difficult to gain a foothold. Although abundantly supplied with waterworks, such as scarped and canyoned streamways, it possesses a minimum of water. These great arroyos are mocking travesties which suggest that nature becomes tired of making this country before turning on the water.

– Robert T. Hill, USGS geologist, 1889

(Maxwell 1985)

"The harsh physically inhospitable arid Big Bend area either attracts and fascinates or utterly repels the visitor…if [he] lingers however, he learns that the higher mountains are a treasure…"

-- Ross A. Maxwell, first superintendent of Big Bend National Park

(Maxwell et al. 1967)

CHAPTER I

INTRODUCTION

To this day, Ross Maxwell's words ring true for those who know the Big Bend region. The Dead Horse Mountains (DH) of Big Bend National Park (BBNP) create a remote and forbidding viewscape on the West Texas park's eastern skyline. The rugged limestone escarpments offer no reliable surface water, nor infrastructure allowing quick access to the interior, leading to claims of it's being uncharted wilderness (Wood et al. 1999). These logistical challenges, in addition to rugged topography and extreme climate, have left the area one of the least botanically understood areas in Texas and the northern Chihuahuan Desert province.

The lack of attention creates a degree of floristic intrigue. The DH occur in an area of large-scale ecological overlap. In this part of the Trans-Pecos Mountains and Basins vegetational area (Fig. 1; Hatch et al. 1990), phytogeographic connections exist with other Texas floristic areas including the High Plains, Rolling Plains, Edwards Plateau, and the South Texas Plains, also known as the Tamaulipan Thornscrub region (Powell 2000). Northerly connections are evidenced by the populations of aspen, Douglas-fir, and other Rocky Mountain species growing well south of their normal distributions. Floristic links reach south to the Sierra Madre Oriental and Occidental, in addition to the greater Chihuahuan Desert of Mexico (Larke 1989). The graminoid flora even has an affinity to the Great Plains grasslands (Powell 2000; Christie 2006).

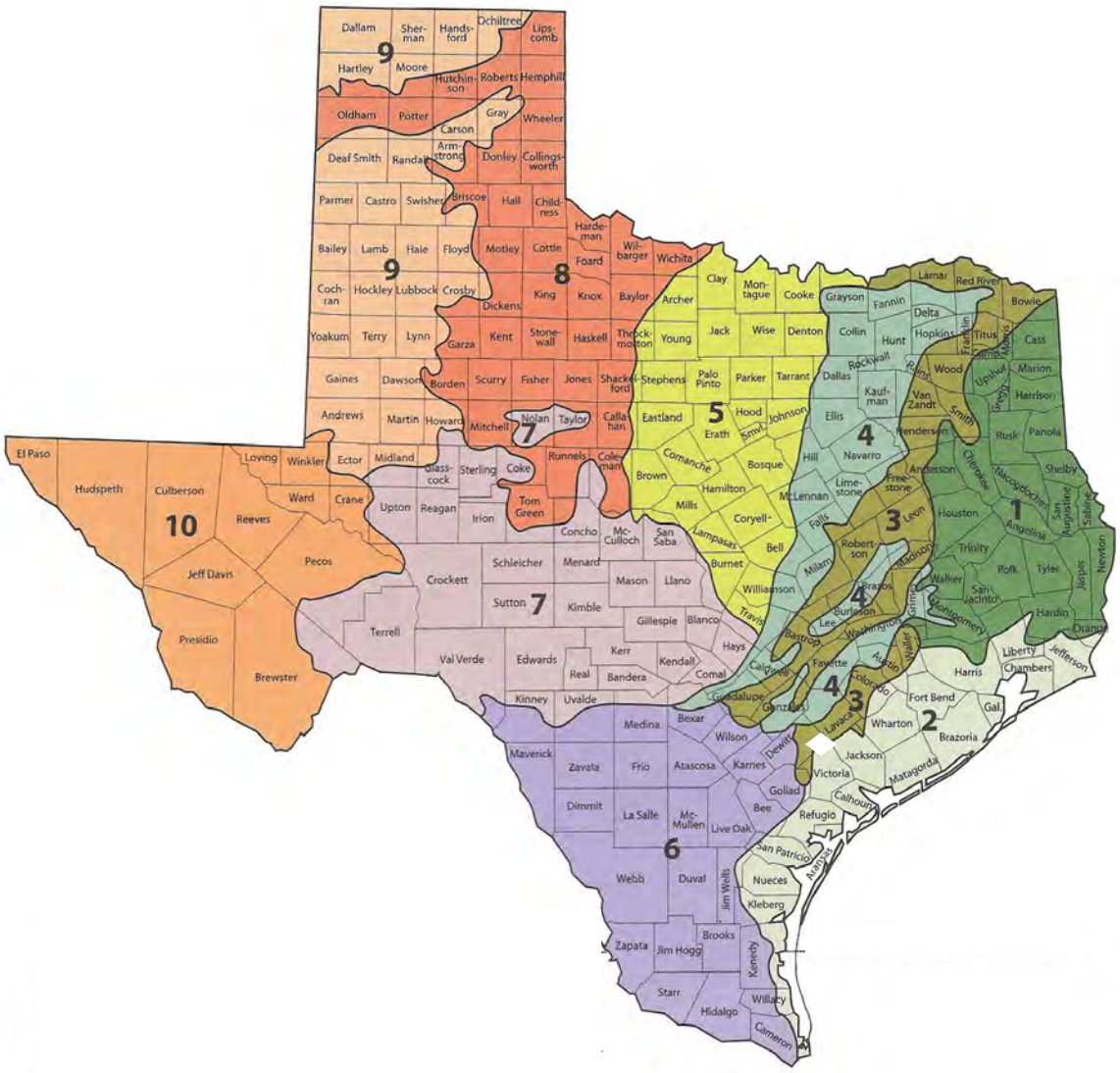


Fig. 1. Vegetational areas of Texas: (1) Pineywoods, (2) Gulf Prairies and Marshes, (3) Post Oak Savannah, (4) Blackland Prairies, (5) Cross Timbers and Prairies, (6) South Texas Plains, (7) Edwards Plateau, (8) Rolling Plains, (9) High Plains, (10) Tran-Pecos, Mountains and Basins. Map produced by the Botanical Research Institute of Texas/Austin College; modified from Correll & Johnston (1970) and Hatch et al. (1990).

Because there are so many intergrading regions, there is high potential for finding species out of their expected ranges. The area is topographically complex, providing microclimates that may have allowed new species a chance to evolve. The Chihuahuan Desert has many endemics, but, instead of being widespread, they have mostly local distributions (Brown 1994), increasing the likelihood of new discoveries in large, remote areas like the Dead Horse. Indeed, in Trans-Pecos Texas, Brewster County tallies the highest numbers of endemic (TAM-BWG 2007) and rare plant species (Alex et al. 2006; Poole et al. 2007, in press). Often, however, species of concern are little known beyond data taken at their original collection site. For example, the bluet *Hedyotis pooleana* (Jackie's bluet) was discovered in the Dead Horse in 1985. Because it is not known from any other location or collection since, much remains unknown about this controversial species and its taxonomy in relationship to its more variable and very similar Mexican cousin *Hedyotis mullerae* (Terrell 1996, 2001; Turner 1997). Providing more information about little-known species is one objective of this study.

The flora of the Dead Horse in its entirety will also be considered. Many collections on the periphery of the mountain range have been made over the past 60 years. This is probably due to the proximity of Sul Ross State University (SRSU) with a significant regional herbarium (SRSC), and the large proportion of state and federal protected lands in the area; areas under public management are typically more accessible to the scientific community than those under private ownership. Despite the history of collection activity, there has been limited effort to catalog DH species or to place the range and its floristics in a larger context. The current study includes all known specimens from the DH, with both the current collections and those found in an extensive

search of herbaria. Putting this area into a regional context and comparing the floras of similar mountain ranges north and south of the international border will help identify patterns of distribution and abundance which can help future studies elucidate details of the establishment and the evolution of the present-day flora.

Beyond limiting area-specific understanding, the lack of data hampers the ability to make responsible management decisions. Species data from field-collected herbarium specimens can be a fundamental tool used in conservation and management (Funk & Richardson 2002). It is crucial that managers know about what they are trying to protect, whether from direct or indirect sources. The species-distribution information gained in this survey can help place the DH and other regional species assemblages in a larger, biogeographical context, help explain previous patterns of establishment and migration, and allow speculation on future developments. One such development might be response to climate change, and this study provides a reference benchmark for species occurrence. If species are found that are obviously occurring at the limits of their ranges, they may be useful as proverbial canaries in the coal mine to signal biologically significant shifts in temperature or precipitation.

The main study objective was to create a collective body of work on the floral composition of the DH, documenting all known vascular plants through field collections and herbarium records. Subsequent analysis demonstrates regional patterns of species richness, both in terms of regions within Texas and as compared to other Southwestern areas.

Geography and Study Area Description

The DH are located in that part of West Texas known as the Big Bend region—generally the land south of the Union Pacific railway bounded to the east, west, and south by the Rio Grande. BBNP is in south Brewster County, bordering Mexico for 118 mi (190 km; Fig. 2). The park comprises over 800,000 acres (323,752 ha) and includes elevations between 1700 and 7854 ft (518 and 2394 m). The closest towns fall along TX Hwy 90, paralleling the railway. Alpine (110 mi/177 km, pop. 6500) is home to Sul Ross State University, and Marathon (70 mi/113 km, pop. 600) is the eastern-most gateway to the park. Directly west of the park are the communities of Study Butte (23 mi/37 km) and Terlingua (30 mi/48 km). Bordering the park to the east is Texas Parks and Wildlife's Black Gap Wildlife Management Area (BGWMA) and a few parcels of private ranchland, including the Adams Ranch, which was recently purchased by Cemex, the Mexican government-owned cement company involved in conservation efforts on both sides of the Rio Grande. The DH are primarily within BBNP, with the eastern extents falling within BGWMA and private property.

Looking at historical accounts and topographic maps of the area, the DH are also considered part of the Sierra del Carmen range that originates in Mexico. South of the border the del Carmens reach elevations over 9000 ft (2750 m) and serve as BBNP's distinctive southeastern skyline of massive, banded cliffs that glow in the sunset. The DH are a smaller, northern extension of the impressive Mexican range.

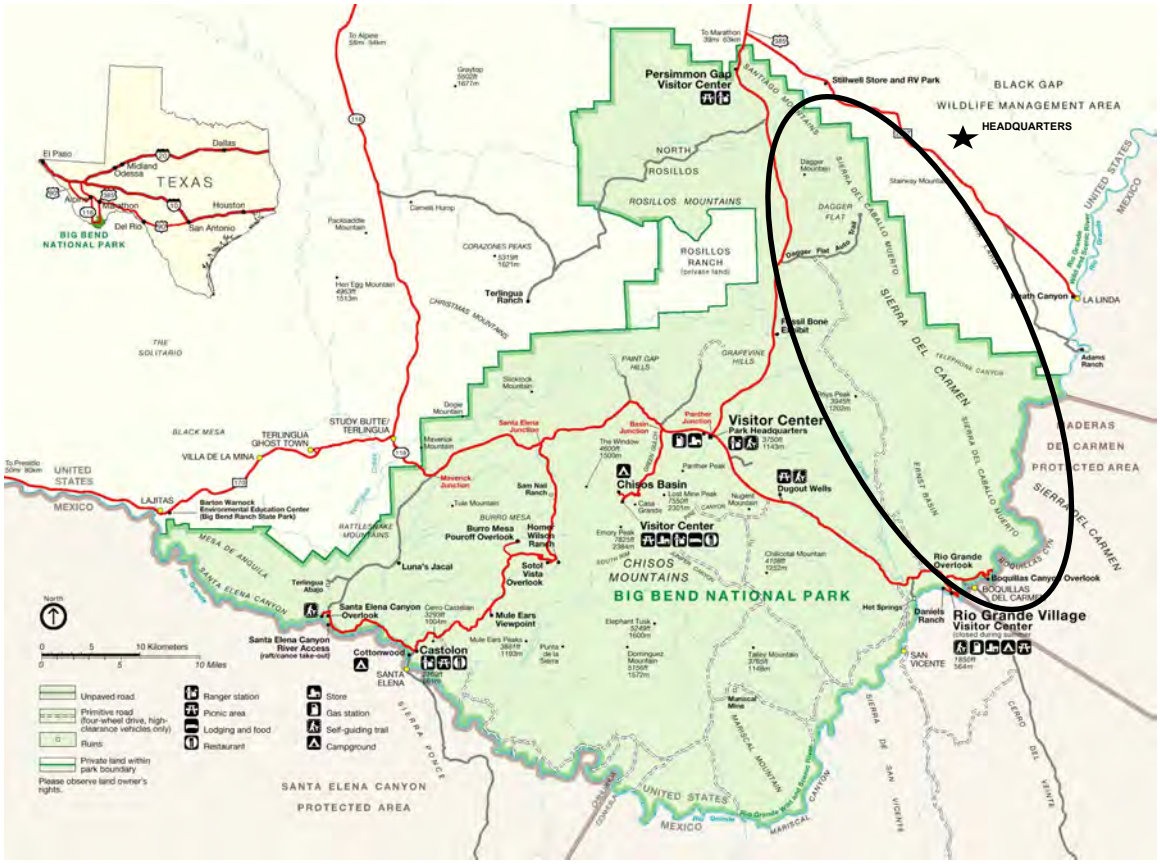
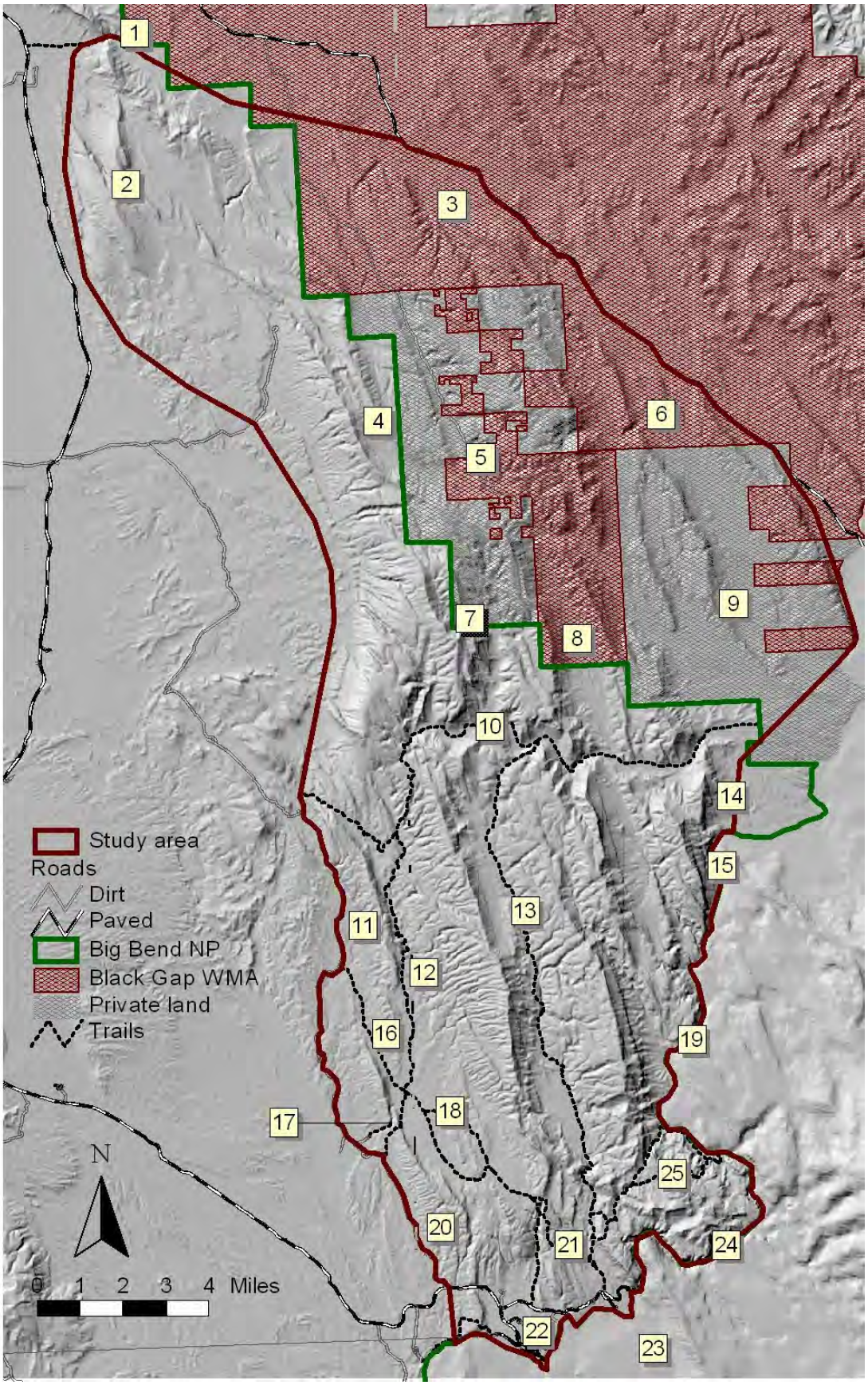


Fig. 2. Map of Big Bend National Park (NPS 2004) with the study area circled. The Dead Horse Mountains are labeled “Sierra del Carmen” and “Sierra del Caballo Muerto”.

There are various stories recorded about how the DH got their name, and all embody the colorful history of the region. The most common theme involves Texas Rangers who were escorting a party of state boundary surveyors down the Rio Grande in the late 1800s. When the party encountered a rugged canyon, they either had to abandon their horses because it was only feasible to continue in rafts or surprised and scattered a band of Indians, who left behind their horses in their escape. The universal conundrum was how to prevent the horses from falling into Indian hands so that they would not be used for future raids against the Anglo community. Thus, the horses were killed with one account describing how all ammunition had been previously lost, so that the horses were blindfolded and knocked in the head with an axe (Maxwell & Dietrich 1965), and the other relating that the 30–40 head were simply shot (Smith 1924). Those historical tales, along with a more modern story that a rancher's horse fell off a cliff while the man was out looking for lost stock (Maxwell 1985) all serve to validate the area's name as a description of the harshness of the region.

Main physical characteristics of the DH include its northwest-trending mountains, with basins in between and sharp peaks overlooking the surrounding desert. Extending 31.5 mi (51 km) N/S and an average of 8.5 mi (14 km) E/W, the study area falls between 29° 37' 22", 29° 10' 17" latitude and 103° 7'14", 102° 52' 26" longitude (Fig. 3). The resulting plot of land covers approximately 176,800 acres (71,548 ha; 276 mi², 716 km²). The elevation range of the study area is approximately 4100 ft (1250 m). All land-feature names used were taken from the eight United States Geological Survey 1:24,000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Black Gap WMA
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Fig. 3. Dead Horse Mountains study area locations: (1) Dog Canyon, (2) Dagger Mountain, (3) Stairway Mountain, (4) Stuarts Peak, (5) Brushy Canyon, (6) Frog Canyon/Frog Tank, (7) Sue Peaks, (8) Margaret Basin, (9) Sierra Larga, (10) Telephone Canyon, (11) Alto Relex, (12) Passionflower Canyon, (13) Strawhouse Trail, (14) Hubert Ridge, (15) Cow Canyon, (16) Arroyo Venado, (17) Cuesta Carlotta, (18) Ernst Tinaja, (19) Ernst Basin, (20) Ernst Ridge, (21) Ore Terminal trail, (22) RGV developed area, (23) Boquillas, Mexico, (24) Boquillas Canyon, (25) Marufo Vega.

topographic quadrangle maps covering the area: Dog Canyon, Black Gap, McKinney Springs, Sue Peaks, Roy's Peak, Ernst Valley, San Vicente, and Rio Grande Village (RGV).

Obvious topographic features of the study area include Dagger Mountain (4160 ft/ 1268 m) to the north, Stuarts Peak (5080 ft/1548 m), and the highest points at Sue Peaks (5840 ft/1780 m). The DH meet their southern end along the river, at 1700 ft (518 m). There the Rio Grande has carved out the spectacular Boquillas Canyon, a 33-mile-long (53 km) slice through massive limestone rock, with canyon walls rising to almost 1500 ft (457 m) tall. The area targeted for this research was chosen using topographic limits as opposed to administrative boundaries, although the majority of current field work was done within BBNP (Fig. 3).

The study area boundary starts to the north at Dog Canyon, and continues south along the western foothills to include Dagger Mountain, Alto Relex, Cuesta Carlotta, and Ernst Ridge. McKinney Springs and Roy's Peak were excluded because of their disjunct volcanic nature. The river makes the southern limit, including the RGV developed area and all of Boquillas Canyon. Heading north, the boundary skirts the lowest foothills of Hubert Ridge, the Sierra Larga, and Stairway Mountain in BGWMA. The current field work extended from BBNP as far east as Brushy Canyon and the mouth of Cow Canyon along the Rio Grande, and as far north as Dagger Mountain. The herbaria search was extended to cover the topographic extent of the entire DH-related uplift.

Over this entire area, the only physical feature that trends east-west besides Boquillas Canyon is 14-mile-long (22.5 km) Telephone Canyon, which bisects the DH. Even though Telephone Canyon is a major drainage, its Heath Creek does not contain

any permanent surface moisture, nor do any of the other major drainages such as Brushy Canyon, Strawhouse, Margaret Basin, Arroyo Venado, or Cow Canyon. These are all host to water at one time or another, but only in the form of ephemeral torrents after summer thundershowers. Surface water away from the Rio Grande is found only in tinajas, stone basins eroded usually out of arroyo or canyon beds with bedrock outcrops. The only reliable source like this is Ernst Tinaja, in the southern part of the DH. Other tinajas can be found, usually just by luck, but they are not large enough to hold more water than will evaporate after a few days. In light of the low frequency of rain events, such tinajas are inherently ephemeral.

Access to the study area was primarily through BBNP, though one trip was made into BGWMA territory. There are few human-created ways to access the DH, mostly on the periphery of the range. The Old Ore Road runs along the western flats and hits the paved road, which continues as a good point of access to the study area as it passes through the tunnel in Ernst Ridge to RGV. Providing good peripheral access to the southern foothills, the Boquillas Canyon road leads to the entrance of Boquillas Canyon. During the study period, the best interior road access was into Brushy Canyon through BGWMA and the Shackelford Ranch, a private inholding. The best trail for interior access was through Telephone Canyon, a 20-mile-long (32 km) path bisecting the DH, following the largest, and the only east-west-draining, canyon in the range. Access to the mouth of Telephone Canyon, by way of ranch roads from the east, was not available during the study period. The only other substantial, established trails within the DH are the 12 mi (19 km) Marufo Vega loop, the Ore Terminal Trail (4 mi/6.5 km), and the Strawhouse Trail (14 mi/22.5 km), all in the extreme southern end of the study area.

Climate

Some fairly comprehensive work has been done to document the climate of the Chihuahuan desert (Morafka 1977; Schmidt 1979, 1986). The general information about the Chihuahuan desert to follow is based on Schmidt's (1986) conclusions. Typical year-round climate for the Chihuahuan desert consists of hot summers and cool-to-cold winters. Temperatures reach lower levels than in the other hot North American deserts due to the higher altitude of the uplifted plains that form the majority of the desert area. Rainfall patterns also differ: being in the rainshadow of both Mexican Sierra Madre ranges limits rainfall to one peak summer season instead of a spring and summer season, as in the Sonoran and Mojave deserts. This regional aridity is more the effect of the orographic barriers than of actual distance from moisture sources.

The higher summer temperatures begin to drop in association with the developing rainy season: higher humidity and increased cloud cover elevate the thunderstorm potential. Summer moisture, in large part, is influenced by storms coming from the Gulf of Mexico. Winter precipitation is dependent on tropical Pacific storms, which push moist air toward the interior of the continent. Though winter is typically a drier time of year, it is these very storms that can cause higher-than-normal precipitation and influence the intensity or existence of the spring and early summer bloom. Summer thundershowers can be quite intense, with hail often falling over limited areas. Snow is always a possibility but is highly sporadic and always ephemeral.

Many mountains in the southwest are high enough to support flora and even fauna that do not fall within typical desert descriptions, though their foothills are solidly rooted in the desert. The altitudinal maximum of the Chihuahuan desert, as delimited by

Schmidt (1986) using climatic conditions, is 5900 ft (1800 m). The DH fall just under that, indicating that climatically the vegetation encountered should be representative of that occurring in the Chihuahuan desert. Being situated in the northern part of the Chihuahuan Desert (Fig. 4), the DH have temperatures registering slightly lower than the average of the Chihuahuan Desert as a whole. The northern cold fronts typical of Trans-Pecos region winters do not extend into the lower latitudes. High temperatures are on par with the desert's averages. It seems that the more northern latitude does not overwhelm the propensity for high temperatures at low elevations: the RGV area falls at the lowest recorded elevations in the Chihuahuan desert.

All temperature and precipitation data were gathered from BBNP files, originating from the National Weather Service or directly from park weather station records. The period of record varies in length and completeness for each weather station. The weather stations most useful for the DH (Fig. 2) are located at both ends of the range. The Persimmon Gap (PGAP) station is just outside the northern edge of the study area and has temperature and precipitation data from 1989–2005. RGV, at the southern limit, has reliable temperature data from 1979–2005, and precipitation records spanning 51 years since 1954. Average annual lows for the two stations are similar, averaging 53°F/12°C (Fig. 5). Highs at RGV, on the other hand, consistently remain about six degrees hotter than the those at PGAP throughout the year: the average annual high at PGAP is 82°F (28°C) and at RGV is 88°F (31°C), making an average annual high of 85°F (29°C) for the DH area.

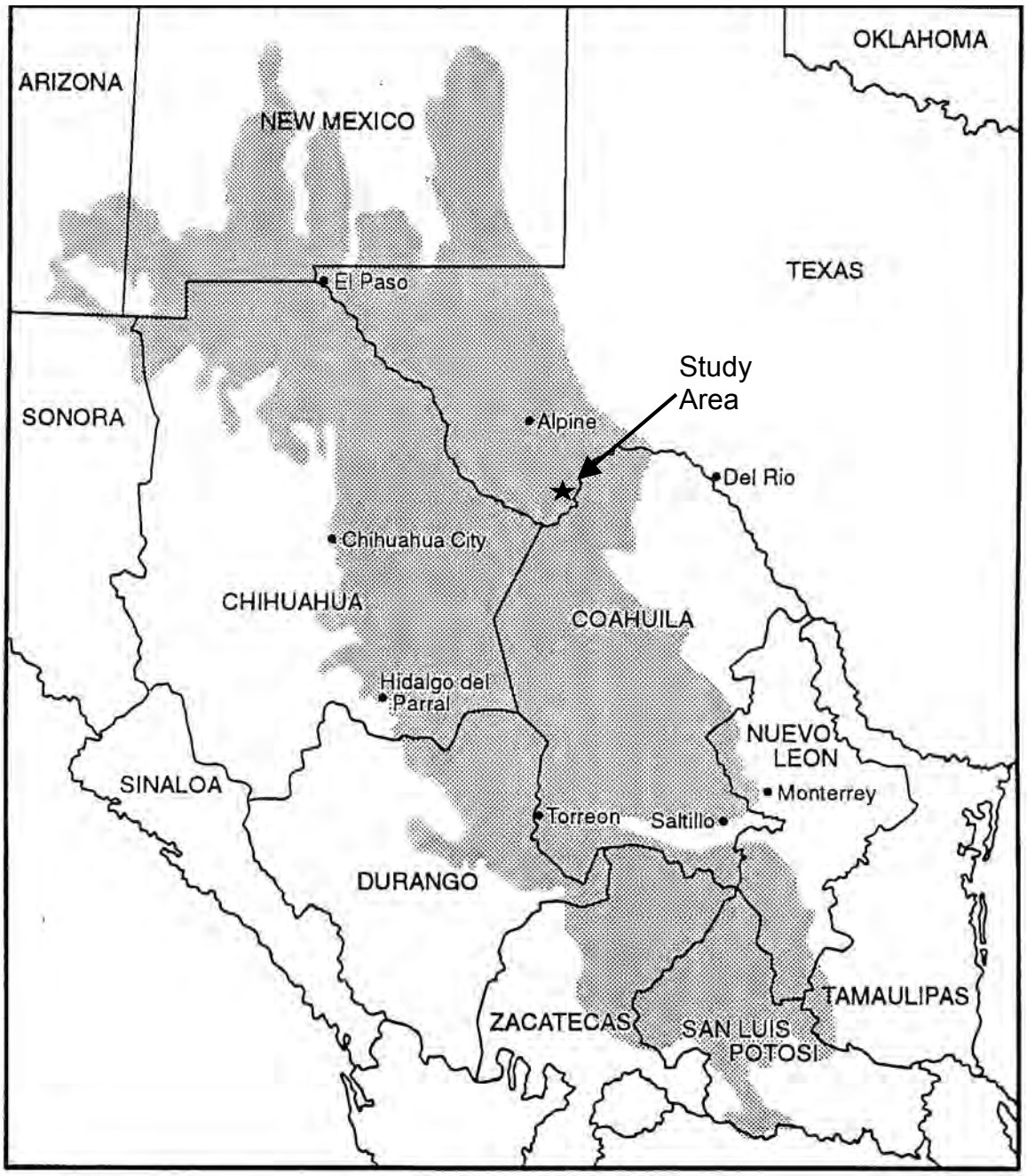


Fig. 4. The extent of the Chihuahuan Desert Region from Hardy 1997, used with permission.

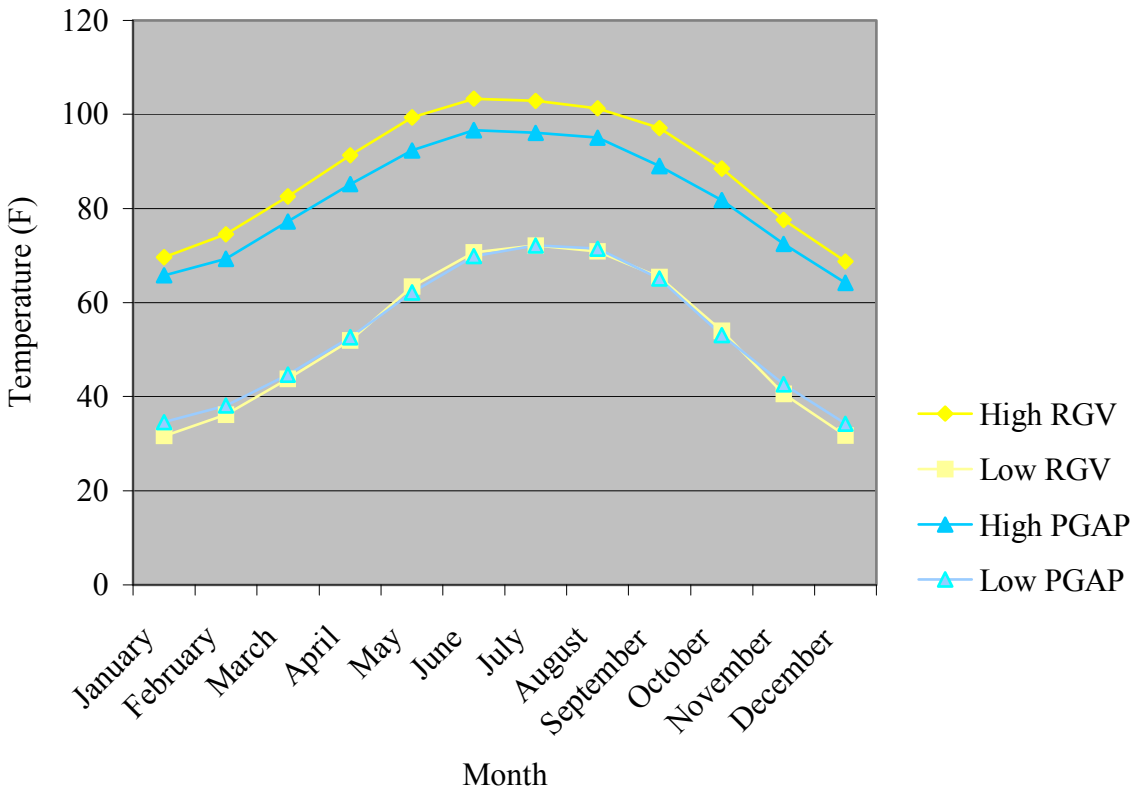


Fig. 5. Average annual high and low temperatures of the Dead Horse Mountains. Period of record varies between stations: Persimmon Gap (PGAP): 16 year record, 1989–2005; Rio Grande Village (RGV): 26 year record, 1979–2005.

The hottest month at both stations is June, with a combined daily average high of 100°F/38°C (max. 117°F/47°C at RGV), while December is coldest, with daily station lows averaging daily 33°F/1°C (min. 4°F/16°C at RGV). High diurnal temperature ranges are common for the Chihuahuan Desert as a whole. In the DH, the daily range can average between 29°F (16°C) at PGAP and 35°F (20°C) at RGV. Maximum daily fluctuations of over 50°F (28°C) can occur, usually in May and December. More stable temperatures coincide with the rainy summer months. Compared to higher-elevation locales in the park (Fig. 6), the DH stations experience lower average temperatures in winter months and temperatures among the highest during summer months. This extreme range of annual mean temperatures is probably due to the area's habitually low humidity and the lack of buffering topography. The lowest annual average temperatures do occur at the highest elevations in the Chisos Mountains, with a minimum low of -3°F (-19°C) recorded at the Basin station in January 1949.

Rainfall data for the DH come from the two park stations and from data recorded at BGWMA headquarters, just east of the DH. The highest rainfall comes predictably in the summer months, peaking between May and October (Fig. 7). Annual totals average close to 10 in. (25 cm) for both stations, which is less than the higher-elevation stations in the park (Fig. 8). The DH are high enough to catch and even create their own weather, but they cover enough area and contain such varied topography that storm cells form patchily. The amount of rainfall within the DH is highly variable, and any calculated average may not be adequately representative of actual precipitation seen in any given location. However, the average DH precipitation would never match that for the Chisos

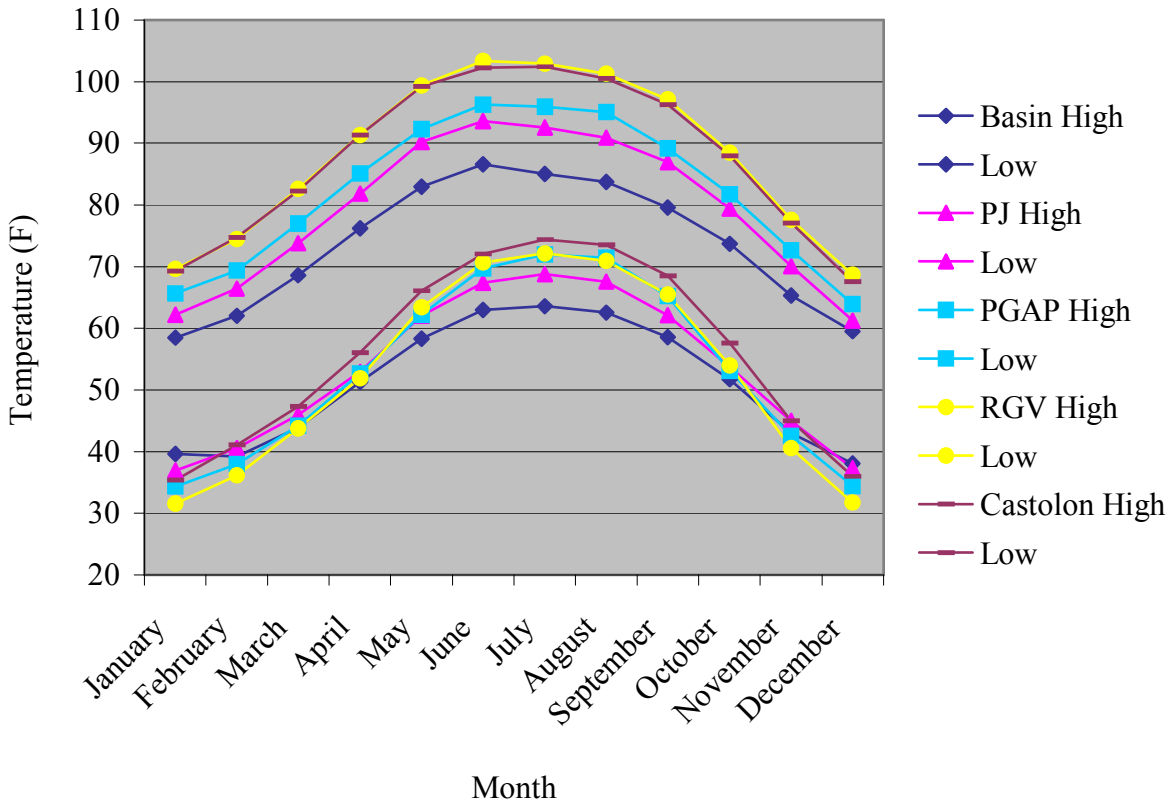


Fig. 6. High and low temperatures of weather stations of Big Bend National Park, Texas. Period of record varies between stations: Basin: 57 year record, 1948–2005; Panther Junction (PJ): 19 year record, 1986–2005; Persimmon Gap (PGAP): 16 year record, 1989–2005; Rio Grande Village (RGV): 26 year record, 1979–2005; Castolon: 19 year record, 1986–2005.

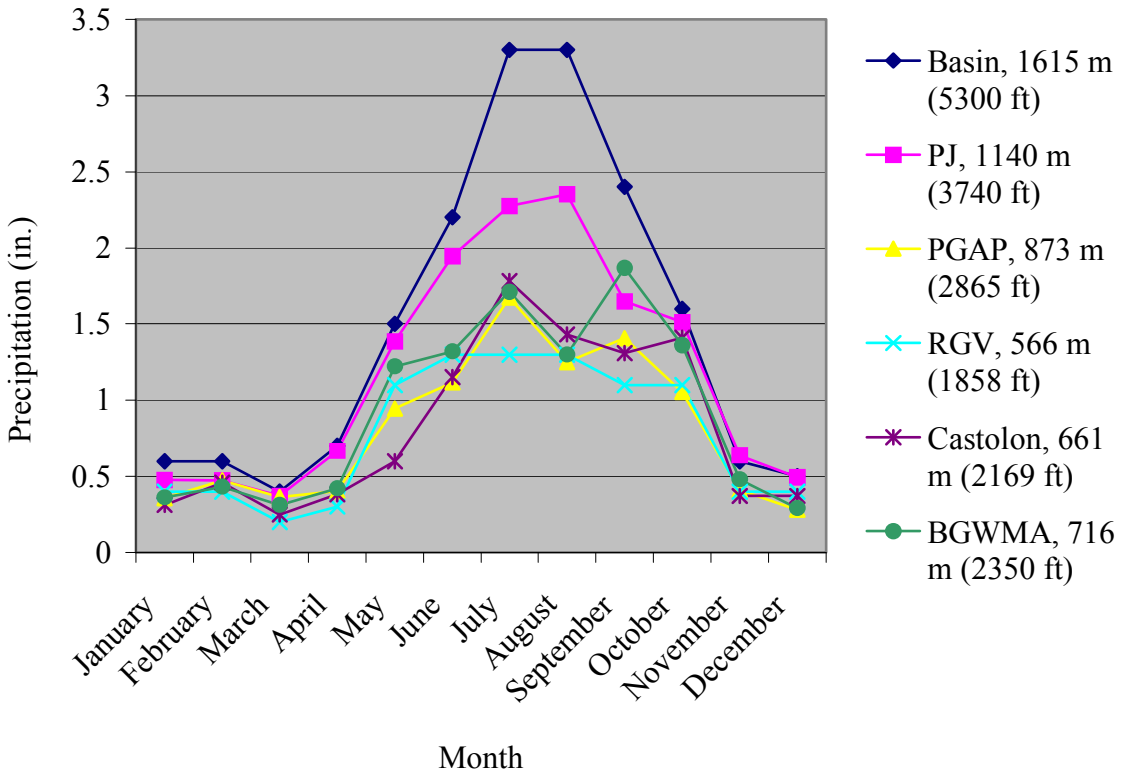


Fig. 7. Average annual precipitation by month for Big Bend National Park weather stations and for the Black Gap Wildlife Management Area (BGWMA); elevation of station listed beside name; the period of record varies between stations: Basin: 28 year record, 1948–2006; Panther Junction (PJ): 30 year record, 1976–2006; Persimmon Gap (PGAP): 18 year record, 1988–2006; Rio Grande Village (RGV): 52 year record, 1954–2006, missing Jun–Sep 2002 and Aug–Sep 2003; Castolon: 20 year record, 1986–2006; BGWMA: 36 year record, 1952–2005, missing data from 1978–1989 and 1991–1996.

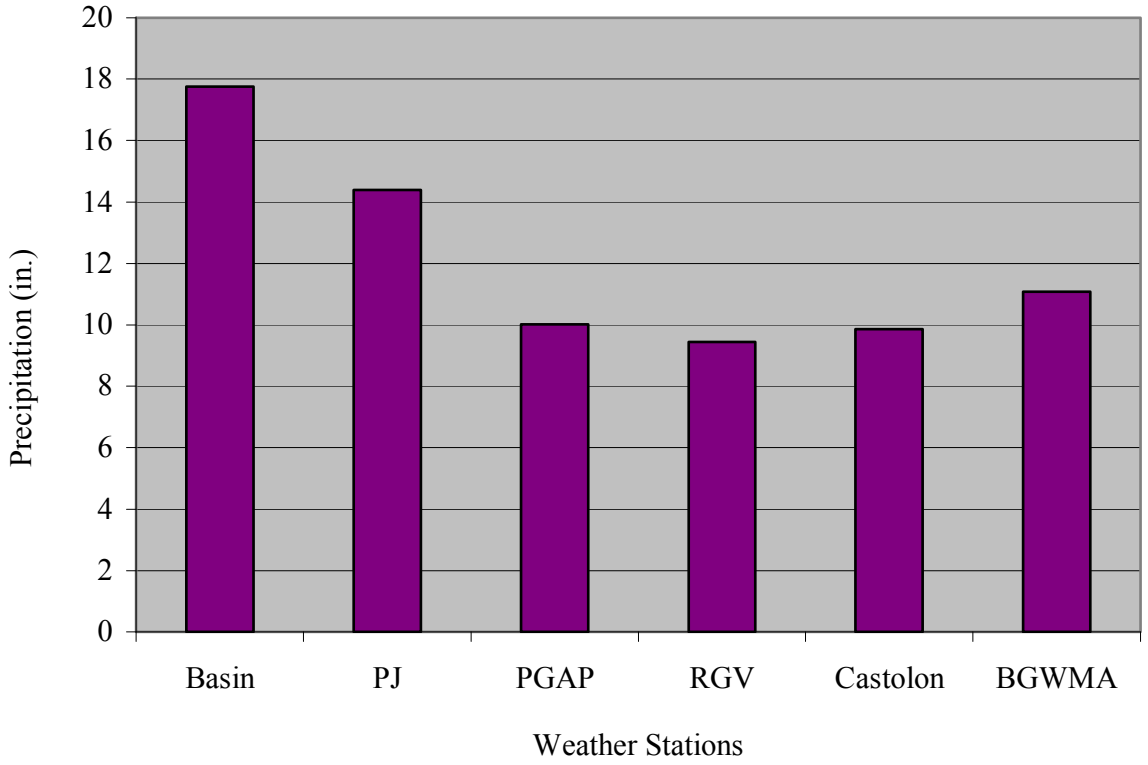


Fig. 8. Average annual precipitation totals for Big Bend National Park weather stations and for the Black Gap Wildlife Management Area (BGWMA); the period of record varies between stations: Basin: 28 year record, 1948–2006; Panther Junction (PJ): 30 year record, 1976–2006; Persimmon Gap (PGAP): 18 year record, 1988–2006; Rio Grande Village (RGV): 52 year record, 1954–2006, missing Jun–Sep 2002 and Aug–Sep 2003; Castolon: 20 year record, 1986–2006; BGWMA: 36 year record, 1952–2005, missing data from 1978–1989 and 1991–1996.

Basin, nor even levels at Panther Junction, due to physiographic differences between the sites. The Chisos Mountains are higher than the DH and, thus, have more powerful orographic lift and vegetative feedback to produce, catch, and/or drive storm cells. Panther Junction sees higher rainfall due to its location on the lower slopes of the Chisos.

During the cooler months, well-developed cold fronts sweep in from the north and sometimes bring snow to the higher elevations of the park. Over the past 57 years, there was snow during 83% of the winters at the Basin station, averaging 2.9 in. (7.3 cm) per snow year. Interestingly, over the last 30 years, there was snow in only 47% of the years, and the average snow-year total dropped to 1.8 in. (4.6 cm). During the last 15 years it snowed in only 27% of the years, averaging 0.43 in. (1.1 cm) per snow year. The peaks of the DH do get snow (J. Fenstermacher pers. observ.), but only as a rare novelty. Recorded snowfall in the DH is minimal: at RGV, 14 events over the last 52 years (av. 0.1 in./0.25 cm), two events during the last 30 years (av. 0.3 in./0.76 cm), and zero snowfall in the last 15 years have been recorded. Recorded precipitation is underrepresented, however; it did snow at least once at RGV in 1999, enough to supply the bulk for three snowmen at the campground (J. Fenstermacher pers. observ.), and until recently the rain gauge at RGV was partially under the eaves of the ranger station and the canopy of a mesquite tree (J. Forsythe pers. comm.).

A sporadic weather phenomenon may supplement moisture levels at higher DH elevations. Occasionally, during the more humid summer months, fog or low-lying clouds lay over the top of the peaks. This seems to occur when west-moving moist air is blocked by the DH and held by an inversion to create a bank of low-lying clouds over the

large alluvial Stillwell/Maravillas plain to the east (Fig. 9). The clouds eventually waft up the slopes of the DH and may sit on the higher elevations for part of a day. This phenomenon may provide significant humidity for some non-vascular and vascular plants at the higher elevations. For example, several lichen species were observed on the rocks around Stuarts Peak that were not seen elsewhere, including Sue Peaks.

Desert plants are highly tuned to the amount and timing of moisture they receive, both in order to bloom and for germination and establishment. Thus, the amount of rain received prior to and during any given study period greatly influences the composition of species found. Yearly rainfall totals for sites in BBNP are not consistent throughout history, though higher-elevation stations receive more precipitation than lower ones (Fig. 10). In the first two years of the study period the area experienced a rebound from the lowest rainfall in years, occurring in 2001. However, 2005 was another lower-rainfall year, especially over the winter of 2005–06 which caused an absence of plants in flower during the spring field season of 2006. Good rains in 2006 began only in August (Fig. 11), finally stimulating the desert to green up.

Geology

The DH are entirely limestone in nature, while the rest of BBNP is characterized by significant igneous features, in addition to isolated sandstone deposits and metamorphic rock. Ross Maxwell was the first superintendent of BBNP and a geologist by training. He was involved in mapping the park's geology in the late 1960s and went on to publish that mapping and other informative treatments in following years (Maxwell

Fig. 9. Low-lying clouds over higher Dead Horse peaks can remain for up to a day, perhaps creating a significant source of available moisture.

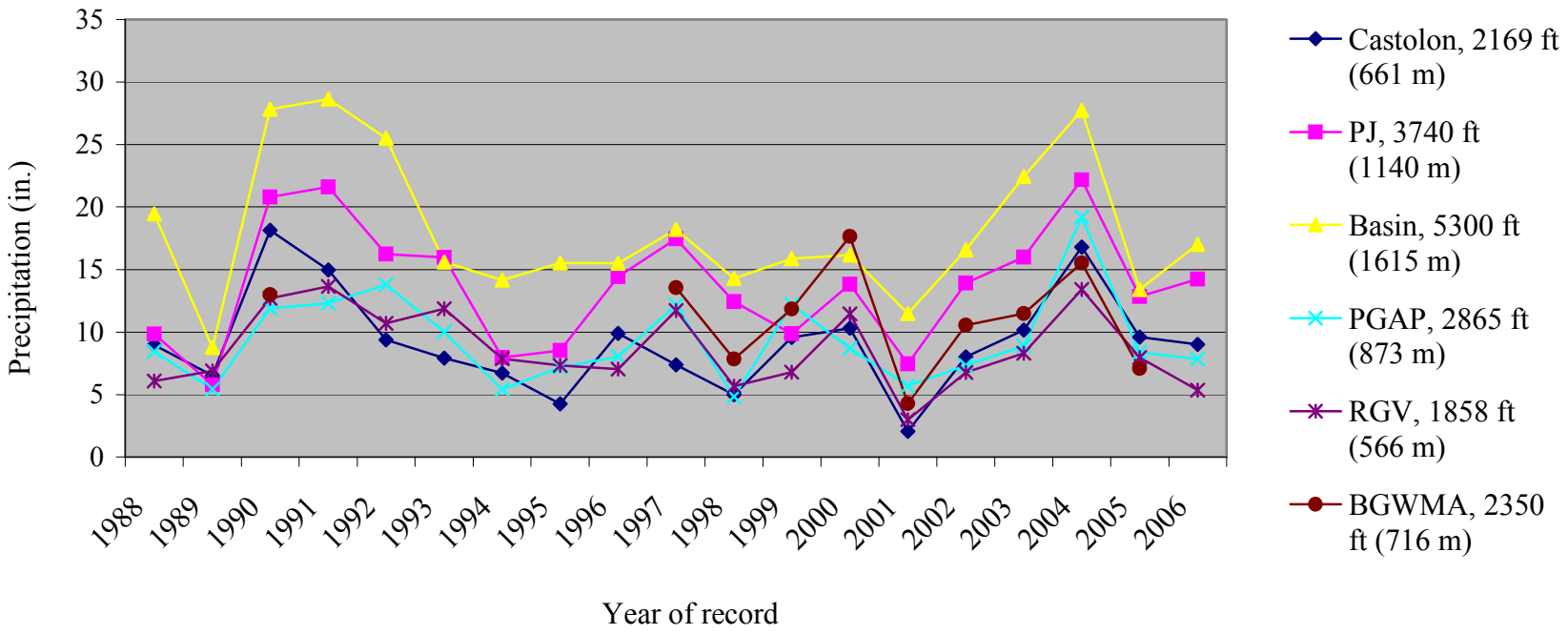


Fig. 10. Historical annual precipitation levels for Big Bend National Park weather stations and for the Black Gap Wildlife Management Area (BGWMA) between 1998 and 2006. BGWMA averages do not include data from the following years: 1988, 1999, 1991–1996, and 2006.

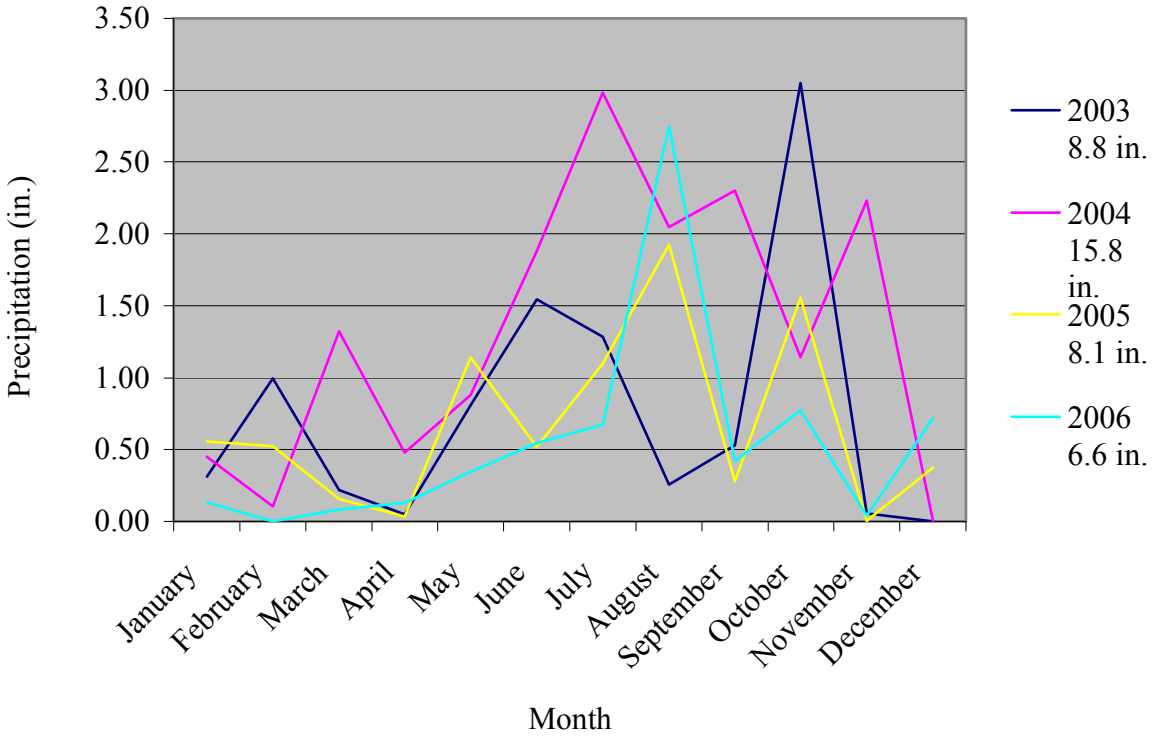


Fig. 11. Yearly precipitation patterns during the study period, 2003–2006, for the Dead Horse Mountains area. Data represents an average between values from PGAP and RGV. The average annual total for the two DH stations is listed by the appropriate year in the legend.

1979, 1985, Maxwell & Dietrich 1965, Maxwell et al. 1967). Unfortunately, the original geological map is not georeferenced, making updated maps desirable. Updating is occurring, but slowly and in pieces.

One current study relevant to the DH involves mapping outcrops of the Boquillas formation (R. Cooper unpub. data). The mapping by Moustafa (1988) is the only project to focus specifically on the DH, but it is not reliable: created using remote sensing, the resulting map was not ground-truthed to accurately map differing geological layers with similar reflectance values (D. Corrick pers. comm.). To this day, Maxwell's work is the best reference and was used to create the following basic treatment of landscape formation and the nature of important stratigraphic layers.

Most of the rocks visible in the DH today were formed during the lower Cretaceous period, ca. 180 million years ago (mya). By that time, the continents were moving into familiar positions, and flowering plants and pollinating insects were becoming an increasing part of the biota (Fig. 12). A large ocean covered the majority of North America, and as the remains of marine invertebrates fell to the bottom, they eventually solidified into different rock layers, depending on the amount of clay (continental deposits), as opposed to silica or calcium carbonate/limestone (marine deposits), that was present. Continental crust movements that shaped the North American continent are recorded in the different rock layers we see today; the type and thickness of deposits correlate with how deep or shallow the sea was and how close or far an area was from the shoreline.

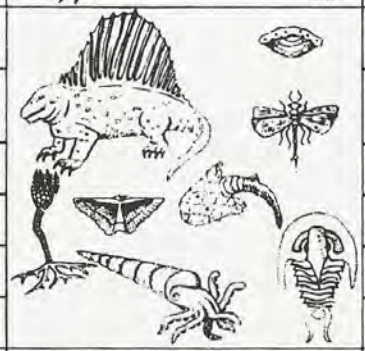
ERA	PERIOD	EPOCH	AGE (Millions of Years Ago)	SUCCESSION OF LIFE	TYPICAL LIFE FORMS	MAJOR GEOLOGIC EVENTS	GEOLOGIC RECORD BIG BEND REGION
CENOZOIC "Age of Mammals"	Quaternary	Pleistocene	1		Man Woolly mammoth	World-wide glaciation	Alluvium Intermontane basin and terrace deposits
	Tertiary	Pliocene Miocene Oligocene Eocene Paleocene	12 25 36 60 63		Saber-tooth cat Horses Primitive mammals	Alps, Himalayas, Cascade ranges formed	Repeated epochs of uplift. Intrusive and extrusive igneous activity. Continental deposits with mammal bones and teeth.
MESOZOIC "Age of Reptiles"	Cretaceous	Upper Lower	135		Dinosaurs First flowering plants	Rocky Mountains formed	Folds, thrust faults, and general uplift at end of period. Marine and non-marine deposition.
	Jurassic		181		First birds	Sierra Nevada Mountains formed	Prolonged period of erosion during which Paleozoic rocks were exposed in Marathon Basin, Solitario, and Persimmon Gap
	Triassic		230		Ammonoids		
PALEOZOIC "Age of Invertebrates"	Permian		280		Reptiles	Appalachian Mountains formed	Folds, thrust faults in Ouachita System trough
	Pennsylvanian Mississippian		310 345		Insects Coal forests Amphibians		Sandstone, shale and novaculite deposited. Uplift in Marathon Basin began.
	Devonian		405		Brachiopods Fish		Novaculite, chert, and shale deposited in late part. Early record not clear.
	Silurian		425		Crinoids		No record
	Ordovician		500		Nautiloids		Chert, shale, and limestone deposited. Many marine shellfish.
	Cambrian		600		Trilobites		Sandstone, shale, and limestone deposited in late part. No early record.
PRECAMBRIAN ERAS PROTEROZOIC ERA ARCHEOZOIC ERA			3,000		Algae Worm tubes Indirect evidence of life		No record
Approximate age of the earth more than 3 billion 300 million years							

Fig. 12. Geologic periods, typical life forms, and general Big Bend geologic record (Maxwell 1979). Used with permission of the Bureau of Economic Geology, University of Texas, Austin.

GEOLOGIC AGE			ROCK UNITS			
			GROUP	FORMATION	THICKNESS (feet)	ROCK TYPE
CENOZOIC	QUATERNARY	RECENT and PLEISTOCENE		Alluvial deposits	100-500	Clay, silt, sandstone, and conglomerate covering extensive slopes surrounding most mountains
CENOZOIC	TERTIARY	OLIGOCENE or YOUNGER	Big Bend Park	South Rim Formation	1,000-1,500	Thick ledge-forming lava flows exposed high in Chisos Mountains, ash beds, tuff, flow breccia, irregularly bedded sandstone and conglomerate
CENOZOIC	TERTIARY	EOCENE, Upper	Big Bend Park	Chisos Formation	1,500-2,600	Indurated tuff interbedded with clay, mudstone, tuffaceous sandstone, ash beds, lavas, sandstone, and conglomerate; crops out median and lower slopes in Chisos Mountains
CENOZOIC	TERTIARY	EOCENE, Middle	Big Bend Park	Canoe Formation	1,170	Base is a massive yellow cross-bedded ledge-forming sandstone overlain by tuff, mudstone, tuffaceous sandstone, indurated tuff, and lavas
CENOZOIC	TERTIARY	EOCENE, Lower	Tornillo	Hannold Hill Formation	356-770	Soft, gray, and yellowish-gray conglomeratic sandstone and varicolored and mottled clay mostly in valleys
CENOZOIC	TERTIARY	PALEOCENE	Tornillo	Black Peaks Formation	850	Varicolored clay interbedded with ledge-forming cross-bedded, yellow, buff, and gray sandstone and lenses of conglomerate
MESOZOIC	CRETACEOUS	GULFIAN	Tornillo	Javelina Formation	350-850	Gray, dull green, blue, red, yellow, purple, brown, black, and white clay, with thin layers of sandstone. Clay commonly bentonitic and forms badlands. Contains fossil wood and dinosaur bones
MESOZOIC	CRETACEOUS	GULFIAN	Tornillo	Aguja Formation	800-1,300	Upper part, 300-700 feet thick. Nonmarine dark-gray carbonaceous clay and some silt and layers of coal interbedded with brown and yellowish-brown sandstone. Contains fossil wood and dinosaur bones Lower part, 500-700 feet thick. Marine sandstone and clay, a shelly sandstone generally present at the base
MESOZOIC	CRETACEOUS	GULFIAN	Terlingua	Pen Formation	220-600	Dark grayish-blue gypsiferous marl and clay that weathers yellow, with concretionary limestone and layers of calcareous sandstone; underlies valleys
MESOZOIC	CRETACEOUS	GULFIAN	Terlingua	BOQUILLAS FORMATION, San Vicente Member	330-400	Gray and bluish-gray chalk and gray to buff argillaceous flaggy limestone; crops out in slopes
MESOZOIC	CRETACEOUS	GULFIAN	Terlingua	BOQUILLAS FORMATION, Ernst Member	475	Gray, buff, and yellowish-brown flaggy limestone interbedded with gray and buff marl; crops out in slopes
MESOZOIC	CRETACEOUS	COMANCHEAN		Buda Limestone	100	Whitish, dense, brittle limestone and nodular limestone interbedded with marl, ledge forming
MESOZOIC	CRETACEOUS	COMANCHEAN		Del Rio Clay	1-125	Light gray and yellow clay, clay-shale, and thin-bedded limestone; forms slopes
MESOZOIC	CRETACEOUS	COMANCHEAN		Santa Elena Limestone	750-850	Mostly massive, thick-bedded, dense, cherty, ledge-forming limestone, with thin-bedded marly limestone near base
MESOZOIC	CRETACEOUS	COMANCHEAN		Sue Peaks Formation	75	Shale, marl, and thin marly, nodular limestone ledges; forms slope below the Santa Elena Limestone
MESOZOIC	CRETACEOUS	COMANCHEAN		Del Carmen Limestone	350-450	Massive, heavy-bedded, dense, cherty, ledge-forming limestone
MESOZOIC	CRETACEOUS	COMANCHEAN		Telephone Canyon Formation	40-130	Thin, nodular, marly limestone and marl; forms slope below the Del Carmen Limestone
MESOZOIC	CRETACEOUS	COMANCHEAN		Maxon Sandstone	10	Medium-grained, calcareous sandstone
MESOZOIC	CRETACEOUS	COMANCHEAN		Glen Rose Formation	600	Dense limestone interbedded with calcareous shale, erodes to form step-like benches. Basal conglomerate and coarse sandstone exposed on flanks of Persimmon Gap and the Solitario
PALEOZOIC				Paleozoic sedimentary rocks (undifferentiated)	Unknown	Strongly folded rocks, including slightly metamorphosed shale, chert, novaculite, and limestone. Exposed at Persimmon Gap and in the Solitario
PALEOZOIC				Metamorphic rocks	Unknown	Fine-grained schist, metaquartzite, phyllite, and marble exposed in the Sierra del Carmen escarpment of Boquillas, Coahuila, Mexico

Fig. 13. Stratigraphic layers in Big Bend National Park (Maxwell 1979). Used with permission of the Bureau of Economic Geology, University of Texas, Austin.

The earliest Cretaceous rock in the DH is the Glen Rose Limestone (Fig. 13). Deposited in a near-shore environment, it is primarily calcium carbonate, with some additional clay and sandstone interbedding. A small outcrop of the Glen Rose is found near Dog Canyon and there is a more substantial exposure in the Marufo Vega area. The majority of this layer is seen in the Mexican Sierra del Carmen.

Telephone Canyon is the succeeding formation. Found in the canyon of the same name, the type locality is described from the arroyo bed in the eastern end. There is also a small exposure in the Marufo Vega area. The Telephone Canyon limestone is a soft lithological unit in contrast to the Glen Rose and its overlying neighbor the Del Carmen Limestone. The Del Carmen was also newly described from local outcrops and corresponds to the Edwards Limestone from central Texas. It is more prominent on the western side of the park; in the DH it is exposed on the eastern flanks of the mountains, out of view to most park visitors unless they hike the Marufo Vega trail. The Del Carmen and the Santa Elena Limestone, the latter an overlying layer of similar massive character, are the main blocks of rock that were uplifted to form the DH. They were both deposited in deep-sea environments, which accounts for the abundance of fossils and the compact, pure nature of the rock, mostly devoid of interbedding or clay content.

Widely found in the rock of both deep-sea layers are nodular or linear inclusions of chert. In the right conditions, silica can precipitate out of seawater and, over time, develop into chert masses—rusty-colored knobs or lens-shaped deposits that, when found in large concentrations, have been used as source rock for arrowheads and other sharp tools. The DH inclusions are only a few inches thick and only periodically seen; thus, they were probably not widely used as source rock by Native Americans.

Sandwiched in between these two massive strata is the Sue Peaks Formation, a softer, thinner unit of marly, buff-colored shale that erodes out, forming a sloping, debris-filled bench between the sheer faces of its neighbors, sometimes leaving the Santa Elena exposed as an overhanging ledge. Stuarts Peak is part of a thin band of this friable formation, otherwise seen on the steep eastern escarpments of the ranges and, to some extent, along the Marufo Vega trail.

The Santa Elena Limestone is the most abundant surface layer in the DH. It has a lighter gray color and a smoother surface than the Del Carmen, but locally they are difficult to distinguish. Fossils are frequently exposed in the Santa Elena, often weathering more quickly than the encasing rock to form small pits. These cavities create unique niches that are utilized by many area plants (J. Fenstermacher pers. observ.). Overlying layers on the steeper slopes and high elevations have long disappeared, the deposits having eroded away down to the resistant surface of the Santa Elena. Weathered material from those younger layers now comprises many of the basin-fill and foothills soils.

The Del Rio Clay is one, younger member that can be found in conjunction with outcrops of Buda Limestone. The Del Rio is seen as thick, greenish clay interbedding with flaggy, silica-rich limestone. The Buda is a more compact limestone that creates scalloped “hogbacks” at the base of the western DH slopes where erosion has not completely erased those components of geologic history.

Mid-to-late Cretaceous deposits are represented as the Boquillas Formation, most easily seen around Ernst Tinaja as the Ernst Member. The silty limestone flags occur with siltstone and calcareous clays, indicating that they were deposited in a near-shore,

shallow environment. Many outcrops are artistically striped with various shades of brown and red, the pigments coming from varying amounts of silica in the rock. The extreme folding and compression evident at the Tinaja are now considered a result of high-pressure activity: as the Cretaceous sea retreated, there were periods when the shoreline waxed and waned, with silty or muddy conditions alternating with clearer, deeper water. Many silty, therefore flexible and slippery, layers were deposited, and it is hypothesized that, due to the accumulated weight, the overlying deposits finally slumped and folded in on themselves, the underlying Buda Limestone having served as a slick surface that enabled friction-free movement (D. Corrick pers. comm.).

The Upper Cretaceous period, ca. 100 mya, was a time of uplift and continental development contemporaneous with the presence of dinosaurs. A critical event of the time was the Laramide Orogeny, which created, among other North American geologic features, the Rocky Mountains. That same compressive activity caused the faults and uplift associated with several mountains in BBNP and the Sierra Madre ranges of Mexico. The intense pressures caused clinal folding, many instances of which are visible in the DH. In the Cenozoic era, crustal stretching, beginning around 30 mya and continuing today, resulted in the basin and range topography common in the desert west and obvious locally in the DH. Resisting the stretching, massive blocks of sedimentary limestone split apart. Faults were created along a NW-SE line, and eventually the blocks were uplifted and tilted (Fig. 14), creating gradual slopes to the west and steeper escarpments to the east. The DH area is a prominent example of this geological process. Also, as a result of faulting and expansion, the central area of the park was down-dropped, which served to further accentuate the DH.

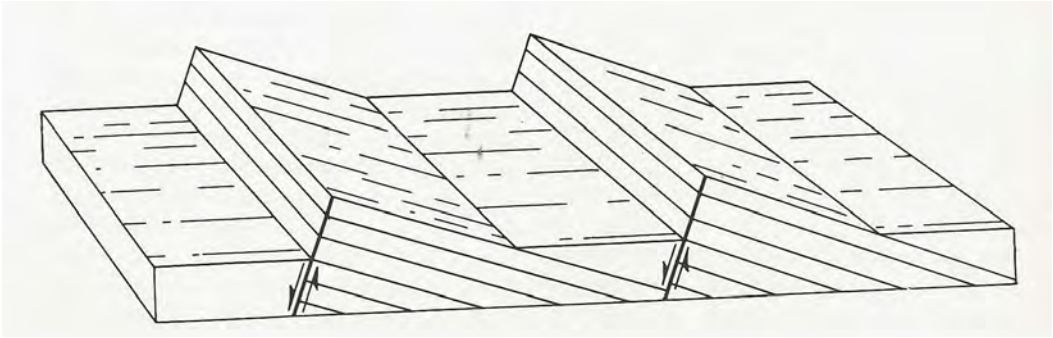


Fig. 14. Diagram of upthrust fault blocks, creating basins in between (Maxwell 1979).

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Repeated mountain-building events in the Cenozoic resulted in a variety of formations. The Chisos Mountains in the center of the park are Tertiary-period, igneous formations (ca. 60 mya); most relevant to the DH, the McKinney Hills and Roy's Peak are eroded laccoliths from the same period. Dagger Mountain is recognized as a fault-banded anticlinal fold, but the power to deform the rock may have come from some kind of igneous intrusion below that is not yet exposed for verification.

The most recent geologic history is that of simple weathering: once the basin and range faulting subsided, the mountains began to weather down instead of building, and the sunken valleys, or grabens, began to fill up with eroded material. Representative stratigraphic layers from this period are the Quaternary gravel and silt deposits (ca. 1 mya). These consist of gravel and silt deposits that in-filled the fault-formed, internally draining basins. Once external drainage developed, arroyos formed and eroded the fill, leaving high-level terrace and pediment gravels in addition to remaining valley-fill deposits. The most recent Quaternary stratum is the general alluvium that forms alluvial fans and terraces. These features are mostly found downstream of Ernst Tinaja, in Ernst Basin and other basins between the uplifted interior ranges, and at the south end of the DH around RGV and the Strawhouse trailhead.

As the internally-drained bolsons were finally finding outlets, major hydrologic patterns began to take shape. The Rio Grande had wound its way through the Big Bend, cutting a course through the softer, overlying layers, when it finally reached more resistant rock such as the Santa Elena and Del Carmen limestone. Already trapped in the

channel it had created, the river was forced to continue, and the tons of silt and particulate matter its waters carried slowly eroded the hard river bed until the canyons of the Rio Grande were formed.

Soils

In general, the DH soils are shallow to very shallow, very gravelly or cobbly, with a high percentage of rock fragments. Rock outcrops are frequent, slopes are steep to very steep, and virtually all soils are limestone-derived, with a high percentage of calcium carbonate. There are small, localized areas on alluvial uplands where the soils are shallow-to-deeper and gravelly, and there are even some deeper, loamy soils found in valleys or near the Rio Grande. It is often stated (Shreve 1942; Powell & Turner 1977) that localized occurrences of gypsiferous soils are important in the Chihuahuan Desert Region (CDR), but this is not the case in the DH. There are areas along the Old Ore Road that may have higher gypsum levels, where the dog cholla *Opuntia aggeria* seems to occur in large part as a monoculture (pers. observ.), in addition to occasional *Larrea tridentata* (creosote) and the purportedly obligate gypsophile *Psathyrotes scaposa* (naked turtleback; Powell & Turner 1977).

Classifying soils can only be done in relation to the surrounding environment. The elevation of a site determines its climate. The climate shapes the community of plants occurring there, and the plants demonstrate what the soil is capable of, or what conditions are present: the amount of organic matter, water capacity/availability, minerals, root zone depth, and soil temperature. Using this pattern of associations, the Natural Resource Conservation Service (NRCS) creates regional soil maps. It is an active process: the soil survey of BBNP first completed in 1985 (Cochran & Rives 1985)

is currently being revised and refined as new information becomes available. Some of the current changes affect the DH and are discussed below as understood from Lynn Loomis (pers. comm.), the Big Bend regional soil conservationist. As the park's map is updated, new information will be available first on the United States Department of Agriculture website (USDA 2006). Information on soils that are not being reclassified is based on Cochran and Rives (1985).

The basic soil units of the DH follow general elevational divisions used in the USDA's concept of regional vegetation communities (Turner 1977). The highest elevations in the DH fall into its Mountain Grassland ecological zone, 4500–6700 ft (1370–2040 m). DH areas with this elevation are on the summits and shoulders of the main DH plateau and continue up to Sue Peaks (Fig. 15). Previously known as Ector soils, these now carry the updated name of Altuda. These soils are classified as loamy-skeletal, carbonatic, thermic, and lithic, calciustolls. These technical terms translate into many important characteristics. The soils at this elevation and on the whole for the DH are evenly balanced and dominated neither by clays nor sands. In most areas of the DH, the soil is shallow (bedrock found within 20 in of the soil surface) and contains a high percentage of rock fragments. The mean annual soil temperature (MAT) is 14–22° C (58–72° F) at the Ector/Altuda elevations and gets progressively warmer in decreasing elevation. Also, at the highest elevations the soil is darker in color because of its high organic content and may be moist more often than dry, although this has not been ground-truthed and may not apply in this area. Throughout the DH, the high amount of

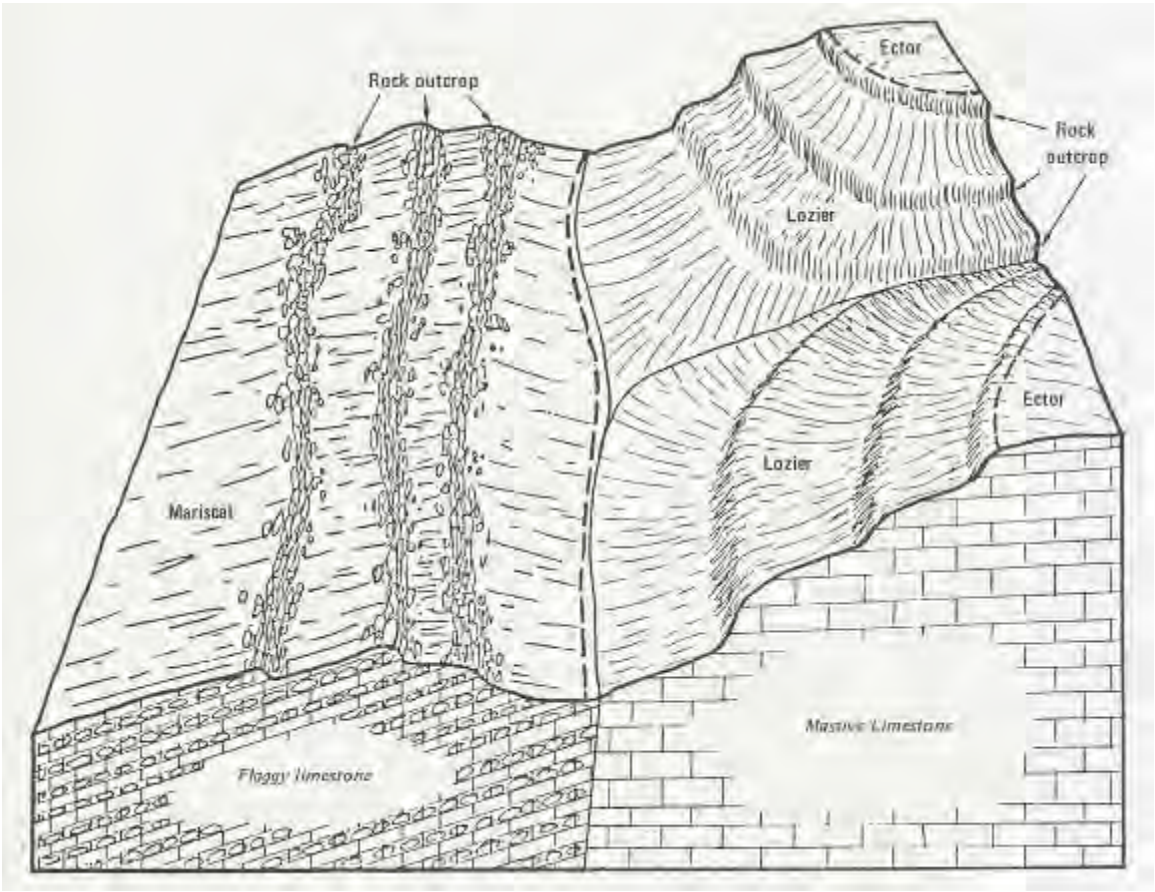

Fig. 15. Schematic drawing of high elevation soil units (Altuda/Ector and Lozier/Bissett) in the DH Mountains (Cochran and Rives 1985).

calcium carbonate in the soil is not leached out by high rainfall and persists in solution in the soil column long enough to precipitate out on the underside of suspended rock fragments.

The Ector/Altuda map unit is found in areas with an approximate 3:1 ratio of soil to rock outcrop, which manifests as limestone ledges, escarpments, and bedrock exposures. Slopes are from 5 to 65%, with rocky outcrops common on slopes over 20%. The water-holding capacity of the soil is generally low because of the high percentage of rock fragments, but after a small rain the availability of water is higher because of the resultant higher water potential. Runoff is rapid and permeability is moderate.

Associated plants in this map unit, as listed by the NRCS for Jeff Davis County (USDA 2006) are short and mid-grasses, with main shrubs being *Quercus mohriana* (Mohr shinoak), *Juniperus pinchotii* (redberry juniper), *Pinus* sp. (pinyon pines), *Nolina texana* (sacahuista), *Dasylirion leiophyllum* (sotol), and *Agave lechuguilla* (lechuguilla). The communities listed at this elevation in the BBNP soil survey are the mountain savannah (>5500 ft) and mixed prairie (4500–5500 ft). Characteristic vegetation listed for mountain savannah are pinyon pine, oak species, *Cercocarpus* spp. (mountain mahogany) *Muhlenbergia emersleyi* (bull muhly), *Bouteloua gracilis* (blue grama), and *Schizachyrium* spp. (little bluestem). Mixed prairie vegetation is expected to contain *Bouteloua curtipendula* and other grama grasses, perennial *Aristida* spp., (threeawns), *Leptochloa dubia*, *Bothriochloa barbinodis* (cane bluestem), *Dalea formosa* (feather dalea), and *Menodora* sp. A combination of these lists gives more suggestions as to what may occur in the DH rather than a true picture of the dominant species at these elevations in the DH: the junipers are not uncommon, pines are very rare, no sacahuista was seen

during the current study, and the shinoak occurs in patchy thickets. More abundant are the monocot rosette species such as *Yucca* spp. (yuccas), *Dasylirion leiophyllum* (sotol), and *Nolina erumpens* (beargrass). Grasses are very important at this elevation and are mainly a mixture of *Muhlenbergia* and *Aristida* species, with *Bouteloua curtipendula* (sideoats grama) being the dominant grama grass.

Moving downslope, what were previously known as two Lozier Rock-outcrop units are currently being redefined; the Lozier name is now associated only with soils in the Pecos River drainage, approximately 95 mi (150 km) east of the DH. The new units are centered around the 3500 ft elevational split that divides the two, lower-elevation USDA vegetation groups. The higher unit is called the Bissett, generally between 3500 and 4500 ft, as is the Desert Grassland vegetative zone. The USDA associates the following plants with the Bissett unit: *Bouteloua curtipendula* (sideoats grama), *Leptochloa dubia* (green sprangletop), *Viguiera stenoloba* (skeleton-leaf golden-eye), and *Leucaena retusa* (goldenball leadtree; L. Loomis pers. comm.). Major differences from the Altuda include steeper slopes, higher percentage of rock outcrop, warmer MAT, and drier soil for a longer portion of the year.

The lower Lozier Rock outcrop unit associated with the DH has been redefined and is now called Black Gap. This new determination was precipitated by newly available soil temperature data. It has become apparent that soils at the lower elevations are hyperthermic: the MAT is over 72° F (22°C), making soil conditions equivalent to those in South Texas. The distinctive plant species of the Black Gap unit are located generally from the river corridor up to 3500 ft (1065 m) and fall into the USDA Desert

Shrub vegetation zone. They are the most drought tolerant encountered so far: *Jatropha dioica* (leatherstem), *Hechtia texensis* (hechtia); and *Euphorbia antisyphilitica* (candelilla).

The previous BBNP soil survey (Cochran & Rives 1985) delineates an area between 2600 and 4500 ft (792–1370 m) as a Desert Grassland vegetative zone, supposedly receiving 10–12 in. (25–30 cm) of rain per year, as opposed to a projected 12–15 in. (30–38 cm) for the Mixed Prairie and over 15 in. (38 cm) within the survey's Mountain Savannah zone. Dominant grasses and shrubs in the BBNP soil survey for Desert Grassland vegetative zone in large part match those suggested for the new Bissett unit but are not as markedly arid-adapted in nature as are those of the Black Gap. The current revelations about soil MAT seem to be appropriately revising the previous vegetation interpretation, moving the transition between grassland and the more arid-adapted desert scrub zone from 2600 ft up to 3500 ft (792–1065 m).

Several other soil units occur at lower and flatter elevations within the DH. Found sporadically along the western foothills, Mariscal soils are in areas of interbedded limestone and shales, resulting in a higher percentage of clay. The Upton-Nickel association is found above and along drainages cutting through pediment valley fill (Fig. 16). This is another unit undergoing reclassification and is now known as Strawhouse-Stillwell. These deep-to-shallow, gravelly soils are well drained, calcic, and coarse-to-sandy loams. Occurring on remnants of erosional fans, alluvial flats, and pediments, they develop along the base of the western foothills and in depositional areas like Dagger Flat and Ernst Basin. Slopes are up to 30 percent. Calcium carbonate leaches through the soil slowly and, in some areas, solidifies below the surface into a hard impermeable layer

called caliche, making soil depths variable. Common plants include lechuguilla, *Fouquieria splendens* (ocotillo), *Bouteloua ramosa* (chino grama), *Tridens mutica* (slim tridens), and *Dasyochloa pulchella* (fluffgrass).

Deeper, finer soils generally associate with the larger drainages of the area like Tornillo Creek and the Rio Grande. Tornillo soils are formed in alluvium across broad valley floors (Fig. 16). When disturbed, this soil erodes easily, resulting in exposed rootstocks and, eventually, badlands-type landscapes (Fig. 17). Historically this soil was believed to support extensive meadows of *Hilaria mutica* (tobosa grass). A small area of tobosa covers the western edge of Ernst Basin, in stark contrast to the sparsely vegetated, more elevated flats over the rest of the basin (Fig. 18). The area contains many deep erosion channels, presumably due to hydrologic action across and along numerous established mammal trails. As water drained across the valley, fine particles may have been transported farther than the rest, then settled out to create good substrate for tobosa. This area may represent a small inclusion of Tornillo soils (L. Loomis pers. comm.).

Along the Rio Grande floodplain at the south end of the DH, cyclic deposition of silt from floodwaters has created the Glendale-Harkey unit. These are deep, well drained, silty-clay loams on nearly level floodplains. Fresh alluvium remaining after each flood would enrich the soil, promoting farming as an important area industry. Today, with a history of heavy use and with natural flood cycles broken by upstream dams, in many places these soils have eroded, and the surface is bare if not occupied by creosote or thickets of mesquite-dominated brush.

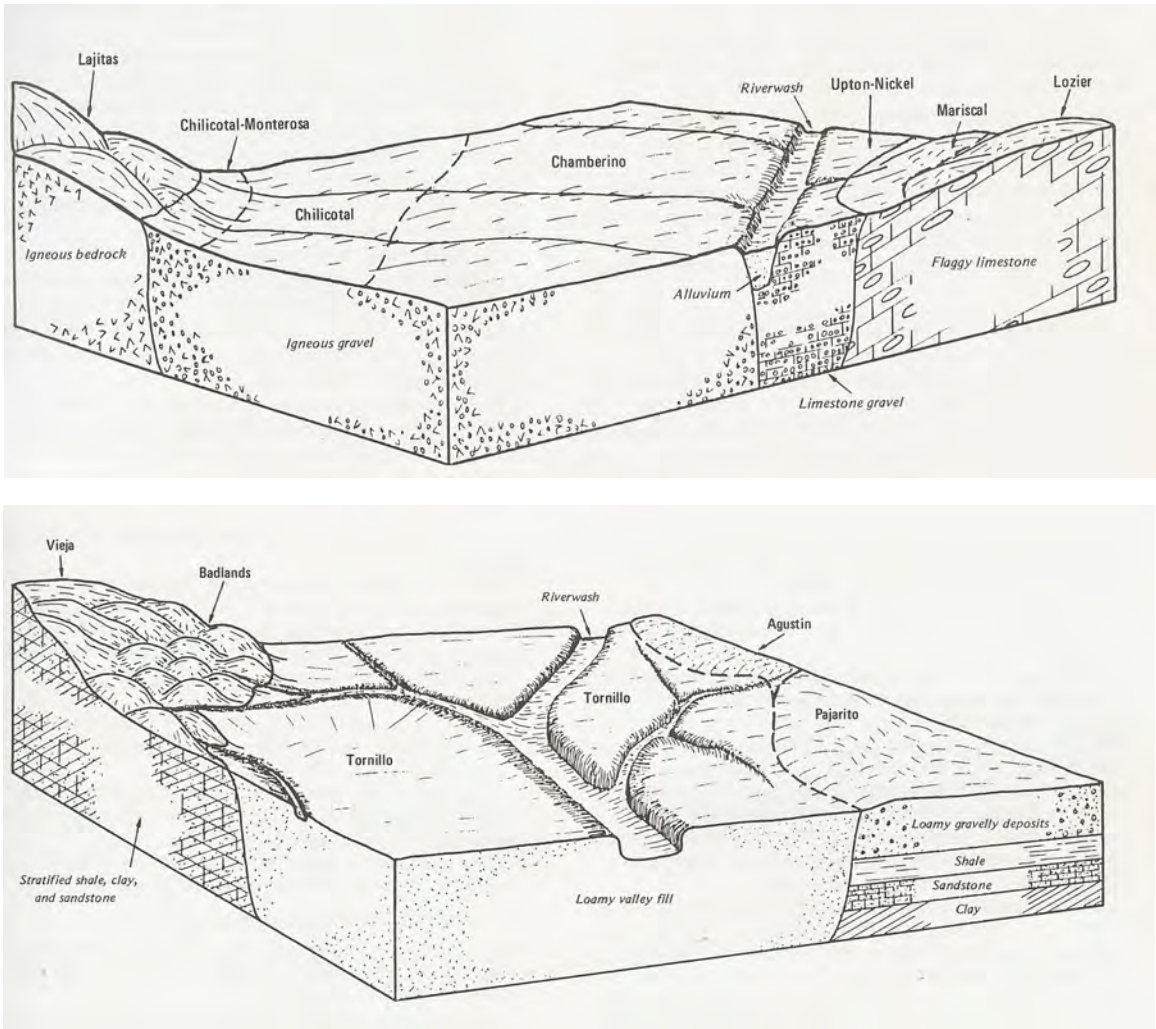

Fig. 16. Schematic drawings of lower elevation soil units (Upton-Nickel and Tornillo) in the DH Mountains and BBNP (Cochran and Rives 1985).

Fig. 17. Erosion of Tornillo soils into badlands formations, north of Tornillo Creek bridge, March 2007.

Fig. 18. Tobosa grassland on the western side of Ernst Basin. Note disturbance of fine soils at bottom center of picture, due to entrenched mammal trails and fluvial erosion.

In all of the major streambeds and drainage channels, the soils are termed Riverwash, consisting of sandy-to-silty, gravelly alluvium. The arroyo beds are expected to be mostly barren. Any plants that might establish themselves in the streambeds would be deep-rooted perennials; annuals are more expected, according to the soil survey descriptions (Cochran & Rives 1985). These areas are subject to frequent flash floods and then are dry for long periods. Erosion rates are high, creating cut banks on both sides of the drainages.

Human History

People have been living in the Big Bend for thousands of years. The research done and literature available about all phases of regional occupation are extensive and highly entertaining. The two sources used to compile the following summary (Tyler 1975; Alex 1990) are a good starting point. The first people thought to occupy the area now encompassed by BBNP were there during the Late Paleo-Indian period (12,000–6,500 BC). At the end of the last glacial period, the climate was cooler and wetter, with more vegetation, and the local people lived a nomadic hunting-and-gathering life. Though few sites in BBNP have evidence of occupation from this time, one happens to be at the foot of the DH. Dated superficially by the type of point (arrowhead) found there, the site is nestled at the southwest foot of Alto Relex. There, nomads may have enjoyed a small, spring oasis that may have existed in the more mesic environment of the time (A. Cloud pers. comm.).

Gradually the climate warmed, and both the flora and fauna adapted to the increasingly arid climate. Humans altered their hunting and gathering techniques by focusing on smaller game, using an atl-atl to propel their spears, and becoming more

dependent on plant foods. Archaeological evidence from this Archaic Period (6500 BC–ca. 100 AD) is abundant in the Big Bend. In a survey of a 5000-acre (2023 ha) area of the DH, 99 sites were found, ranging from general lithic scatter to pictographs and obvious cave utilization. On a few, higher-elevation precipices, low, crescent-shaped rock walls were found, thought to be vision quest sites (A. Cloud pers. comm.). In a side drainage downstream of Passionflower Canyon, a mid-Archaic (4000 BC) point was found below a previously occupied cave. The shelter had a fire-blackened roof and was full of significant artifacts, including a storage pit lined with a woven, sotol-leaf mat, a metate (rock used for grinding and processing food), fiber sandals, yucca- and lechuguilla-fiber cordage, and various implements, including a wooden scoop (Niebuhr 1936).

The nomadic life was slowly transformed as the Jornada-Mogollon culture began to influence the region. During the Prehistoric Period (1000 AD–1535 AD), the bow and arrow replaced the atl-atl, and lifestyles focused more on agrarian settlements; ceramic shards are some of the common artifacts observed today. Remains of this culture are most abundant west of BBNP at La Junta, where the Rio Grande meets the Mexican Río Conchos. This area figures prominently in the Historic era (1535 AD– present), as the site of the first documented interactions between Europeans and Native Americans in the region.

In 1581, Spaniards exploring from their New World kingdom to the south recorded their encounters with local natives, groups commonly known as the Chisos and Jumanos Indians. Initially welcoming, the native peoples became more hostile due to poor treatment from their southern neighbors. The Spanish, amidst conscripting slaves

and souls, were focused on using the Big Bend as a safe foothold from which to find the riches imagined by many to be awaiting discovery and extrication in the North American interior. However, as the Mescalero Apache were forced southward by the plains-dominating Comanche, the peaceful frontier envisioned by the Spanish deteriorated. Missions and presidio forts were established but, ultimately, to no avail as Indian raids increased south of the Rio Grande.

Regional instability was a major factor in the European loss of control; between the 1821 Mexican independence from Spain and the ensuing Texan independence from Mexico in 1836, no government existed that could provide the stability needed to neutralize Indian hostilities. An established cycle developed: Apache, and eventually Comanche, bands would summer to the north in New Mexico and Oklahoma, sweep down through the Big Bend into northern Mexico, raiding anyone and any place they chose, and then return with livestock, horses, and other spoils. Their travels resulted in a wide, beaten path along this route. The Comanche Trail was clearly visible for many years after the cycle was broken and consisted of several routes heading north from the river. These routes converged at Persimmon Gap, which formed an important conduit during the annual migration.

The next, non-Indian presence in the Big Bend was slow to develop. A few early ranchers and traders in the mid 1800s strove to take advantage of the abundant grasses and economic opportunities offered by trading with the Mexican interior. The U.S. military established a fort in the Davis Mountains in 1854 to help protect the fledgling trade routes. Searching for a way to match Native Americans' survival abilities in the harsh desert, the army brought camels to the region as an experiment in arid military

operations. The camel corps passed through Dog Canyon and traveled on the flanks of Dagger Mountain in 1859 as they moved in and out of the rough country to the west and south. The Civil War brought that experiment to an end, as well as any protection and stability that the U.S. military had brought, as all troops were recalled east. Despite the threat of constant raids and loss of cargo or livestock, trading increased. By 1881, after several violent attacks had eliminated the remaining, resistant Native American bands, Indians were no longer a threat to the new settlers. The railroad came to the region in 1882, enabling towns like Alpine and Marathon to be established along the route. Ranching became more logistically feasible, and amid reports of unending amounts of forage and opportunity (Langford 1995), a wave of settlement moved out in all directions from the railway.

Ranching was successful in many areas of the Big Bend, but the DH, as a whole, never provided a consistent range for grazing animals. The Adams family headquartered on the eastern side of the DH near Hubert Ridge and the mouth of Telephone Canyon. They originally ran mohair goats, a popular choice during the early 1900s in Big Bend, but, eventually, it was not a successful venture due to low prices and environmental challenges (Adams 1978). One of the stories about how the DH were named tells of a rancher who took his horses to the higher plateaus to graze on the belly-high grasses, only for them to die of thirst (Fulcher 1959). Few remnants of human use persist in the mountains—old pieces of wood, some wire—but the lack of water was probably the primary limitation. The Adamses did finally find success but only through utilizing another biological resource.

Euphorbia antisyphilitica (candelilla) was harvested and rendered to produce blocks of wax for commercial sale. One of the main factories was in the McKinney hills, just west of the DH proper. The Adams family had an extensive system of wax camps on the eastern side, clearing $125,000 in one year, above and beyond $15,000 of product lost to fire (Adams 1978). Many residents lining both sides of the Rio Grande were involved in wax production, since the river provided the large quantities of water needed in the rendering process. This small-scale industry continues along the river today, providing wax used, most notably, in lip balm and other cosmetics.

Rubber was another product to come out of the Big Bend: a high-grade natural product can be extracted from the shrub *Parthenium argentatum* (guayule). In 1909 a factory was built in Marathon and produced rubber intermittently for twenty years, but it was determined that the natural population would not produce enough rubber to be economically sustainable. Interest in the industry eventually faded. A consistently utilized plant, though not for human consumption, was *Bouteloua ramosa* (chino grama), extensively harvested to feed the area's increasing numbers of working mules, burros, and horses.

Mining was an important industry in turn-of-the-century Big Bend. While cinnabar or mercury mining was flourishing in other parts of the Big Bend, important minerals in Sierra del Carmen history were silver, lead, and zinc. The Puerto Rico mine, on the western front of the Mexican Sierra del Carmen, was the source for tons of ore to be smelted at Boquillas, Mexico. A store supplying the mining community opened after a supply road finally connected Marathon with Boquillas, Texas, in 1894 (Maxwell 1979). When the smelter shut down in 1914, the ore was transported into the U.S. by a

six-mile, aerial tramway over the Rio Grande. At the terminal in Ernst Basin, 7.5 tons (6804 kg) of ore per hour were loaded into mule-drawn carts, which then completed the journey north to the railroad (Pearson 1990). Today the Old Ore Road travels the route almost as it was at the turn of the century.

The southern end of the DH, as a whole, was an especially popular commercial area of the time. A succession of post offices, trading posts, and even a hot springs "resort" on the river were among the amenities available in the early 1900s. The services targeted residents on both sides of the river, who lived as friends and neighbors, depending heavily on each other in light of their isolation. For a short time, however, unrest and banditry associated with the Mexican revolution caused the US military to station troops in the Big Bend. Apart from two significant raids, which occurred before most troops were deployed to the area, the soldiers spent much of their time grumbling about their plight, stranded in the desert with no maneuvers in sight. Some of their time was put to good use, however, stringing a telephone line across the DH to add yet another modern convenience to the area. Remnants of that project can still be found along the Telephone Canyon trail. True to the resourceful nature of area pioneers, the Adams family used abandoned caches of poles to outfit a large cave in which they lived for a time (M. Paredes pers. comm.).

Partly due to the military-era publicity, word spread about a spectacular place in western Texas, with rugged scenery and impressive, river-carved canyons, a place certainly worthy of national park status. Momentum built until the Texas legislature created Texas Canyons State Park in 1933, destined to become part of the National Park Service eleven years later. The Civilian Conservation Corps worked in the new park,

improving access and accommodations at the original park headquarters in the Chisos Basin. Over time, however, other areas in the park that had seen so much life and death through the steady flow of human occupiers were left to crumble back into the desert. Most settlements and signs of life are but lumps of melted adobe or twisted, rusty wire barely emerging from the ground. Today, the only humans seen in the DH are hardy souls from our current times: those willing to forgo a soft bed and air conditioning to adventure into what was many peoples' backyard and now is our wilderness. Each year up to 400,000 people visit Big Bend park, participating in a wide variety of recreational pursuits. Hiking, camping, river running, bird watching, geology and nature tours, and ranger activities are among the many opportunities available to today's visitors.

Disturbance Regimes

Human-induced disturbance regimes that have affected DH vegetation include grazing, natural-resource harvesting, fire, non-native species establishment, and recreation. The absence of surface water in the DH has most likely saved it from most of the historical grazing-induced impacts. Early park biologists noted that good grass was found only where no water was available. According to these early reports, whereas *Euphorbia antisyphilitica* (candelilla) and *Bouteloua ramosa* (chino grama) had been collected almost to the point of extirpation in more accessible areas of the park, the populations in the interior of the DH appeared untouched (McDougall 1936). This contrasts with sites with available surface water, such as man-made tanks and dams. At one time, perhaps 8,000 goats watered at Ernst Tank, leaving hardly any remaining plants in the surrounding area (NPS 2003). Today there is a small strip of tobosa grassland

there, with the rest of the basin being gravelly creosote flats. Since the advent of the National Park, the land has been allowed to rest and recover, although in the DH it would be difficult to show whether this area has returned to its original stature.

Tornillo Flats, extending west of the DH, once supported good grazing (Langford 1995), but the soils are fine and silty. When the grass cover was disturbed, the soil eroded, creating the barren flats and badlands-type areas that are visible today when driving through the National Park south of Persimmon Gap. Some grassland areas have seen improvement since the removal of stock animals, most notably in the Dog Flats area west of Dog Canyon.

Noticeable remains from human use of the DH include header dams, built across narrow drainages to catch runoff from thunderstorms, and tanks, built with berms to catch water in more open areas. They may hold water for extended periods if rain falls in the right place, but generally are not permanent sources. There is a dam along the Telephone Canyon trail, where a few non-native grasses, e.g. *Eragrostis lehmanniana* (Lehmann's lovegrass) have occurred but likely will not spread into the arid surroundings. Tanks often develop into mesquite thickets or provide wallows for javelina and non-native feral hogs. The two mapped tanks, in Dagger Flat and Ernst Basin, were not visited during this study.

The harvesting of *Euphorbia antisyphilitica* (candelilla), *Bouteloua ramosa* (chino grama), and *Parthenium argentatum* (guayule) probably impacted the area to some extent, but again, without water, the possibility for people or animals of burden to spend long amounts of time in the area was low. There is no historical quantitative basis from which to compare pre- and post-harvest plant densities with the current populations, but

the populations of grasses and "weed," as *Euphorbia antisyphilitica* (candelilla) was called, today appear healthy and widespread. *Parthenium argentatum* (guayule) is not common at lower elevations in the DH, which may have restricted its collection to areas closer to the factory at Marathon. This resource harvesting does not seem to have been a significant impact in the DH.

Fire may be a significant factor in creating patchiness of higher elevation vegetation. NPS fire records date from 1948. Over the last 57 years, a total of 84 recorded fires have burned in the DH (Fig. 19), five occurring outside of BBNP, in total covering 12,153 acres, or 4918 ha (J. Morelock pers. comm.). In many places, one yucca struck by lightning would constitute a "fire." Often vegetation is so patchy that flames will not spread beyond the spot where they started. In higher elevations or in some major drainages, it would be possible for larger fires to maintain themselves, because the vegetation is denser and larger than on more arid slopes and flats. Fifty of the recorded fires covered less than one acre; six of those were human caused. In the twelve fires larger than 20 acres (8 ha), lightning strikes burned 12,082 acres (4,889 ha). Human-caused fires do not seem to be a significant impact, especially outside of developed areas.

Long-term impacts to vegetation from fire have not been thoroughly researched in the Chihuahuan Desert. In current, land-management philosophy, it is commonly believed that fire is a positive and necessary force in the environment but one that has been suppressed by humans for too long, thus unnaturally changing the vegetative character of (especially western) landscapes. There has been little suppression effort in the DH, so current states should be considered normal. Henrickson and Johnston (1986)

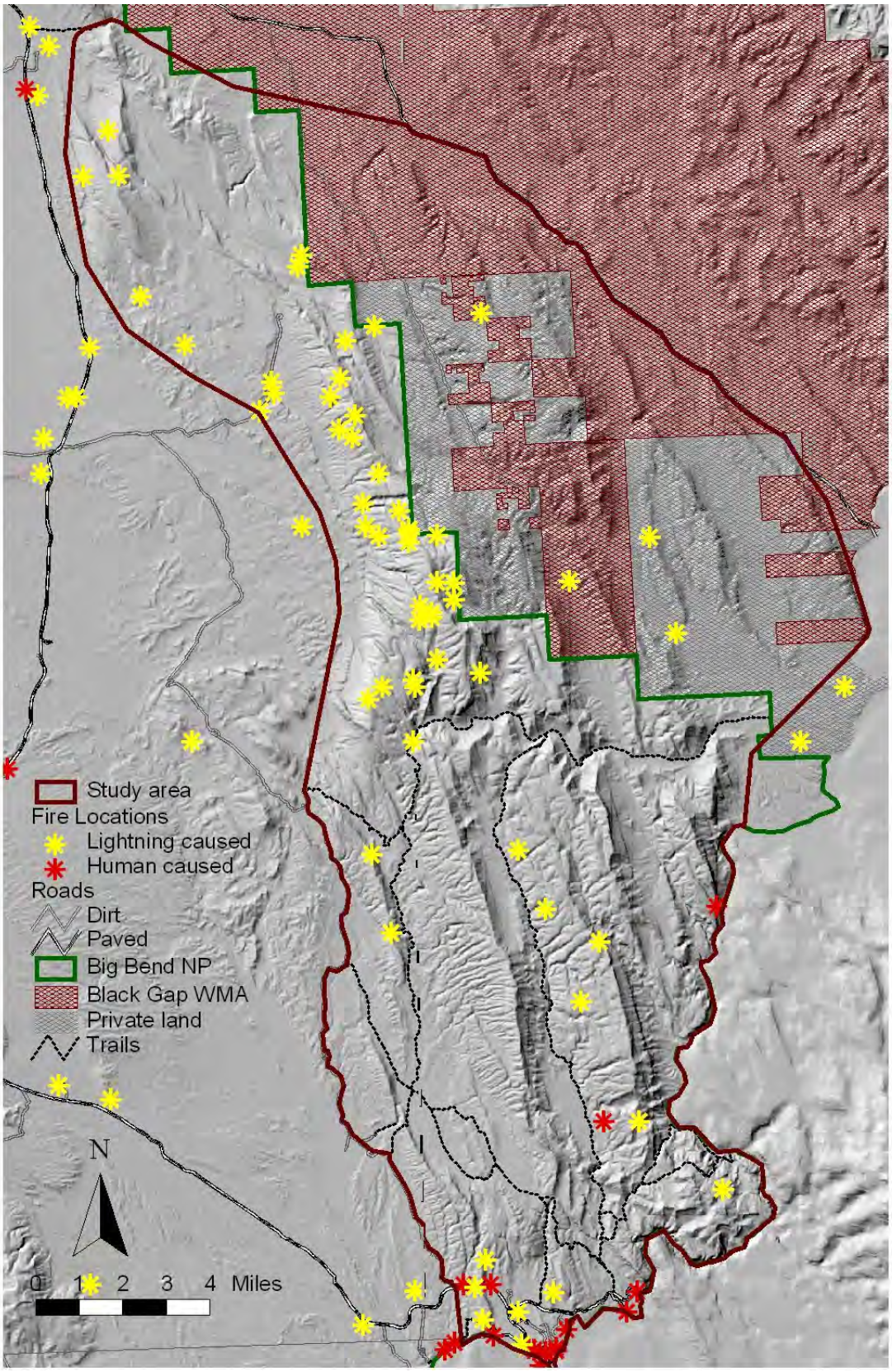

Fig. 19. Recorded fires in the Dead Horse Mountains, 1946–1998 (B. Alex pers. comm.).

suggest that the unique Yucca Woodland community at higher Chihuahuan Desert elevations may be maintained by fire, favoring the semi-succulent monocots over more woody species. This hypothesis could be looked at in the DH, where woody chaparral thickets occur in patches within the Yucca Woodland and where fires have impacted both life forms.

The establishment and spread of non-native vegetation is a significant issue, most striking along the river corridor. The invasion of the southwest by *Tamarix* spp. (tamarisk, salt cedar) is well known and is a major issue along the Rio Grande. This species can also be a problem at inland springs because its tiny seeds are easily transported by birds. The non-native *Arundo donax* (giant river cane) is also densely present along the river, interspersed with smaller populations of its similar native (Saltonstall 2003) cousin *Phragmites australis* (common reed). These three species create a homogeneous thicket along miles and miles of riverbank (Fig. 20). The dense canopy cover, in addition to increased soil salinity levels created by the tamarisk, prohibits the establishment and/or success of previously existing native species. The dense growth of roots and cane rhizomes stabilize the sandy banks. With upstream dams breaking the historic flood cycles, the river channel does not see the regular scouring and replenishment of beaches and gravel bars, places where native *Salix* spp. (willows), *Populus* spp. (cottonwoods), and other riparian species would normally take root. The stabilized banks entrench the river, limiting the possibilities for native species and leaving non-natives as the dominant riparian species on the Rio Grande. Currently there

Fig. 20. Non-native *Arundo donax* (a.) growing densely along the Rio Grande, with a *Tamarix* sp. (b) thicket established slightly higher up the riverbank.

is a bi-national effort underway to clear selected areas of tamarisk and cane within Boquillas Canyon and then track the success of exotic removal and the hoped-for reestablishment of native species (J. Sirotnak pers. comm.).

Pennisetum ciliare (buffelgrass) is another invasive, non-native species that is well known in the southwest. The robust African grass was introduced as a drought-tolerant range species and has spread, excluding much of the native flora and fauna where it takes hold. In BBNP it is increasing at the lower elevations, and on the flanks of Boquillas Canyon *Pennisetum ciliare* (buffelgrass) can be seen almost to the top of the canyon walls. Though ubiquitous, it is not as dense as it has become in other low-elevation areas, perhaps being held in check by other non-native species, burros and horses.

Though legal grazing was eliminated from BBNP by the mid 1950s, some livestock still forage within the park along the river corridor. Termed "trespass livestock," many horses, burros, and even cattle cross the river from Mexico, taking advantage of all forage available during their free-range existence (there are no fences at the river along the NPS boundary, and the few on the Mexican side are discontinuous). It is unclear whether *Pennisetum ciliare* (buffelgrass) seeds are spread through dung or if the stock are, in truth, limiting seed establishment by grazing. What is certain is that the animals trample and eat native vegetation (Fig. 21). Collecting trips through Boquillas canyon revealed that the sides of the canyon did not support much diversity; the few plants able to exist on rocky outcrops and ledges that were not frequented by burros were the only ones to remain. Biological crusts that form on the sandy surfaces were relegated to sunken areas between rocks and thin margins of soil that escaped being trodden. At

Fig. 21. Impacts from trespass livestock: a. burro eating prickly pear, b. trampled vegetation and disturbed fine soils.

the mouths of side canyons feeding into the Rio Grande, some slopes were almost denuded and the soil churned up to a fine powder due to the stock traffic. Park rangers are only just beginning to assess the impacts to park resources due to trespass livestock (D. VanInwagen pers. comm.).

Humans are also potential sources of disturbance, but recreational use in the DH is minimal. There are many ways for visitors to enjoy the DH: driving the high-clearance/4-wheel-drive Old Ore Road, hiking, camping, and floating the river through Boquillas Canyon. Front-country use is intensive at the RGV developed area, where there are a campground, RV hook-up site, ranger station, store, and boat ramp. There, human activity does not stray far from these impacted areas. For those who want to hike, several trails are available throughout the DH, with those at Ernst Tinaja and Boquillas Canyon being the most heavily used. Impacts are minimal along the trails, as hiking cross country means difficult navigation between the spines of lechuguilla, cacti, ocotillo, and catclaw, not to mention the possibility of encountering various venomous creatures; this scenario does not appeal to the majority. The lack of water sources limits recreational use of longer trails in the DH, such as the Telephone Canyon and Strawhouse trails. The Marufo Vega loop is the most-used longer trail of the DH, but the numerous search-and-rescue operations that have involved this area attest to its challenging environment.

For those wishing for an overnight backcountry experience, permits are available for the primitive car-camping sites along the Old Ore Road (offering only a cleared area for parking and a tent), backpacking, or river trips. In 2005, only 13% of BBNP backcountry users chose to recreate in the DH area (NPS 2006; S. McAllister pers.

comm.). That is only 0.5% of the 400,000 visitors to the park in 2005. Only 14% of those backcountry visitors went backpacking, meaning a very small impact to more pristine areas. Twice as many people used the river than went backpacking, but any human-caused disturbances along the river corridor are are focused around the few usable campsite areas in the canyon, and the floodplain is naturally a highly impacted area to begin with. Human use in the riverine portion of the DH appears less significant long term than are the increasing non-native vegetation or damage done by trespass livestock.

On the whole, the impacts of current human use do not seem significant over most of the DH backcountry. People can serve as vectors in transporting and dispersing non-native seeds, on their cars, shoes, clothing, and through stock use, but no buffelgrass was observed away from the river or the lower Old Ore Road. The few tanks may support non-native species, but these species are likely restricted to those areas due to moisture requirements. It is the human impacts on a larger scale, i.e. the changes in river dynamics and regional dominance of non-native riparian species, that are most obvious today. Increasingly, impacts from trespass livestock are becoming apparent as well. In the end, the most realistic outlook may be to rely on the old axiom: good vegetation will be found only where there is no water.

Paleoenvironment

There has probably never been a unified CDR flora, and the modern vegetation is as sparse as at any time during the current Holocene period (Van Devender 1990). Since the glacial period during the late Wisconsin, species ranges have expanded and contracted due to climate changes and the environmental tolerance of individual species. The changes in climate have been mediated largely by alterations of large-scale,

atmospheric flow cycles, similar to the forces that have caused the El Niño/La Niña weather patterns and the successes and failures of fisheries in more recent years (Neilson 1986). The resulting characteristics of vegetation communities present at different points through paleohistory can be interpreted from analyzing the contents of packrat middens. These nests consist of material gathered within a 98–164 ft (30–50 m) radius of the site. The nests are reused through time and, if sheltered well, can accumulate as much as 40,000 years of local biotic history (Van Devender et al. 1987).

Vegetative remains in middens across the Southwest, dating from the last glacial period through to the present, suggest a progressively warming and drying climate (Van Devender 1990). During the late Wisconsin period (20,000–11,000 years ago) North America was in a full glacial period. At this time, an extensive pinyon-juniper-oak woodland covered the entire elevational range of the CDR. It is hypothesized that the region experienced cooler, overall temperatures, along with dominant winter rains, in order to support this type of vegetation. At this time, a more equable climate with few winter freezes is envisioned, likely created by the blockage of arctic air masses by the continental glaciers (Bryson & Wendland 1967 in Van Devender 1990). This situation may have allowed warmer-adapted species to migrate north and more cold-adapted species to extend south, creating a level of vegetative complexity that no longer exists (Van Devender 1990) yet could still be reflected by relicts occurring in local floras.

During the early Holocene (11,000–9000 years ago), glaciers retreated, and pinyon pines disappeared from the midden record; increased summer temperatures combined with winter rain and increasing summer monsoons most likely precipitated the shift to an oak-and-juniper dominated flora. By the middle Holocene (9000–4000 years

ago), winter rainfall is thought to have ceased, while summer temperatures and rainfall increased substantially, favoring the increase of graminoids. A vast, unbroken grassland spanned the entire central section of North America from Canada down through the Mexican highlands, with warm-season perennial grasses (utilizing the C4 photosynthetic pathway) replacing cold-adapted C3 grasses in the central Great Plains (Van Devender et al. 1987). Winter freezes, with higher intensity and frequency than the region sees today, most likely continued through the middle Holocene, preventing subtropical elements from becoming an established part of the regional flora.

Moving into the late Holocene (4000–present), temperatures continued to increase. The advent of milder winters and continued abundant summer rain, with variable drought periods, favored the establishment of subtropical desert shrubs and a decrease in the primacy of grasslands by the lower Holocene. This period also saw the reestablishment of a corridor connecting the Chihuahuan and Sonoran Deserts. The modern, plant-community composition of the Big Bend and larger Southwest is thought to have been established more recently than 4,300 years ago.

In the DH area, middens from Dagger Mountain, RGV, and Maravillas Canyon (in BGWMA, ca. 15 mi/24 km east of Sue Peaks) have been examined (Wells 1966; Van Devender et al. 1987, Van Devender 1990). There are clear differences between the species able to persist throughout the known paleohistory and those that disappeared or appeared, presumably because of changing environmental conditions. *Agave lechuguilla* (lechuguilla), *Ephedra aspera* (Mormon tea), and *Opuntia phaeacantha* (variable prickly pear) were the only species consistently represented throughout the entire 40,000-year record at RGV. Cold-adapted species, or at least those currently requiring more mesic

conditions, dominated the late Wisconsin period. *Juniperus pinchottii* (red-berry juniper) was the most abundant species represented in the midden data, accompanied by *Pinus remota* (papershell pinyon), *Dasylirion leiophyllum* (sotol), *Koeberlinia spinosa* (allthorn), and *Quercus hinckleyi* (Hinckley oak). In the Dagger Mountain middens, *Quercus pungens* (shrub oak) replaced *Quercus hinckleyi* to become the dominant scrub oak of the DH today. Beginning about 9000–10,000 years ago, the previously dominant species at RGV were replaced by a more xeric shrub assemblage, initially dominated by *Prosopis glandulosa* (mesquite) and *Lycium puberulum* (silver wolfberry), with an increased representation of *Agave lechuguilla* (lechuguilla) and *Opuntia phaeacantha* (variable prickly pear). Over the middle Holocene, more xeric-adapted species began to occur, including *Larrea tridentate* (creosote), *Opuntia rufida* (blind prickly pear), *Fouquieria splendens* (ocotillo), *Acacia greggii* (Gregg catclaw), and even *Castela stewarti* (crucifixion thorn) for a short time.

The midden data create a slightly different picture at the Maravillas Canyon site. During the late Wisconsin, while RGV showed a more xeric-oriented species assemblage, with *Juniperus* spp. (junipers) and some *Pinus* spp. (pinyon pines), *Dasylirion leiophyllum* (sotol), *Koeberlinia spinosa* (althorn), *Ephedra aspera* (Mormon tea), and *Agave lechuguilla* (lechuguilla), the Maravillas Canyon site recorded more of a woodland association, being dominated by pine, juniper, and oak, with none of the above-listed shrubs that were occurring contemporaneously at RGV. Around 9000–10,000 years ago, as more xeric-tolerant species began to occur at both sites, the increased diversity at Maravillas, unlike RGV, included species that today are typical of the larger, protected drainages of the DH: *Purshia ericifolia* (heath cliffrose), *Guaiacum angustifolium*

(guayacan), *Shaefferia cuneifolia* (desert yaupon), and *Acacia roemeriana* (Roemer acacia). This discrepancy between the vegetations of the two sites, in terms of the degree to which each has adapted to xeric conditions, highlights an important difference between the sites. They are both found at the same elevation (ca. 1970 ft/600 m), which suggests that the Maravillas site has a less arid microclimate. Van Devender (1990) attributes this simply to the Maravillas Cave's northern aspect and its being geographically closer to the eastern edge of the CDR. However, the topography of the region should also be considered highly significant.

The Maravillas Cave is on the eastern side of the DH, the DH being the northern extension of the Sierra del Carmen of Mexico, which is itself an extension of the Mexican Sierra Madre Oriental range. Van Devender (1990) suggests that because desert scrub elements, such as *Agave lechuguilla* (lechuguilla), *Koeberlinia spinosa* (allthorn), and *Dasylirion leiophyllum* (sotol), were present in the RGV area during the late Wisconsin and because those species were mainly absent in the Maravillas samples dating to that time, the environment west of the DH has apparently been more xeric for the last 28,000 years. He continues to extrapolate that the DH, as an extension of the Sierra Madre Oriental, may serve as an important air mass barrier that influences the local climate. Throughout this report, this idea is supported based on findings during the current study.

General Vegetation Description

The plant life characteristic of the study area is that of the CDR. This in and of itself does not provide detailed insight, however, beyond assumptions that the plants will be adapted to extreme heat and aridity and that *Agave lechuguilla* (lechuguilla) and *Larrea tridentata* (creosote) may figure prominently in the species composition. Many

workers have proposed vegetation classification systems relevant to the region. For the Chihuahuan Desert as a whole, there exist excellent overviews of basic and detailed vegetation structure (Morafka 1977; Henrickson & Johnston 1986, 2004; Brown 1994; Powell & Hilsenbeck 1995). Descriptions in several local floras (Rogers 1964; Butterwick & Strong 1976; Amos & Giles 1992; Hardy 1997) demonstrate the degree of local diversity possible within hierarchies created by the above publications. Two vegetation maps, produced through remote sensing and some vegetation sampling, generally include the study area (Plumb 1991, 1992; Wood et al. 1999). However, neither study adequately sampled representative DH vegetation nor ground-truthed the resulting maps and should not be considered definitive representations of what actually occurs in the DH.

Giving a sense of foreshadowing, Plumb (1992: 386) makes a discerning statement that no one classification system is universally the best and that researchers should "…select the one that most appropriately suits their purposes." Beyond an overall tendency towards homogeneity (Brown 1994), the DH and larger CDR have basic plant-community types that intergrade and change in abundance and dominance in response to the complex physiography. Perhaps Whittaker, as quoted in Takhtajan (1986), has offered the best explanation for general Chihuahuan Desert vegetation patterns: in warm, semi-arid deserts there is no clear convergence of dominant forms as can be found in cool semi-deserts. Warm deserts may be too dry to support arborescent life-forms or consistent canopy cover. However a diversity of non-arborescent growth is supported in pockets of higher moisture availability, maintained by the right combination of aspect, slope, elevation, and substrate. Larger plants, such as shrubs and *Yucca* spp. (yuccas),

can also create special microclimates. Many species take advantage of the shade and wind protection that these larger nurse plants provide. This could be considered the canopy of the Chihuahuan Desert—low and discontinuous, but functional.

The vegetation types used herein to describe the DH are based on observations made during the study period in addition to the classifications by Henrickson and Johnston (1986) for the CDR and Plumb (1992) for BBNP. Henrickson and Johnston (1986) comment on the high degree of intergradation between types in the CDR, which makes it difficult to place many areas into an exact classification, especially when many sub-types are recognized, as in their and Plumb's (1992) work. Henrickson and Johnston's 16 general vegetation groups incorporate the communities of the entire CDR. Not all of their communities occur in the DH, and because of the high degree of intergradation, the basic categories used to describe DH vegetation have been combined and simplified, though their names are taken from, and basically correlate to, the Henrickson and Johnston terminology (Table 1).

Plumb's categories (1991, 1992) are extremely specific, utilizing 24 categories for vegetation types within just BBNP. Park managers found that level of specificity unwieldy and, therefore, combined some categories (Table 2). Plumb's combined categories can also be generally correlated with those chosen to describe the DH, and because the vegetation class types were based on remote sensing data, they are computerized and able to be analyzed for coverage percentages within the study area (Table 3). The vegetation type with the largest coverage is the Lechuguilla Scrub, at 50.4% of the study area. This type includes Plumb's lechuguilla-prickly pear-grass and

Table 1. Outline of plant communities of the Chihuahuan Desert Region (Henrickson & Johnston 1986). Types in bold are used to describe DH vegetation.

I. Desert Scrub and Woodlands	II. Grasslands	III. Chaparral	IV. Montane Woodlands
A. Chihuahuan Desert Scrub	A. Grama Grassland (*Bouteloua* spp.)	A. **Montane Chaparral**	A. Juniper-Pinyon Woodland
1. Larrea Scrub	B. Sacaton Grassland (*Sporobolous* spp.)		B. Oak Woodland
2. **Mixed Desert Scrub**	C. Tobosa Grassland (*Pleuraphis* spp.)		C. Pine Woodland
3. **Sandy Arroyo Scrub**			D. Mixed Fir Forest
4. **Canyon Scrub**			
5. Sand Dune Scrub			
B. Lechuguilla Scrub			
C. Yucca Woodland, Sotol Scrub (Rosetófilo)			
D. *Prosopis-Atriplex* Scrub			
E. Alkali Scrub (halophiles)			
F. Gypsophilous Scrub			

Table 1, continued. Outline of plant communities of the Chihuahuan Desert Region (Henrickson & Johnston 1986). Types in bold are used to describe DH vegetation.

I. Desert Scrub and Woodlands	II. Grasslands	III. Chaparral	IV. Montane Woodlands
G. Cactus Scrub			
H. Riparian Woodland			

Table 2. Vegetation types of Big Bend National Park, as circumscribed by BBNP staff from Plumb (1991, 1992).

BBNP category	Plumb's categories
Upland Riparian	Mesquite Thicket
	Desert Willow
Riverine Riparian	Reed Grass
	Cottonwood Grove
	Mixed Riparian
Lechuguilla Scrub	Lechuguilla-Prickly Pear-Grass
	Lechuguilla-Candelilla-Grass
Creosote Scrub	Creosote Flats
	Creosote-Tarbush
	Creosote-Lechuguilla
	Creosote-Grass
High Desert Grasslands	Sotol-Lechuguilla-Grass
	Lechuguilla-Grass
	Lechuguilla-Grass-Viguiera
	Sotos-Nolina-Grass
	Yucca-Sotol
	Creosote-Yucca-Grass
Scrub Woodland	Mixed Scrub
	Oak Scrub

Table 3. Percent composition of vegetation types in the BBNP portion of the study area, as translated from remote sensing (Plumb 1991, 1992).

Vegetation Type	Percentage of Study Area
Lechuguilla Scrub	50.4
High Desert Grassland	45.1
Creosote Scrub	1.6
Scrub Woodland	1.5
Upland Riparian	0.9
Bare	0.3
Riverine Riparian	0.2
Water	0.01
Total study area in BBNP	117, 659 acres (47,615 ha)

lechuguilla-candelilla-grass categories. This type is closely followed by the High-Desert-Grassland type at 45.1%, which includes the subcategories with the Rosetófilo species like *Nolina erumpens* (nolina), *Dasylirion leiophyllum* (sotol), and *Yucca* spp. (yuccas), with grass species as co-dominants.

Previous Work, Notable Species

Many people have collected in and around the DH but are remembered only by their names on herbarium labels. Vernon Bailey made the earliest known collections in 1901 around the Boquillas area (*Bailey 34, 355* TEX-LL), and with the exception of the author of the current study, Barton H. Warnock remains the most prolific collector from the area. Specific scholarly work in the DH has been attempted twice previously as unfinished master's theses, most notably by Miller Talbot, whose collections reside at SRSC and TEX. Tom Rogers (1964) produced an MS thesis dealing with the vegetation of BGWMA, and many of his collections added depth to the current effort.

Only one formal publication focuses on the vegetation of the Dead Horse Mountains: Philip V. Wells, in the course of his packrat midden research, spent time in the DH and subsequently published a paper of his observations during two hikes to Sue Peaks (Wells 1965). The paper includes an excellently characterized description of vegetation patterns and a species list; although incompletely vouchered (C. Morse pers. comm.), the list is still a useful tally of species present at the time.

The most extensive data documenting DH taxa were compiled for an unpublished report (Amos & Giles 1992) completed for the Nature Conservancy when it owned the parcel of property including Brushy Canyon. This property has since been deeded to Texas Parks and Wildlife (TPWD) as part of BGWMA. The report on the Brushy

Canyon flora is the only other intensive, documented work to be done in the DH prior to the current research. Qualitative descriptions of vegetative communities are given in the report, in addition to notes on species of concern tracked by the TPWD. The species list of 276 vascular taxa was compiled using collections and observations made during six, one-day fieldtrips over two years. It includes flowering time, general habitat, and abundance and notes voucher collections made. Only one of the five species of concern noted in the report, *Physaria mcvaughiana* (McVaugh bladderpod), was located growing abundantly in the creekbed of Big Brushy Canyon. The other four species of concern, *Senna orcuttii* (Orcutt senna), *Hedyotis pooleana* (Jackie's bluet), *Perityle bisetosa* var. *scalaris* (stairstep rockdaisy), and *Cirsium turneri* (cliff thistle), were expected to be present and had been located there previously by TPWD biologists.

Species that were of particular import as the current project began included relatively unknown taxa and historically collected species that had not been seen for many years. *Hedyotis pooleana* (Jackie's bluet), a species described as endemic to the Dead Horse, is known from only two collections. Not mentioned in the current literature (Powell 1998, Turner et al. 2003), *Quercus intricata* (Coahuila scrub oak) was collected by Wells (1965) near the summit of Sue Peaks (*Wells s.n.* KANU); this species was previously known to occur in the U.S. only in the Chisos Mountains of BBNP and in the Eagle Mountains of Hudspeth County (Fig. 22). Another historical record, the northern Chihuahuan Desert endemic *Andrachne arida* (Trans-Pecos maidenbush) had not been verified as extant since 1958. Unconfirmed historical reports of *Quercus hinckleyi* (Hinckley oak) should not be entirely dismissed (J. Sirotnak pers. comm.); it currently occurs with *Andrachne arida* in the Solitario, a limestone area 40 mi (64 km) west of the

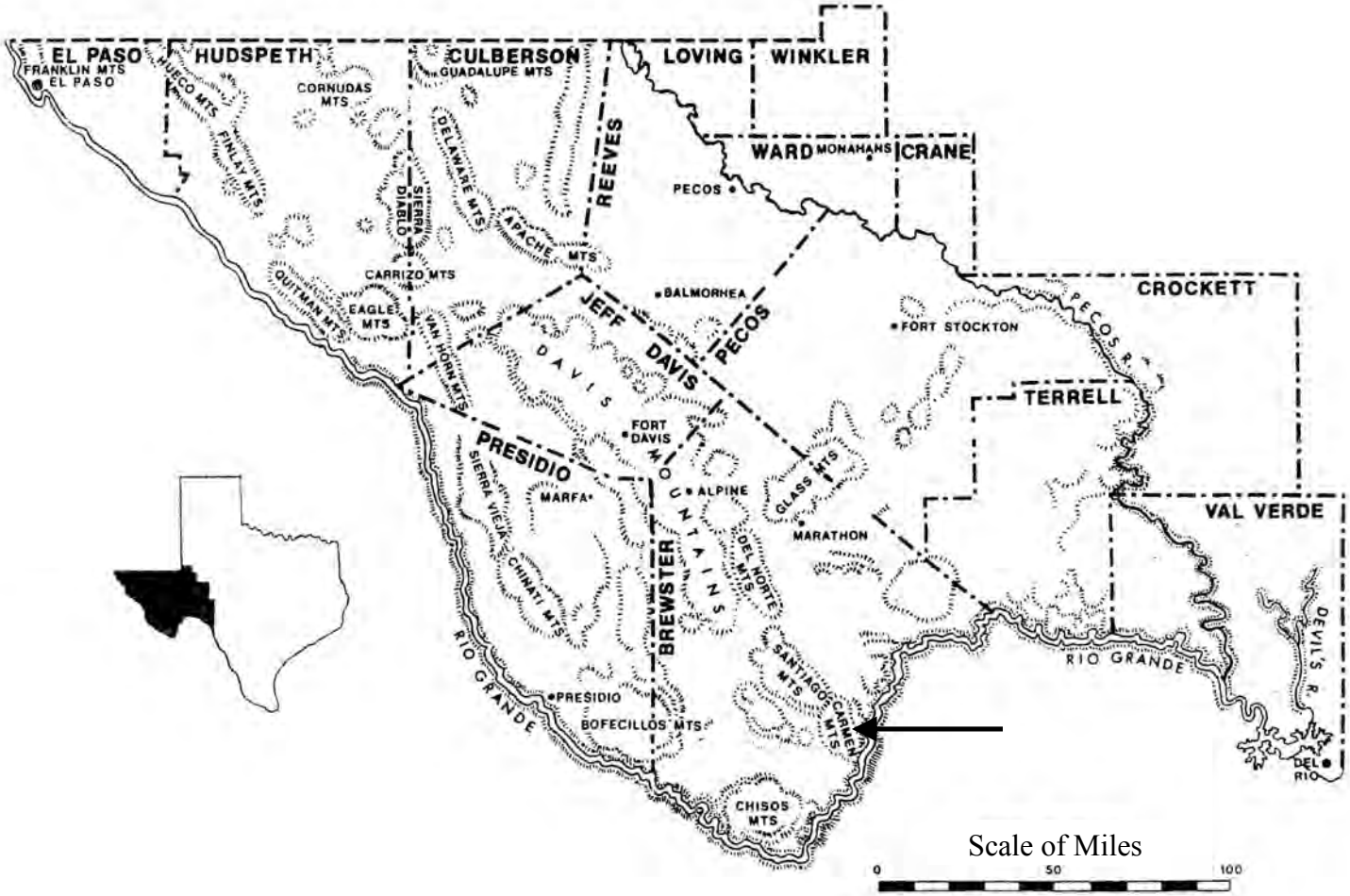

Fig. 22. Schematic map of Trans-Pecos mountain ranges, created for use in the Sul Ross State University herbarium and used by permission. The Dead Horse Mountains are labeled “Carmen Mts”.

DH. This oak species figures abundantly in packrat midden records (Van Devender et al. 1987), indicating that it is a cooler-weather, more mesic species. This could suggest it is relegated to protected niches at the higher elevations, but individuals have been found in the Solitario (Bofecillos Mountains, Fig. 22) at only 3500 ft/1066 m (*BHW 21571* BBRSP).

Other work that relates to DH flora includes a recent, rare-plant project by park personnel (Alex et al. 2006), which has added to the previously known extent of special plant populations (Louie 1996). An overall plant list of BBNP exists (Clelland 2001), in addition to accounts of and a key for BGWMA vegetation (Rogers 1964, Mahler 1971), but these may not adequately represent the full complement of species found in the DH. While useful for determining presence or absence on a larger scale, these reports do not list all collection locations and are not clear as to whether any herbaria were searched to add known species that may occur only within the DH.

The main study objective was to create a collective body of work on the floral composition of the DH, documenting all known vascular plants through field collections and herbarium records. Goals to accomplish this objective included gaining more field-based information on rare and little-known species, obtaining historical records and collections through research, and increasing voucher collections through focused effort in under-botanized areas. Subsequent analysis was used to interpret the DH flora in a regional context, both within the Trans-Pecos and the larger Southwest.

CHAPTER II

METHODS

Herbarium search

Herbaria thought to hold specimens from the DH were contacted and, when possible, electronically searched. These included institutions that sponsored botanists known to collect in the Big Bend, those geographically close to the study area, and those that were otherwise promising and electronically available: Angelo State University (SAT), the Botanical Research Institute of Texas (BRIT), the New York Botanical Garden (NYBG), Sam Houston State University (SHST), Sul Ross State University (SRSC), the Texas A&M University Biology Department herbarium (TAMU), Texas A&M's Tracy herbarium (TAES), Texas State University (SWT), University of Kansas (KANU), University of Texas at Austin (TEX-LL), the University of Texas at El Paso (UTEP), and the on-site holdings of BBNP and BGWMA. Sheet-by-sheet searches were conducted at SRSC and BGWMA.

The relevant herbaria that were part of the Flora of Texas Consortium (SAT, SHST, SWT, TAES, TAMU, TEX-LL,) were searched through the project's website (FTC 2003). The University of Texas, Austin herbarium was also searched on its gateway website (PRC 2006), which had a larger and more current body of digital records available. Specimen information for the majority of Brushy Canyon collections (Amos & Giles 1992) was retrieved by an onsite search of the SAT database. Inquiries

were made to KANU about Philip Wells's possible collections mentioned in his publication (1965). Collections, and their whereabouts, made by William Mahler, previous faculty member at Southern Methodist University and long-time collector at BGWMA, were investigated. The collections of NYBG have the potential to house historical collections from early expeditions to the Big Bend area and were easily searchable online (NYBG 2006).

Search parameters used to limit digital searches were county (Brewster) and, when practical, the following key words, entered individually: alto, Arroyo Venado, Boquillas, brushy, Cow Canyon, dagger, devil's, Dead Horse, dog, Ernst, frog, Hubert, McKinney, ore, persimmon, Sierra Caballo, Sierra Larga, stairway, strawhouse, Stuart, Sue, telephone, tunnel. Names of collectors besides Mahler who are known to have worked in the region were also used as database search parameters: M.S. Young, E. Butterwick, B.H. Warnock, P.V. Wells, O.C. Wallmo, and O.E. Sperry. A spreadsheet was created in Microsoft Excel to house the accumulating specimen records. To populate the spreadsheet, TEX-LL search results were received directly from the curator as text files and converted, the SAT and sheet-by-sheet search results were manually entered, and the rest were downloaded as text files and converted or were copied and pasted directly into the spreadsheet from the internet.

Each entry in the resulting list was then reviewed for accuracy of occurrence within the study area. Any localities that were vague (e.g. "between Hot Springs and Marathon") or did not seem to fall within the study area (e.g. "15 miles down

Boquillas road from Panther Junction") were deleted. Locations not included in the study area, but that were often returned using the above key words, included McKinney Springs, Hot Springs, Roy's Peak, Muskhog Spring, and Dog Flats.

The majority of specimens at institutions outside of SRSC were not examined to verify their identification. All determinations of species found through the digital searches were assumed to be correct unless Turner et al. (2003) did not support that species' occurrence in the DH. Specimens with such suspect records were requested for examination from the relevant institutions, annotated, and included or excluded from the final flora (Appx. A) as appropriate. Unvouchered species that were listed in Wells (1965) or Amos and Giles (1992) and species collected close to but not within the study area were excluded from the DH flora and placed on a "possible" or "unlikely" list of taxa (Appx. B, C). Species that were observed in the field during the current study but were unable to be vouchered were included in the DH flora only if they were within an expected range according to Turner et al. (2003); these are noted accordingly in the annotated list (Appx. A). The resulting "historical" species list was cross-checked against the collections made for the current study, with nomenclature updated and matched as accurately as possible with current taxonomic standards.

Field Collections

Field work occurred between August 2003 and September 2006. An attempt was made to collect in all seasons and throughout the entire range. All species found in flower were collected during every trip. Often sterile specimens were collected, mostly to improve the author's field identification abilities but also to document the presence of an unfamiliar or previously unobserved taxon. Collection of rare species or plants of

uncertain identity and/or distribution was guided by BBNP protocol: no more than 10% of the viable reproductive population of rare plants should be harvested. This could mean no more than 10% of a flowering population in any given area or only one flower out of ten on a lone individual. Most collecting was done within the National Park, due to easier and quicker access to more areas. Access was mainly on foot, but two river trips allowed limited southern access. A few extended, overnight trips were enabled by water caches previously transported into the backcountry by NPS trail crew personnel and packstock.

Sampling areas were chosen based on intricacy of topography such as deep and/or sinuous canyons, unvisited but probably unique areas such as the higher peaks, and otherwise intriguing spots identified on USGS 1:24000 topographic maps. Search methodology was a directed meander (Goff et al. 1982) at each locality visited, focusing on promising microhabitats and moving from patch to patch as the observable species diversity was documented.

Field notes and resulting label data included collection location, habitat, habit and description of notable plant features, and associated species. Spatial location data were often taken onsite, recorded in Universal Transverse Mercator (UTM) projection for zone 13 using a Compaq iPac 3850 with a World Navigator Global Positioning System (GPS). The iPac operating system was ArcPad 6.0.2 for Windows, and data entry was facilitated by an application developed by NPS Geographic Information System specialist Betty Alex in ArcPad Application Builder 6.0.1. When time or GPS satellite availability were

compromised, digital coordinates were approximated and/or generalized post-field in the office, using ESRI's ArcPad 6.0 software and hypsography layers derived from one-meter Digital Elevation Model files for the Big Bend National Park.

Specimens were harvested, placed in a large plastic bag carried by hand during the field trips, and eventually pressed between newspapers and cardboards for several days until dry, either in the back of a closed pickup truck or over light bulbs to provide a heated drying environment. When dry, specimens in their newspaper were labeled with collection number, and name, if known, and then transferred to a freezer for two weeks to kill any insects, larvae, or eggs. When sterilized, the majority of specimens were mounted by SRSC herbarium technicians per SRSC specifications, using watered-down Elmer's glue, acid-free specimen sheets and labels, and packets of regular, white copy paper.

Identifications and Nomenclature

Specimens were identified using multiple sources, including Correll and Johnston (1970), Warnock (1970, 1974, 1977), *Flora of North America* Poaceae and Asteraceae volumes (FNA 2003b, 2006, 2007), Powell (1998, 2000), Yarborough and Powell (2002), Turner et al. (2003), and Powell and Weedin (2004). The majority of specimens were determined by B.L. Turner at the time of writing. The remaining specimens were of common species and thought to be correctly identified by the author. Turner et al. (2003) was the primary source for nomenclature and distributional data, and various online sources (ITIS 2007, MBG 2007) provided author information. Though the *Manual of Vascular Plants of Texas* (Correll & Johnston 1970) could be considered the taxonomic underpinning of this work, numerous updated sources provided the bulk of reference

material, most notably Powell (in prep.) and Powell et al. (in ms.) for non-woody vascular species and genera, the *Flora of North America* volumes for the Poaceae and Asteraceae (FNA 2003b, 2006, 2007), and Powell and Weedin (2004) for the Cactaceae.

CHAPTER III

RESULTS

Herbarium Search

No DH specimens were found at UTEP or BRIT: UTEP had no records in its electronic database, and BRIT's specimens were not available electronically and, unfortunately, were not able to be manually searched for inclusion in this project. Using the Flora of Texas Consortium website (FTC 2003), 64 collections were returned from SAT, two from SHST, 10 from TAES, and only one specimen was held by SWT, while TAMU returned no records. The on-site search of the SAT digital database revealed 245 DH specimens, only three of which were also found during the consortium search. According to its online database, TEX-LL houses 390 DH specimens (PRC 2006). The databased DH holdings of BBNP and SRSC tallied 163 and 579 specimens respectively (Automated National Catalog System 2006). KANU reported 23 known specimens (C. Morse pers. comm.), and NYBG holds five vascular DH collections (NYBG 2006).

The sheet-by-sheet search at SRSC uncovered 490 DH specimens, the vast majority from the BGWMA side, though there were a few BBNP specimens that had escaped documentation in the NPS databasing effort. The Black Gap herbarium houses 203 specimens from the study area. Recent collections made by BBNP staff as part of ongoing projects increased the historical specimen count by 44. The previous reports by Amos and Wells list 22 unvouchered taxa (entities at or below the species level) that fall either in the "possible" or "unlikely" categories.

Taking the above records into account, the historic baseline flora of the DH is based upon 2212 specimens, representing 570 taxa (564 species) from 85 families and 294 genera. Beginning with the first known collections in 1901 by Vernon Bailey, 126 collectors have contributed to the documentation of the Dead Horse flora (Appx. A). Barton H. Warnock has been the most prolific collector; he and Bonnie Amos, with the help of many collecting partners, have contributed more than half of the historically collected specimens.

Vegetation Patterns

For the purposes of this research, six vegetation types are distinguished in the DH, separated generally by elevation and water availability. The three dominant types follow elevational zones, with Mixed Desert Scrub at lower to mid elevations, Sotol-Yucca Grassland at mid to high elevations, and Chaparral appearing in patches at the highest elevations within the Sotol-Yucca Grassland. These types are similar to the previously mentioned vegetation zones created by the USDA for use in classifying soils (Turner 1977). The remaining three vegetation types involve anything riparian-related, including arroyos, canyons, and the Rio Grande corridor. The Sandy-Desert-Arroyo and Desert-Canyon types interlace with and intersect mainly lower elevations of the Mixed Desert Scrub but can allow intermixing of high- and lower-elevation species in steep, protected drainages on mountain slopes. The Rio Grande Riparian Corridor is the only vegetation type that occurs in association with permanently flowing water and mainly occurs within Boquillas Canyon, although the developed areas around RGV have significant riparian

habitats that are important to the diversity of the study area. The six types correlate well to the existing classifications (Table 1) but do have some significant differences and omissions.

Mixed Desert Scrub

The Mixed Desert Scrub vegetation type extends from the lowest elevations to about 4000 ft (1220 m), nearing the higher plateaus within the Dead Horse (Fig. 23). Though certainly there are distinct community associations that occur sporadically within this elevational range, they are so interconnected with the entire matrix that it is easier to refer to the overall community as a whole, discussing notable associations in due course. The lowest elevations and flattest terrain of the park are dominated by *Larrea tridentata* (creosote), which is seen most often on low, foothill approaches and interior basins of the DH. A few other species intermingle, including *Opuntia aggeria* (clumped dog cholla) and *Opuntia grahamii* (Graham dog cholla), *Parthenium incanum* (mariola), *Nama hispidum* (bristly nama), and *Acacia neovernicosa* (viscid acacia).

Flourensia cernua (tarbush) is often cited as being important, even co-dominant, in this ecological zone of the Chihuahuan Desert, but it was rarely seen during this research, perhaps indicating that what is considered *Larrea* Scrub by Henrickson and Johnston (1986) and others is not a true component of the DH vegetation matrix. Also not officially included in the DH is Henrickson and Johnston's Sand Dune Scrub. There are limited sand dunes at the mouth of Boquillas Canyon, but they are not significant enough to support a distinct vegetative zone. It is, however, a unique habitat for a few species including the rare *Chamaesyce golondrina* (Boquillas sandmat) and the sand-

Fig. 23. Examples of the Mixed Desert Scrub vegetation type: a. North Dagger Mountain flats, b. Marufo Vega trail, c. south of Dagger Mountain, d. looking north towards Dagger Canyon, e. ridge above and southwest of Telephone Canyon, f. dam along the Telephone Canyon trail.

loving *Heliotropium convolvulaceum* (phlox heliotrope), *Corispermum americanum* (American bugseed), and *Dalea terminalis* (woolly dalea). Other CDR Desertscrub types (Table 1) that are absent from the DH are the *Prosopis-Atriplex*, Gypsophilous, and Cactus scrubs.

Moving upslope, various shrubs, succulents, and grasses become more important. Species commonly encountered and expected include the following: *Parthenium incanum, Tiquilia greggii* (plume tiquilia), *Prosopis glandulosa* (mesquite), *Condalia* sp., *Ziziphus obtusifolia* (lotebush), *Buddleja marrubiifolia* (butterfly bush), *Leucophyllum minus* (Big Bend silverleaf) and *Leucophyllum candidum* (Boquillas silverleaf), *Viguiera stenoloba* (skeletonleaf goldeneye), *Chrysactinia mexicana* (damianita), *Menodora scabra* (rough menodora), *Polygala* spp. (milkworts), *Croton* spp. (crotons), *Koeberlinia spinosa* (allthorn), *Ephedra aspera* (mormon tea), *Fouquieria splendens* (ocotillo), *Dasylirion leiophyllum* (sotol), *Agave lechuguilla* (lechuguilla), *Euphorbia antisyphilitica* (candelilla), *Chamaesyce* spp. (ground spurge), *Jatropha dioica* (leatherstem), *Yucca torreyi* (Torrey yucca), *Opuntia leptocaulis* (pencil cholla, tasajillo), *Opuntia* spp. (prickly pears), *Echinocactus horizonthalonius* (eagle-claw or turks-head cactus), *Ariocarpus fissuratus* (living rock cactus), *Echinocereus mariposensis* (mariposa cactus), *Bouteloua ramosa*, (chino grama), *B. trifida* (red grama), *Aristida* spp. (three-awns), *Tridens muticus* (hairy tridens), *Dasyochloa pulchella* (fluffgrass), and others. Usually associated with higher elevations, *Hedyotis intricata* (bluet) and *Purshia ericifolia* (heath cliffrose) are sometimes seen at lesser elevations where bedrock outcrops are sufficiently protected. Also intergrading with lower-elevation species is *Dasylirion leiophyllum* (sotol), which begins to occur as low as 3500 ft (1066 m). *Dasylirion leiophyllum* and

Bouteloua ramosa (chino grama) are commonly thought of as occurring in a vegetation type called Sotol Grassland, but these two species occur so widely between lower and high elevations, and with such different associate species, that this name was considered too ambiguous in scope for use in defining DH vegetation dynamics.

Some areas within the Mixed Desert Scrub are dominated by lechuguilla, which can form dense concentrations as it spreads by rhizomes; these areas were even accorded a separate phase within the CDR Desertscrub and Woodlands community by Henrickson and Johnston (Table 1). These patches of lechuguilla are perhaps best developed on rockier, exposed, and well-drained slopes. In many places the plants grow so densely that the only way to walk through the thickets is on top of the plants themselves. *Hechtia texensis* (hechtia) also occasionally forms dense stands, typically on south-facing, steeper slopes with shallow soils and sharply-eroded bedrock outcrops. In addition to the species included in Mixed Desert Scrub, areas with higher concentrations of lechuguilla and/or hechtia often include more obvious occurrences of the following species: *Selaginella lepidophylla* (resurrection fern), *Selaginella wrightii* (Wright spikemoss), *Astrolepis* spp. (starcloak ferns), *Argyrochosma microphylla* (small-leaf false cloak fern), *Calliandra iselyi* (Isely stickpea), *Opuntia rufida* (blind prickly pear), *Opuntia* spp., and others. Other interesting components of the Mixed Desert Scrub, and, actually, all throughout the DH, are the ubiquitous *Selaginella* spp. (spikemoss), biological soil crusts, and various species of ferns. *Selaginella wrightii* (Wright spikemoss) may not, at first glance, be noticed or its extent appreciated. After a good rain, however, this plant unfurls, turns bright green instead of looking yellowed and dead, and makes a majority of inter-rock spaces appear covered by a lush carpet (Fig. 24a). *Selaginella lepidophylla* (resurrection

fern) is well known in the region to turn a previously barren-looking limestone hillside into a riot of verdant growth (Fig. 24b). Biological soil crusts are also important members of the inter-rock spaces, harboring various species of cyanobacteria, mosses, lichens, and other cryptogamic components (Figs. 24c–d). Ferns may be more expected in wetter areas, but they are surprisingly abundant throughout the arid landscape of the DH. Certainly there are habitat preferences, with certain species such as *Asplenium resiliens* (blackstem spleenwort) and *Cheilanthes alabamensis* (Alabama lipfern) occurring only in more protected habitats, but the majority of species are commonly encountered in harsher environments.

Desert Arroyo

Many of the general, Mixed-Desert-Scrub species overlap into the arroyos and canyons that intersect the region, where two xeric-riparian phases are generally distinguishable, according to the amount of moisture available. The Desert Arroyo, or Sandy Arroyo Scrub as named by Henrickson and Johnston (Table 1), occurs in more open, low-elevation drainages. The margins are rich with perennial plants, which often grow into impenetrable thorny thickets across the wash. *Fallugia paradoxa* (apache plume) and *Brickellia laciniata* (splitleaf brickellia) are common species present in the wash cobbles of larger drainages, while *Prosopis glandulosa* (mesquite), *Guaiacum angustifolium* (guayacan), *Forestiera angustifolia* (narrowleaf forestiera), *Celtis pallida* (spiny hackberry), *Lycium berlandieri* (wolfberry), and *Porophyllum scoparium* (shrubby poreleaf) are common throughout.

Fig. 24. Potentially less-appreciated members of the DH flora: a. *Selaginella wrightii* forms a lush carpet covering soil surfaces after good rains; b. *Selaginella lepidophylla* turns hillsides green after a rain; c. lichens grow on top of soil held together with cyanobacteria and fungal hyphae; d. cyanobacteria (dark areas, especially at edges of drainage) are primary colonizers of bare soils and can help to decrease erosion.

Desert Canyon

In rockier habitats and larger drainages and within canyons that provide partial shade, the Desert Canyon vegetation type includes additional species, including *Berberis trifoliolata* (agarita), *Fraxinus greggii* (gregg ash), *Diospyros texana* (Texas persimmon), *Clematis drummondii* (virgin's bower), *Eysenhardtia texana* (Texas kidneywood), *Lippia graveolens* (scented lippia), *Mimosa* spp. (catclaw), *Acacia roemeriana* (Roemer acacia), *Shaefferia cuneifolia* (desert yaupon), *Rhus virens* (evergreen sumac), *Passiflora tenuiloba* (passionflower vine), *Maurandya antirrhyniflora* (snapdragon vine), and *Tecoma stans* (yellow bells). Common wash-associate grasses are *Bothriochloa laguroides* (silver bluestem), *Heteropogon contortus* (tanglehead), *Setaria leucopila* (bristlegrass), and *Aristida* spp. (Fig. 25).

More water-dependent species such as *Ungnadia speciosa* (Mexican buckeye) and *Chilopsis linearis* (desert willow) occur infrequently, restricted to the largest drainages. *Juglans microcarpa* (little walnut) is not a typical DH species within BBNP; it was seen only once at the north end of the range but is reported to be dominant in BGWMA's Brushy Canyon (Amos & Giles 1992). In the same Amos and Giles (1992) report, *Cercis canadensis* var. *mexicana* (Mexican redbud) was listed as a dominant in Brushy Canyon; it was not observed in the National Park portion of the DH. Canyon walls throughout the range provide a unique habitat for cliff-dwelling species, including *Cirsium turneri* (Turner thistle), *Perityle aglossa* (rayless rockdaisy), and *Perityle bisetosa* var. *scalaris* (stairstep rockdaisy).

Fig. 25. Desert Canyon environment: a. Dagger Canyon, b. north of the Barker House.

Rio Grande Riparian Corridor

A more traditional riparian woodland vegetation type exists only along the Rio Grande (Fig. 26), where the consistent water table can support species such as *Populus fremontii* (cottonwood) *Salix* spp. (willows), *Baccharis salicifolia* (seepwillow), and *Phragmites australis* (common reed) and the introduced *Arundo donax* (giant cane) and *Tamarix* spp. (salt cedars). A few solitary individuals of more water-dependent genera (e.g. *Salix*, *Baccharis*, and *Tamarix*) occur in at least one other place in the DH interior: above Ernst Tinaja, where their water-hungry roots may have found a perched water table. Also important along the Rio Grande are *Acacia farnesiana* (huisache), *Nicotiana glauca* (tree tobacco), *Prosopis glandulosa* (mesquite), and *Chilopsis linearis* (desert willow).

The major, non-native species have altered and continue to alter the riparian landscape. Thickets of cane with abundantly dense rhizomes have solidified the river banks, channelizing the watercourse. This creates, in many cases, an irreversible cycle: the channel concentrates the river flow, which increases its velocity and thus erosive power, which, in turn, creates a deeper channel that does not allow flooding over its banks as easily as before. With over-bank flooding decreased due to channelization and a generally reduced flow/flood cycle due to upstream dams, dense canopies of *Arundo donax* (giant cane) and *Tamarix* spp. (salt cedar) are allowed to establish, precluding the formation of native *Salix* spp. (willow) and *Populus* spp. (cottonwood) bosques (Howe & Knopf 1991, Bell 1997).

Fig. 26. Riparian Corridor vegetation along a slightly less-channellized, more flood-prone lee shore on the Rio Grande near Marufo Vega.

Sotol-Yucca Grassland

Found on the higher elevation slopes and plateaus to the highest peaks, Sotol-Yucca Grassland is the dominant vegetation above the Mixed Desert Scrub. The vegetational split seems to occur, at least on the western side of the range, at around 5000 ft (1524 m), where the steep slopes break out onto the main plateau of the DH range. Stuarts Peak, though slightly lower at 4800 ft (1463 m), should also be included, due to its many, unique floristic characteristics, including a diverse lichen flora and, in the DH, the only known populations of two species that are more expected in montane forested vegetation—*Philadelphus microphyllus* (littleleaf mockorange) and *Achnatherum curvifolium* (Guadalupe ricegrass).

The Sotol-Yucca Grassland is a visually distinct zone where large yuccas and sotol stand out from the shrub- and grass-dominated understory. Also known as Izotal, Sotolal, and Rosetófilo (Table 1; Henrickson and Johnston 1986), this vegetation type is considered by some to be shrub-dominant (e.g. Henrickson & Johnston 1986), and, thus, many omit the term "grassland" in official terminology. The DH do seem to have a persistent shrub component dominated by *Dasylirion leiophollym* (sotol), *Nolina erumpens* (beargrass), and *Yucca* spp. (yuccas), even when the grass diversity and abundance increase with elevation (Fig. 27). However, the two life-forms seem to be co-dominant, and the term "grassland" is used here to convey the importance of bunch grasses in the inter-shrub spaces. On the main DH plateau, *Nolina erumpens* becomes a significant, visual member of this group, creating, along with the sotol, large masses of thick vegetation standing almost head high in some places.

The DH are virtually the only area in the park where the giant dagger, *Yucca faxoniana*, occurs. Usually growing at higher elevations, they can easily be seen along the Dagger Flat road. Alhough quantitative data on density or abundance are not within the scope of this study, these giant daggers generally do not seem to occur as densely as in some pictures of this vegetation zone further south in the CDR. The only comparable area observed during the study was in BGWMA, on a higher plateau above the head of Brushy Canyon. The giant daggers on the higher plateaus associated with Sue Peaks did not seem as abundant or as tall as those at the lower-elevation plateau in the Black Gap. This comparison and the aforementioned differences in the plant community of Brushy Canyon lend support to the idea that the highest elevations of the DH limit the moisture-laden air flowing westward from the Gulf of Mexico.

Common plants associated with the Sotol-Yucca Grassland of the DH include *Yucca torreyi* (Torrey yucca), *Yucca rostrata* (beaked yucca), *Yucca thompsoniana* (Thompson yucca), *Nolina erumpens* (beargrass), *Agave lechuguilla* (lechuguilla), *Fouquieria splendens* (ocotillo), *Chrysactinia mexicana* (damianita), *Gymnosperma glutinosum* (gumhead), *Parthenium argentatum* (guayule), *Parthenium incanum* (mariola), *Bouchea spathulata* (spoonleaf bouchea), *Leucophyllum* spp. (silverleafs), *Viguiera stenoloba* (skeletonleaf goldeneye), *Bernardia obovata* (desert myrtlecroton), *Vauquelinia angustifolia* (slimleaf vauquelinia), *Mortonia scabrella* (sandpaper bush), *Zinnia acerosa* (spinyleaf zinnia), *Coryphantha tuberculosa* var. *tuberculosa* (cob cactus), *Coryphantha echinus* (sea urchin cactus), *Neolloydia conoidea* (Texas cone cactus), *Epithelantha macromeris* (common button cactus), *Bouteloua curtipendula*

Fig. 27. Sotol-Yucca Grassland: a.–b. Western ridgetop and saddle near Telephone Canyon, c. western ridge on approach to the DH plateau, d. west aspect near Sue Peaks, e.–f. mesa top NW of Shackelford cabin in BGWMA.

(sideoats grama), *Aristida* spp. (three-awns), *Enneapogon desvauxii* (feather pappusgrass), *Leptochloa dubia* (green sprangletop), *Muhlenbergia tenuifolia* (mesa muhly), and *Selaginella wrightii* (Wright spikemoss).

True grasslands, though included in reviews of Chihuahuan Desert vegetation types, are not functionally a part of the DH flora. These areas that are clearly dominated by the Poaceae without a significant shrub component are more commonly associated with the higher plains around Marathon, Alpine, and Marfa, to the north. In the DH, small areas dominated by grasses do occur but on the scale of remnant patches rather than functional ecosystems. In a small area of Ernst Basin is the previously mentioned stand of *Pleuraphis mutica* (tobosa grass). The area west of Dog Canyon is in a recovery state; bands of grasses and shrubs stretching across the flats with bare soil in between can hardly be called a grassland. Interestingly, Amos and Giles (1992) considered the highest portion of Margaret Basin in BGWMA a "high elevation grassland"; unlike in the scrub-filled Brushy Canyon to the north, only scattered *Yucca faxoniana* (giant dagger) reportedly were present. Presumably, the grass understory of the giant daggers was a *Bouteloua* (grama grass) mix; however, this area was not investigated during the current study. Perhaps some of the other interior basins also support a grassland-like community, but it remains to be documented.

Grasses are important components of the shrubby slopes and higher plateaus, and a few species occurring at the higher elevations are important components of the vast grama grasslands to the north. However, they are not dense or contiguous enough, nor dominated enough by the typical grassland species *Bouteloua eriopoda* (black grama) and *Bouteloua gracilis* (blue grama), to be considered a true grassland. This seems to

follow a general trend of grama grasslands' being established on igneous soils, whereas limestone substrates in similar conditions will support only desert-scrub assemblages (Henrickson & Johnston 1986).

Chaparral

Small pockets of shrub thickets, or chaparral vegetation, occur within the Sotol-Yucca Grassland on plateaus and eastern slopes associated with the high elevations of the Sue Peaks area (Fig. 28). Small and sometimes dense clumps of *Quercus pungens* (sandpaper oak), some *Quercus mohriana* (Mohr shinoak) and *Quercus grisea* (grey oak), *Cercocarpus glaberoides* (mountain mahogany), *Berberis trifoliolata* (agarita) and *Rhus virens* (evergreen sumac) associate with large *Dasylirion leiophyllum* (sotol) and *Nolina erumpens* (beargrass), all overshadowed by occasional but conspicuous *Yucca faxoniana* (giant dagger). Associated species include *Fraxinus greggii* (Gregg ash), *Garrya ovata* (eggleaf silktassel), *Ptelea trifoliolata* (common hoptree), *Bouteloua curtipendula* (sideoats grama), and *Muhlenbergia parviglumis* (longawn muhly). Oaks and other more mesic species also occur at the highest summits and in more protected parts of drainages, even in steep drainages and lower elevations of the western slopes. These micro-niche species include *Malacomeles denticulata* (toothed serviceberry), *Quercus pungens, Fendlera falcata* (cliff fendlerbush), *Fraxinus greggii, Prunus havardii* (Havard plum), and *Cheilanthes* spp. (lip ferns).

Junipers, including *Juniperus coahuilensis* (rose-fruited juniper) and *Juniperus pinchotii* (red-berry juniper), occur sporadically on the high plateaus amongst the chaparral clumps and, very rarely, in large, lower-elevation canyons. Pinyon pines are

Fig. 28. Chaparral, interspersed in Sotol-Yucca Grassland, as thickets of larger shrubs: a. DH plateau looking at Sue Peaks, b. mesa top NW of Shackelford cabin in BGWMA, c. east side of the south sister of Sue Peaks looking into Heath Creek drainage.

rare, documented only at a few eastern-slope locations. These species are probably relicts from the previously extensive juniper-pinyon-oak woodland covering the region between 22,000 and 11,000 years ago. The main pine of the DH is *Pinus remota* (papershell pinyon), a limestone specialist (Powell 1998). Once more widespread, *Pinus remota* (papershell pinyon) in the Trans-Pecos is limited to isolated pockets, being more abundant on the Edwards Plateau and in Mexico. Records of *Pinus cembroides* (Mexican pinyon) in the DH are unusual; it is a higher-elevation taxon, although the two species are known to occur together elsewhere in the Big Bend region (Powell 1998).

Field Collections

Between August 2003 and September 2006, a total of 49 days and approximately 400 hours were spent in the field. The 1549 voucher collections made during those three years, with four observations without vouchers, represent 84 families, 283 genera, and 490 species, totaling 493 taxa when including all subspecies and varieties. The herbaria search revealed 7 families, 58 genera, and 173 species (178 taxa) that were not encountered during the current study. However, many new taxa were added to the historic baseline in this current study, with seven additional families, 45 additional genera, and 120 additional species (121 taxa) vouchered. Fifty-five of those additional species were new records for the DH, representing a 10% increase in known species. The remaining 65 species (67 taxa) were considered simple voucher collections of more common species that were expected to occur or that had been previously observed in the DH but not collected.

These new collections increased vouchered DH taxa by 22%. Four additional species were observed over the past three years that were not vouchered but were included in the final flora. After the combination of the current and historical records, including specimens and observations, and after editing for nomenclatural consistency and currency was done, the total known flora of the DH to date consists of 91 families, 344 genera, and 663 species (671 total taxa when including all subspecies and varieties; Table 4). The flora includes 75 taxa recognized at the varietal or subspecific level. An annotated list, including common name, synonymy, life form, abundance, habitat notes, and a list of all known specimens of every taxon, is given in Appendix A.

The Asteraceae is the most prominent family in the DH, with 80 species (12.0% of the flora) found in the DH (Table 5). Other important families in the DH include the Poaceae (75 species, 11.3%), Fabaceae (52 species, 7.8%), Euphorbiaceae (34 species, 5.1%), Cactaceae (31 species, 4.7%), Pteridaceae (20 species, 3.0%), Boraginaceae (20 species, 3.0%), Brassicaceae (16 species, 2.4%), Nyctaginaceae (16 species, 2.4%), and the Solanaceae (15 species, 2.3%). The eight most species-rich families comprise 50% of the flora while 24 families are represented by an individual taxon. The most abundant genera represented in the DH are *Chamaesyce* (ground spurges, 13 species) and *Dalea* (dalea, 13 species), while *Opuntia* (opuntia, 12 species), *Acacia* (acacia, 8 species), *Bouteloua* (grama grass, 8 species), *Polygala* (milkworts, 7 species), *Cheilanthes* (lip ferns, 7 species), and *Muhlenbergia* (muhly, 7 species) are also well represented (Table 5). Collections were made throughout most of the Dead Horse range, but interior locations, such as along the Strawhouse trail, the eastern end of Telephone Canyon, Margaret Basin, and areas interior to Boquillas Canyon, remain undercollected (Fig. 29).

Table 4. Top 20 plant families and top 10 genera of the Dead Horse Mountains, ranked by number of species.

Family	Number of Genera	Number of Species	Percent of Flora
Asteraceae	52	80	12.1
Poaceae	38	74	11.3
Fabaceae	22	52	7.8
Euphorbiaceae	10	34	5.1
Cactaceae	12	34	4.7
Pteridaceae	5	20	3.1
Boraginaceae	7	20	3.0
Brassicaceae	12	16	2.4
Nyctaginaceae	8	16	2.4
Solanaceae	8	15	2.3
Malvaceae	8	15	2.3
Scrophulariaceae	6	14	2.1
Asclepiadaceae	4	14	2.1
Onagraceae	4	13	2.0
Cyperaceae	6	11	1.7
Verbenaceae	8	11	1.7
Liliaceae	5	10	1.5
Convolvulaceae	5	10	1.5
Lamiaceae	4	9	1.4

Table 4, continued. Top 20 plant families and top 10 genera of the Dead Horse Mountains, ranked by number of species.

Family	Number of Genera	Number of Species	Percent of Flora
Polygonaceae	4	9	1.4
Genus			
Chamaesyce	–	13	2.0
Dalea	–	13	2.0
Opuntia	–	12	1.8
Acacia	–	8	1.2
Bouteloua	–	8	1.2
Polygala	–	7	1.1
Cheilanthes	–	7	1.1
Muhlenbergia	–	7	1.1
Oenothera	–	6	0.9
Heliotropium	–	6	0.9

Table 5. Taxonomic composition of the flora of the Dead Horse Mountains.

Taxonomic group	Families	Genera	Species		Total Species
			Native	Non-native	
Ferns and fern allies	3	7	24	0	24
Gymnosperms	3	3	7	0	7
Monocotyledons	10	57	100	7	107
Eudicotyledons	75	277	508	17	525
Totals	91	345	639	24	663

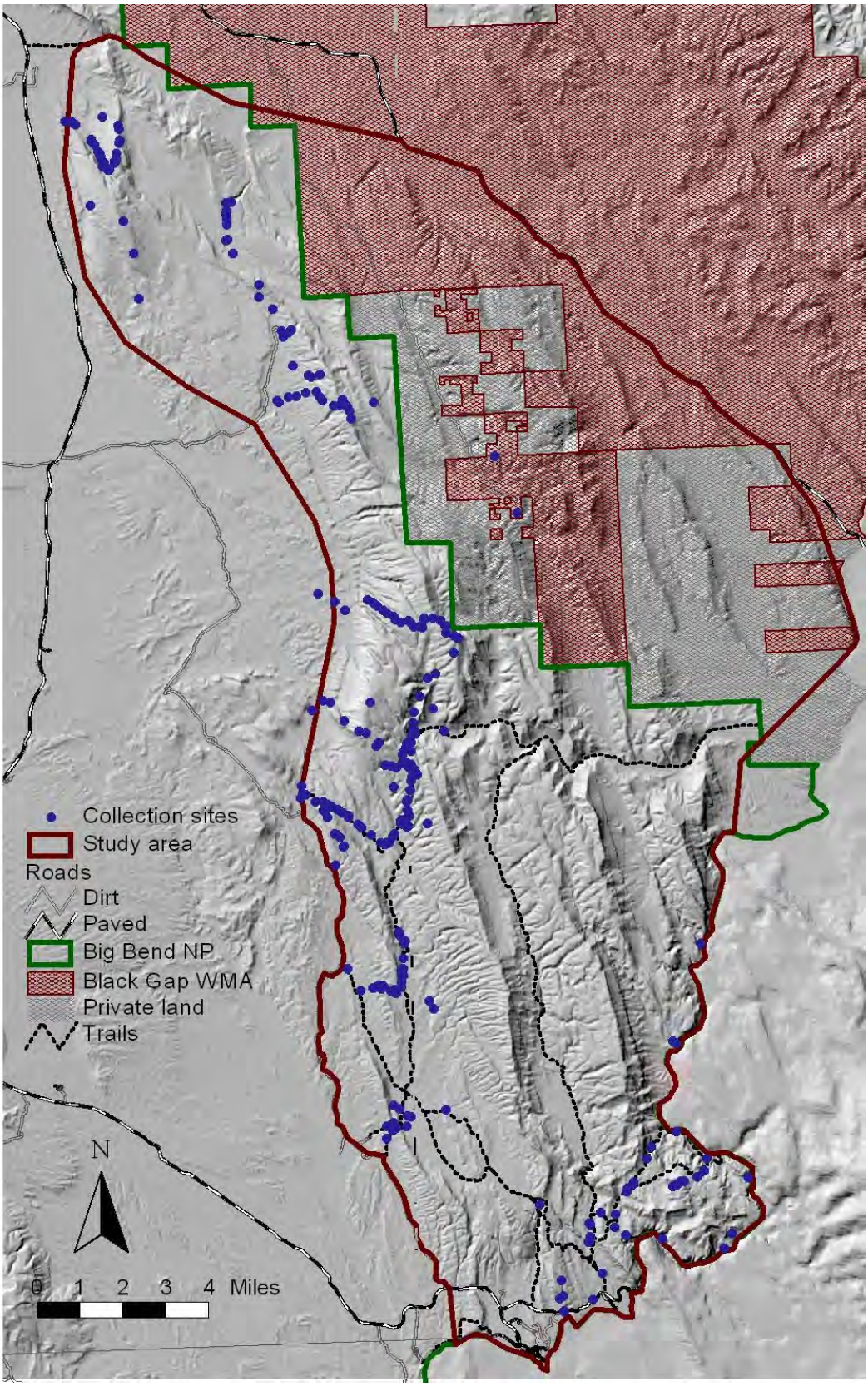

Fig. 29. Study area collection locations between 2003 and 2006.

A taxonomic breakdown of species found in the DH shows that eudicots make up the largest proportion of the flora at 78.9% (Tables 4 & 5). Gymnosperms comprise the smallest portion of the flora after monocots and the ferns and fern allies (Table 5). Perennial herbs were the most abundant life form encountered, followed by annual herbs, shrubs, subshrubs, succulents, vines, and trees (Table 6). Non-native species constitute a small part of the DH flora. The USDA considers 24 species collected in the DH as exotic (USDA 2007; Table 7). Six of those species are considered invasive, and three are state-listed noxious weeds: *Arundo donax* (giant cane), *Tamarix aphylla* (salt cedar), and *Tamarix chinensis* (salt cedar; PTI 2006). Significantly, *Pennisetum ciliare* (bufflegrass), an introduced grass from Africa, is not among the Texas-listed invasives; however, it is a demonstrated threat to native ecosystems throughout the southwest (e.g. TNC 2005) and is listed by the state of Arizona as a noxious weed (AZDA 2005). The fact that it is widely planted in Texas and northern Mexico as a range grass makes its listing perhaps unlikely. Overall, non-native species constitute 3.6% of the DH flora.

Eleven species found in the DH are endemic to Texas, according to the Texas A&M Bioinformatics Working Group and updated taxonomic and distribution information (TAM-BWG 2006; Table 8). The occurrence of *Matelea sagittifolia* (arrowleaf milkvine) is not currently reflected on the referenced website, but it was collected during the present study and also during a recent survey of the Lone Mountain area of BBNP (Fenstermacher et al. 2006). *Lycium puberulum* var. *berberioides* (silvery wolfberry) is also not listed by the Bioinformatics Working Group as occurring in Brewster County but should be; it has been a known member of the BBNP flora for

Table 6. Summary of the Dead Horse Mountain flora by life form (USDA 2007). The semi-succulent members of the Agavaceae, Liliaceae, and Bromeliaceae were included in the shrub category. Eight taxa can be either trees or shrubs depending on the habitat. These were divided equally between the tree and shrub categories. Twenty-eight taxa were listed by USDA as both annual and perennial herbs. These were split evenly between the two herb categories. Graminoid species were included under herbs.

Life Form	Number of Species	Percent of Flora
Trees	27	4.1
Shrubs and semi-succulents	97	14.6
Sub-shrubs	55	8.3
Vines		4.4
Annual herbaceous	1	0.2
Perennial herbaceous	24	3.6
Woody	4	0.6
Herbs		63.6
Perennial	278	41.9
Annual	143	21.7
Cacti and succulents	34	5.1

Table 7. Non-native species (USDA 2007) collected in the Dead Horse Mountains. NAT = naturalized; ! = invasive; !! = state-listed noxious weed (PTI 2006).

Species	Status
Amaranthus blitoides	
Arundo donax	!!
Atriplex rosea	
Cynodon dactylon	!
Echinochloa colona	
Eragrostis lehmanniana	!
Leptochloa dubia	
Malva parviflora	
Medicago sativa	
Melilotus indicus	
Nicotiana glauca	! NAT
Opuntia ficus-indica	
Pennisetum ciliare	
Polygonum persicaria	
Polypogon monspeliensis	
Rumex crispus	
Salsola tragus	!
Sisymbrium irio	
Sonchus asper	
Sonchus oleraceus	

Table 7, continued. Non-native species (USDA 2007) collected in the Dead Horse Mountains. NAT = naturalized; ! = invasive; !! = state-listed noxious weed (PTI 2006).

Species	Status
Sorghum halepense	!
Tamarix aphylla	!!
Tamarix chinensis	!!
Tribulus terrestris	!

Table 8. Species endemic to Texas occurring in the Dead Horse Mountains.

Bouteloua kayi
Chamaesyce golondrina
Hedyotis pooleana
Lesquerella mcvaughiana
Lycium puberulum var. *berberioides*
Matelea sagittifolia
Opuntia aureispina
Oxalis drummondii
Perityle bisetosa var. *scalaris*
Prunus havardii
Tradescantia wrightii var. *glandulopubescens*

some time (Powell 1998). *Hedyotis pooleana* (Jackie's bluet), though included in this DH-endemics list, is another species not listed by the Bioinformatics Working Group, perhaps due to the lack of consensus over its taxonomy. However, whether it is a variety of *Stenaria mullerae* or a species unto itself, the only known populations thus far are within the Dead Horse Mountains. Endemic species account for 1.7% of the DH flora.

Many noteworthy collections were made during the study period. The Wildlife Diversity Program of TPWD, in conjunction with the Texas Conservation Data Center of the Nature Conservancy of Texas, tracks seventeen rare species that were collected in the DH (Table 9; TPWD 2006). Several of these species were collected at new locations. *Bouteloua kayi* (Kay grama; Fig. 30a) was previously known only from one location east of the DH; it is now known that it is one of the dominant grasses at higher elevations near Sue Peaks. *Hedyotis pooleana* (Jackie's bluet; Fig. 30 b–d) was discovered as a new species and first collected in the DH in the mid 1980s. Subsequently it remained uncollected until the present study, in which it was found throughout the majority of the range in higher-elevation bedrock exposures.

Andrachne arida (Trans-Pecos maidenbush; Figs. 31 a–b) was last collected in the DH in the 1960s, and during the study period it was relocated in the general vicinity of the historical collections. One localized population of the diminutive legume *Senna ripleyana* (Ripley senna; Figs. 31 c–d) was discovered, clarifying its status as having remained extant north of the international border since its last documented collection in northern Brewster County in the 1940s. Another historically collected taxon, *Sedum nanifolium* (dwarf stonecrop; Figs.31 e–f), was encountered in shallow soil pockets on the DH plateau. Locally, it was previously known from one collection; it was labeled

Table 9. Rare species collected in the Dead Horse Mountains that are tracked by the Texas Parks and Wildlife Department and the Nature Conservancy of Texas (TNC 2004).

Species	Global rank	State rank	Federal status	State status
Bouteloua kayi	G1	S1		
Perityle bisetosa var. *scalaris*	G2T1	S1		
Streptanthus cutleri	G2			
Coryphantha duncanii [syn: *Escobaria dasyacantha* var. *duncanii*]	G3T1T2	S1S2		
Coryphantha sneedii	G2G3	S2S3		
Echinomastus mariposensis	G2	S2	LT	T
Opuntia azurea var. *aureispina* [syn: *Opuntia aureispina*]	G1	S1		
Andrachne arida	G2	S1		
Chamaesyce golondrina	G2	S2		
Chamaesyce triligulata [syn: *Chamaesyce chaetocalyx* var. *triligulata*]	G5T1	S1		
Croton thermophilus [*C. pottsii* var. *thermophilus*]	G5T2	S1		

Table 9, continued. Rare species collected in the Dead Horse Mountains that are tracked by the Texas Parks and Wildlife Department and the Nature Conservancy of Texas (TNC 2004).

Species	Global rank	State rank	Federal status	State status
Senna orcuttii	G2	S2		
Senna ripleyana	G1	SH		
Phacelia pallida	G2	S1		
Gaura boquillensis	G2	S2		
Polygala maravillasensis	G2	S1		
Hedyotis pooleana [syn: *Stenaria mullerae* var. *pooleana*]	G1T1	S1		

G1 = less than 6 occurrences known globally; critically imperiled, especially vulnerable to extinction; G2 = 6–20 occurrences known globally; imperiled and very vulnerable to extinction throughout its range; S1 = less than 6 occurrences known in Texas; critically imperiled in Texas; especially vulnerable to extirpation; S2 = 6–20 known occurrences in Texas; imperiled in the state because of rarity; very vulnerable to extirpation; SH = historical in Texas, not verified within the past 50 years but suspected to be extant; T = following a global rank denotes the rank for subspecific taxa. Two G or S ranks together (e.g. G2G3; S1S2) indicate that the plant is borderline between the ranks.

Fig. 30. Rare species in the Dead Horse Mountains: a. *Bouteloua kayi* (Kay grama); b. *Hedyotis pooleana* (Jackie's bluet) and example of unique habitat (utilized by both species) created by differential weathering of fossilized marine organisms and the surrounding parent material; c. *Hedyotis pooleana* with woody taproot exposed; d. *Hedyotis pooleana*, plants range in size from this small individual to several times this size, either forming dense mats or sometimes exhibiting more elongated stems and leaves.

Fig. 31. Reconfirmed and newly collected rare species of the Dead Horse Mountains: a.–b. *Andrachne arida* (Trans-Pecos maidenbush) in fruit and flower; c.–d. *Senna ripleyana* (Ripley senna) in flower and fruit, legume is at top center of Fig. 31d; e.–f. *Sedum nanifolium* (dwarf stonecrop), habitat and habit. Fig. 31e. shows a few plants at the lower left of photo in gravel.

Sedum robertsianum and was commonly seen by Warnock in the Del Norte and Glass mountains of northern Brewster County (Warnock 1977). More common in the Mexican highlands, its overall extent in the U.S. is in question, although this species has been observed also on hilltops of the Cox and Guadalupe ranches, about 15 mi (24 km) west of Sanderson (M. Terry pers. comm.).

One taxon, a member of the genus *Galactia* (milkpeas; Figs. 32 a–d), as yet is not identified to the specific level. It does not fit descriptions of known Texan taxa (B. Turner pers. comm.) and is waiting for further review when appropriate herbarium specimens become available. Several populations have been found in several southern DH locations; the plant is seemingly most common near the Rio Grande within Boquillas Canyon. It is a sprawling, procumbent perennial from a central taproot, often growing vine-like within larger, surrounding vegetation. It has dense, silvery pubescence on all vegetative parts but more pronounced on the leaves, those having prominent under-surface veins. The flowers are pink, which is unusual for this genus (B. Turner pers. comm.), with the banner having a green-yellow base. Upon dessication, the petals turn a deep blue-purple, giving no sign they were ever lighter in color. Alhough this taxon may be undescribed, or simply a new record for the U.S., many definitive new records were made during this study. *Seymeria falcata* var. *falcata* (falcate blacksenna; Figs. 32 e–f) was collected for the first time in the United States, actually, in 1994, but it was not recognized until collections for the current study spurred a review of previous collections of its more widespread relative *Seymeria scabra* (limpia blacksenna; Fenstermacher 2006). Eight other species were newly recorded for Brewster County, according to Turner et al. (2003) and known herbarium specimens: *Achnatherum curvifolium*

Fig. 32. Unusual species of the Dead Horse Mountains: a–d: *Galactia* sp. (milkpea), a–b. pink inflorescence, c. dried corolla showing the original pink has faded to blue-purple, d. sprawling habit at base of a *Yucca torreyi* (Torrey yucca), e.–f.: *Seymeria falcata* var. *falcate* (falcate blacksenna), e. habit and habitat, f. flower just emerging from bud.

(Guadalupe needlegrass), *Atriplex rosea* (red orache), *Argemone mexicana* (Mexican pricklepoppy), *Hedeoma serpyllifolia* (Reverchon false pennyroyal), *Matelea sagittifolia* (arrowleaf milkvine), *Maurandya wislizeni* (balloonbush), *Nama dichotomum* (wishbone fiddleleaf), and *Rumex maritimus* (golden dock). Three of these species, *Atriplex rosea*, *Argemone mexicana*, and *Maurandya wislizeni*, were collected by NPS staff in conjunction with the restoration site at the mouth of Boquillas Canyon. Many of the newly collected species for the DH are taxa that normally occur in much less arid conditions at the highest elevations in the Trans-Pecos.

Achnatherum curvifolium is a C3 grass previously known from a restricted range in the Guadalupe Mountains of Texas and New Mexico (Powell 2000). *Nama dichotomum* is another elevation-restricted species, previously known from the Franklin, Davis, and Guadalupe Mountains. Its distribution ranges from Colorado down through the Mexican highlands and into temperate South America (Correll and Johnston 1970; Turner et al. 2003). In addition to the sparsely occurring relict taxa of *Juniperus* (junipers) and *Pinus* (pinyon pines), several other species were found whose presence was not expected in such relatively arid conditions: *Philadelphus microphyllus* (littleleaf mockorange) and additional C3 grasses *Achnatherum eminens* (southwestern needlegrass), *Achnatherum lobatum* (littleawn needlegrass), *Hesperostipa neomexicana* (New Mexico feathergrass), and *Melica montezumae* (Montezuma melicgrass).

Several unique habitats were encountered during the course of the study; they all would profit from further exploration. The remnant tobosa grassland in Ernst Basin was previously mentioned and was unique not only for the *Pleuraphis mutica* (tobosa grass), but also for other species that were collected only there, including *Malvella leprosa*

(alkali mallow), *Leptochloa panicea* (mucronate sprangletop), and *Chamaesyce serpens* (matted sandmat). The possibility of the occurrence of similar sites in other large basins in the DH should be explored, in particular at the northern end of the Ore Terminal trail, in Margaret Basin, and along the Strawhouse trail.

An interesting area was encountered in a high saddle just north and west of Sue Peaks. The saddle, at 5300 ft (1615 m), is a dividing point between two drainages, one flowing north and the other draining the western side of Sue Peaks and flowing south. The vegetation in this area was unique, being completely different than the immediate surroundings of *Dasylirion leiophyllum* (sotol), *Nolina erumpens* (beargrass), *Agave lechuguilla* (lechuguilla), and *Bouteloua* spp. (grama grasses). The soil was finer, deeper, and less rocky than the surroundings; old wire, pieces of wood, and many prehistoric rock flakes and partial tools were found on the ground surface (Fig. 33). Many plant species found there are reminiscent of the tobosa grassland area north of the Rosillos Mountains in the Harte Ranch area of BBNP, *Pleuraphis mutica* (tobosa grass), *Panicum obtusum* (vine mesquite), and *Hoffmanseggia drepanocarpa* (sicklepod rushpea) in particular. Other species making up the unique community included *Sporobolus airoides* (alkali sacaton), *Sporobolus cryptandrus* (sand dropseed), *Aristida adscensionis* (six-weeks three-awn), and *Muhlenbergia arenicola* (sand muhly).

The other habitats deserving of more attention are the unique niches of the high elevation peaks, especially Sue Peaks and Stuarts Peak. They each have different characteristics that make them interesting. Stuarts Peak is rather narrow, with not much area forming the actual summit ridge (Fig. 34). However, many plants collected there

Fig. 33. Environment of the high saddle northwest of Sue Peaks. a–b. prehistoric point bases found on soil surface in saddle area, c. a view of the saddle looking north. Note the fine soil without the typical surface gravel layer, and the lack of the surrounding area's Sotol-Yucca Grassland plants, instead replaced by *Parthenium incanum* (mariola), *Pleuraphis mutica* (tobosa), and several other grass species.

Fig. 34. Views from Stuarts Peak: a. looking south from peak, b. a view of the peak looking north.

were surprising to find in such a seemingly arid location, including *Achnatherum curvifolium* (Guadalupe ricegrass) and *Philadelphus microphyllus* (littleleaf mockorange). The lichen and moss flora on the summit ridge was impressive in its diversity, which was not observed to the same extent anywhere else during the study period. Also notable was that the summit ridge was one of the few places encountered where the cactus *Neolloydia conoidea* (Texas cone cactus) was growing so densely that it was difficult to walk and not be forced to step on some of the plants.

Sue Peaks, though not having a monopoly on harboring all of the unique and unusual discoveries of this study, is the highest spot in the study site. Chaparral is the best developed in this area, with shrub oaks being very common in the whole DH plateau area. The peaks themselves are rather bare of large shrubs, those being relegated to niches between boulders and ledges (Fig. 35). Several species, found only in this area, were observed and collected on a trip following significant rains in the area: *Phemeranthus brevicaulis* (dwarf fameflower), *Ipomoea costellata* (crest-rib morning glory), *Nama dichotomum* (wishbone fiddleleaf), and *Mirabilis linearis* (linearleaf spiderling). These species in addition to others known only from the peaks or the surrounding area, including *Asplenium resiliens* (blackstem spleenwort), *Asclepias sperryi* (Sperry milkweed), *Quercus mohriana* (Mohr shinoak), *Fraxinus cuspidata* (fragrant ash), *Quercus lacyei* (Lacey oak), and *Pinus remota* (papershell pinyon), indicate that conditions, on the whole, are relatively mesic and that the Sue Peaks area may harbor additional, interesting species.

Fig. 35. Views of Sue Peaks: a. south sister from the north, b. north sister from the south.

CHAPTER IV

DISCUSSION

Herbarium Search

It is highly probable that more DH collections exist at various regional herbaria. Digitalizing herbarium holdings is a supremely helpful advent in floristic research; however the digital records are only as good as the data entered. This is relevant for many reasons. Undoubtedly, BRIT has specimens collected in the DH; W. Mahler collected extensively in BGWMA, and after the Southern Methodist University (SMU) herbarium was closed, his specimens, along with the rest of SMU holdings, were donated to BRIT. Unfortunately, these collections are not electronically inventoried. When the staff and funding exist at BRIT to digitalize their records, many more DH specimens will most likely be discovered there. This is a problem at many herbaria, not only at small ones.

The SRSC collection is perhaps the third largest in Texas but is not available in digital format. Computerized specimen information for part of the SRSC collection was available for this study due only to an effort by the NPS in 2001 that compiled a list of known BBNP herbarium specimens. The digital records included all specimens housed in the park museum facility, in addition to those specimens found through a sheet-by-sheet search of SRSC. DH specimens collected on the BGWMA side of the study area were found only through physically searching SRSC. Even the significant herbaria are not digitally accessible in their entireties, a problem caused by the sheer size of their

holdings and the staff time required for data entry. TEX-LL is searchable online, but their entire collection has not been entered into the system. Also, not all databases are created equal: searching the TEX-LL website returned a smaller and perhaps different set of results than a search through the Flora of Texas Consortium website. This is also true for SAT. The onsite search at Angelo State (245 records) and a search of the Consortium website (64 records) resulted in only three records in common. The rest of the returns were all different specimens. Perhaps those from the FTC website have been loaned or gifted to other herbaria, or perhaps the data are lost within the SAT system due to data input errors, a highly possible occurrence when using low-paid, under-skilled, workers or databases that are not sufficiently structured (B. Alex pers. comm.). The availability of herbarium collections through the internet is a boon to the botanical research community, but the limitations should be clearly understood, so that the usefulness and limitations of the resulting data are taken into consideration.

Collector bias is also worth mentioning as a potential, hidden source of under-representing diversity. Not all collectors are interested in common weeds or traveling much beyond easily negotiable access points, whether they be roads, trails, or easy topography. This is reflected in the majority of historical specimens being collected along the periphery of the DH at places such as RGV and Boquillas, in the Ernst Tinaja area, and along the Old Ore Road. That the interior area of Brushy Canyon has many historical collections is likely the result of the jeep road's presence along the drainage. It seems that the only significant departure from easily accessible areas was the visit Wells made to Sue Peaks. The Brushy Canyon survey, although increasing the species list by a great deal, took place within a mile or two of the entry road.

Field Collections

A significant increase in known plant species was attained as a result of the current study. In the entire history of collection efforts in the study area, including those during the past 15 years, there was a significant rise in species found, without any evident leveling of return for effort (Fig. 36). This is to be expected, with much new territory having been covered by the Amos survey of Brushy Canyon in addition to the current work. However, when looking at a curve of new species collected over the past three years, a different picture emerges: there is a slight leveling of new species collected per field-year (Fig. 37).

The tapering return of new species over the course of the current study could be used to indicate that the DH flora is close to being completely sampled. However, it is important to keep in mind the vagaries of desert floras. The precipitation regime over the preceding year, or even longer, has a profound effect on not only the annual flora but also the timing – and even the possibility– of reproductive activity in perennial plants. The search image and the ability of the collector to notice novel taxa are also important. When we consider the results of making repeated visits to one location over several years (Fig. 38), we find that three visits over the same path to the same area during the same season failed to produce any leveling of a species/effort curve. Bearing in mind that after winter rains a completely different cohort of species may exist, there is much potential, not only here but in other areas, to find more species. The potential may vary from site to site, however, based on climate and the inherent diversity-encouraging/limiting properties of the area. In another example, two visits made to the highest peaks in the range differed by exactly one year and only somewhat in route. Additionally, the second visit

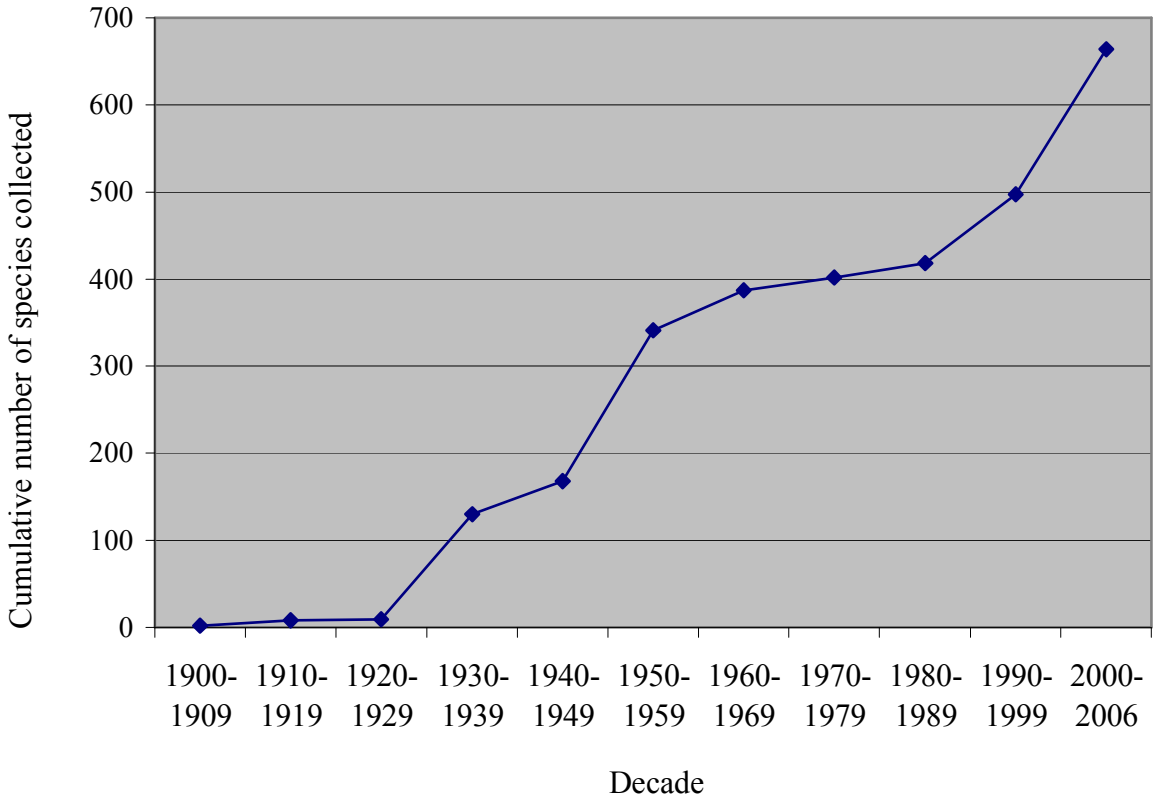

Fig. 36. Species/time trend after 100 years of collecting effort in the Dead Horse Mountains, showing cumulative number of novel species collected by decade.

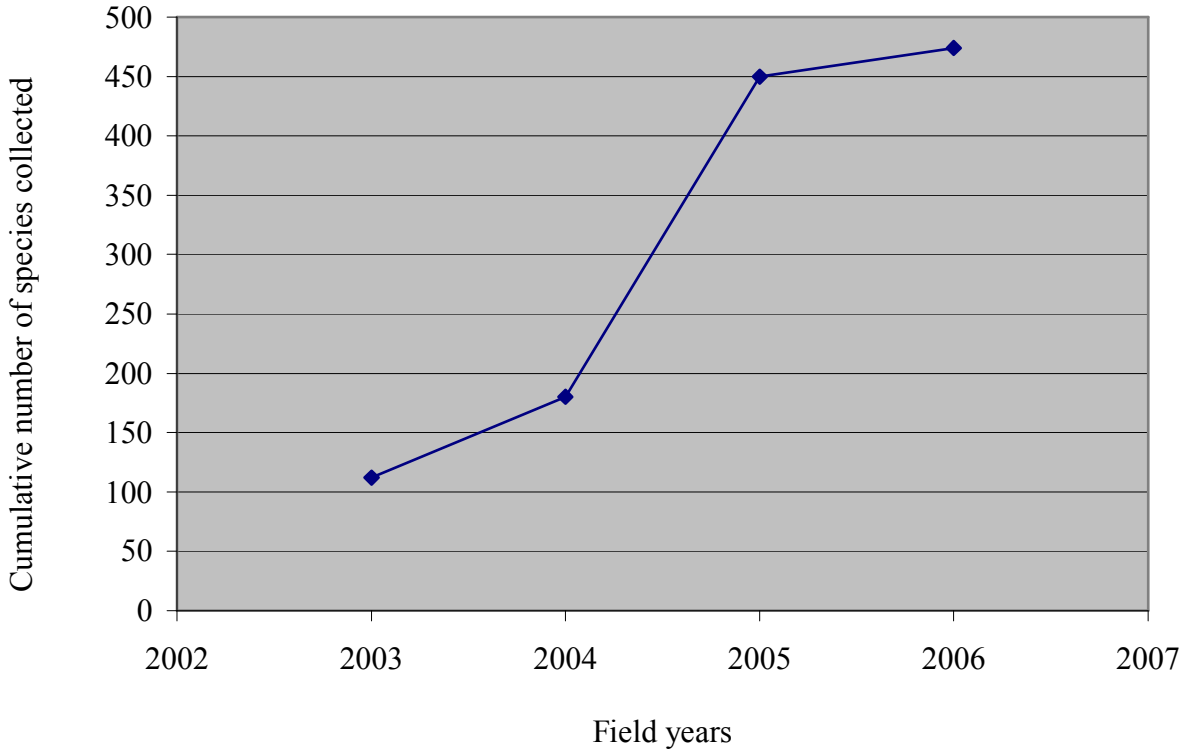

Fig. 37. Cumulative number of species collected between 2003 and 2006 in the Dead Horse Mountains.

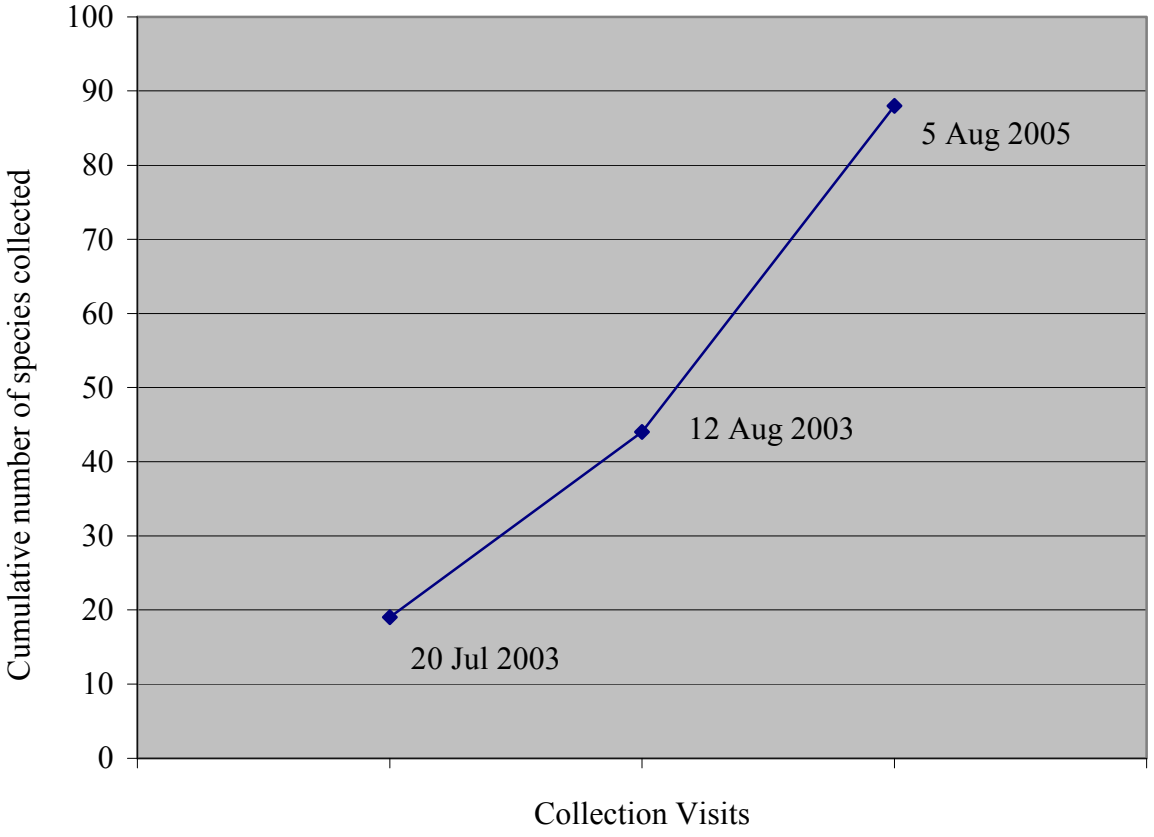

Fig. 38. Species/effort trend after three visits to the Passionflower Canyon area, summer 2003–2005.

followed a significant rainy period such that many new finds were anticipated. Several new collections were made on the second trip, but they numbered about half as many as those made in the initial foray (Fig. 39). Because this area is one of the unique habitats in the range, there may be other important finds yet to reveal themselves, but results thus far suggest that future collection efforts there will continue to diminish over time.

Bearing in mind the potential for discovery of previously unrecorded species for the DH, this study still failed to encounter 127 species previously collected within the study area (Appx. A). This, in some part, is due to sampling away from major riparian habitats like tanks and the Rio Grande and other historical collection localities. including Dog Canyon. There are also thirty-eight species that were not included in the final known flora list, but they are likely to occur, whether in unvouchered observations or as specimens that need verification before being accepted into the official list (Appx. B). These taxa that were not seen by the author in the course of this study amount to 26% of the entire flora, a significant number when attempting to determine floristic completeness.

Previously unrecognized, unique habitats also contribute to the ever-changing nature of a flora. Niches utilized by rare species and newly created habitats can be significant sources of diversity. *Seymeria falcata* var. *falcata* (falcate blacksenna), *Bouteloua kayi* (Kay grama), and *Hedyotis pooleana* (Jackie's bluet) were all seen utilizing a similar habitat niche observed only in the higher DH elevations: small holes that have developed in slick bedrock outcrops of Santa Elena limestone, where it is hypothesized that fossilized marine organisms have weathered out faster than the surrounding parent rock (Fig. 30b). Newly available habitat like that at the Boquillas

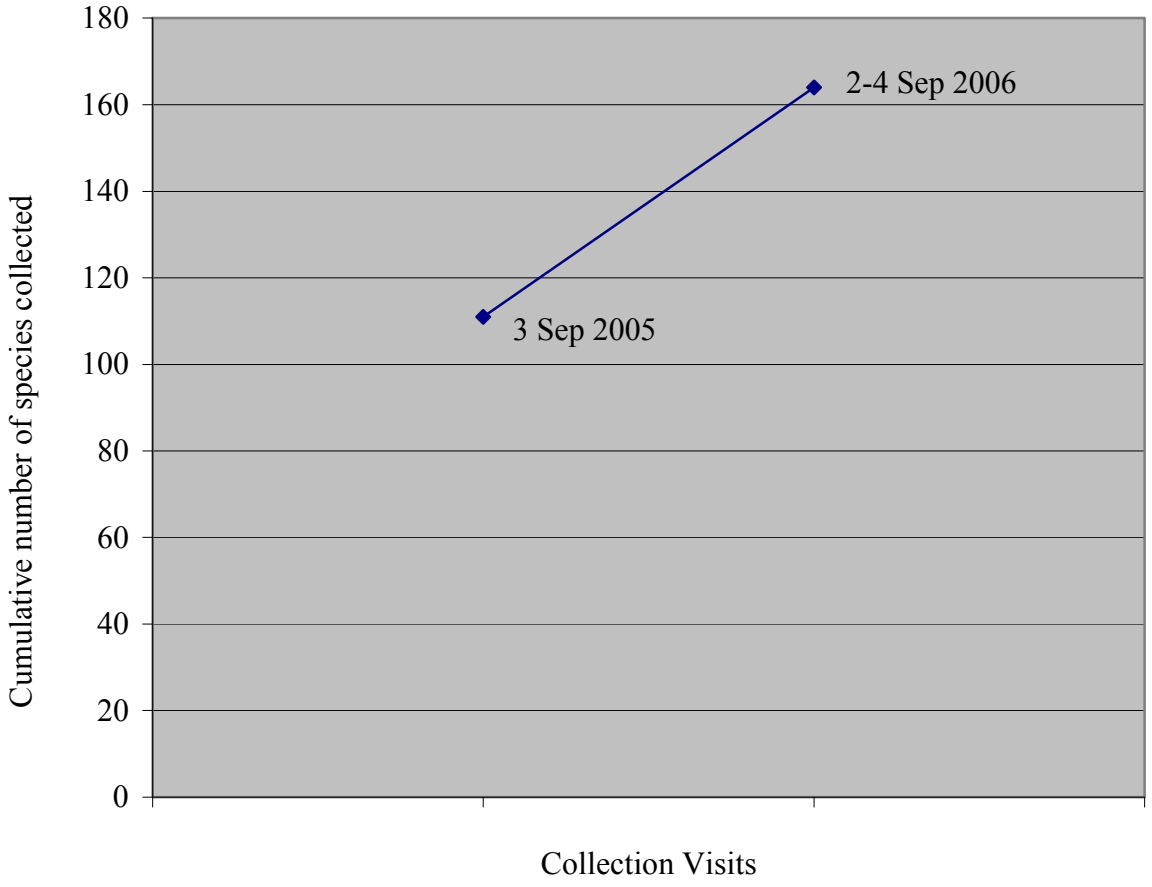

Fig. 39. Species/effort trend after two visits to the Sue Peaks area, September 2005 and 2006.

restoration site, where a dominant canopy of tamarisk and giant cane was removed, allowed species such as *Maurandya wislizeni* (balloonbush) and *Argemone mexicana* (Mexican pricklepoppy) to germinate from seeds that had apparently been dormant in the native seed bank for an unknown number of years until the right conditions for growth occurred. The potential for increasing the size of known floras is great, and as more data become available for the region, predictive equations based on floristic statistics may prove to be a useful method to estimate the completeness of area floras more accurately (Bowers & McLaughlin 1982).

Floristic Analysis and Comparison: Local level

The Dead Horse Mountains are just one range in a larger, regional picture. As a portion of Big Bend National Park, the flora of the DH is 54% of the park's listed total (NPS 1996) yet is found only on 24% of the land area. Clearly, this eastern side of the national park, with its riverine and high-elevation habitats, is an important source of area diversity. But how do the DH compare with similar regional areas? Many initial studies have been done on areas in the Trans-Pecos, but they are not comprehensive enough to accurately represent the true flora of the area (e.g. Carignan 1988), lacking large enough sample areas, an adequate collection history, or both. However, floras of BBNP, BGWMA, and the Solitario have sufficient depth to be useful for exploring floristic relationships of the southern Big Bend region.

The Solitario flora provides an excellent comparison for the DH flora, because it is based on several years of field collections, in addition to a compilation of numerous historical collections. Being located only 40 mi (64 km) west and having a similar limestone substrate, the Solitario could be expected to present a similar floristic picture to

that of the DH. While this is generally true, there are some interesting differences. To begin, both areas share eight of the top 10 families, in terms of percent composition of the flora (i.e. importance; Table 10). In this discussion, the term "importance" denotes a larger proportion of the total number of known species that comprise an area's flora rather than a subjective judgment or statement of overall abundance. The two families not in common in the top 10 make it into the top 13 of the other flora, so the difference is not so great. Asteraceae and Poaceae dominate the two floras and are split slightly more equally in the DH. The Poaceae account for one-third more species in the DH than in the Solitario, which could be a result of the 79% larger area sampled in the DH (40,700:176,800 acres; 16,471:71,548 ha). However, it is more likely a result of the higher elevations encountered in the DH, where many of the different grass species were collected.

This increased habitat sampling may be responsible for the higher proportion of leguminous species in the DH, yet may not be a contributing factor for increasing cacti diversity. While a similar number of cactus species are found in the two areas, almost twice the number of leguminous genera and 39% more leguminous species were found to occur in the DH. This may reflect the importance of the Fabaceae in the Tamaulipan Thornscrub vegetation zone (WWF 2001), found to the east and downriver of the Big Bend area. The DH harbor other Tamaulipan species, and this trend may be a continuation of that influence. Within the Fabaceae, species in the genus *Dalea* are responsible for a large proportion of its diversity in the DH and may be explained by its importance statewide, after the more mesic monocots like *Carex* that are not significant

Table 10. Top 10 families of the Dead Horse Mountains and the Solitario (Hardy 1997), including the number of genera and species recorded in each family, listed in order of species percentage of the total flora for each site.

Dead Horse Mountains	Total genera	Total species	% of flora
Asteraceae	52	80	12.0
Poaceae	37	75	11.3
Fabaceae	22	52	7.8
Euphorbiaceae	10	34	5.1
Cactaceae	11	31	4.7
Pteridaceae	5	20	3.0
Boraginaceae	7	20	3.0
Brassicaceae	12	16	2.4
Nyctaginaceae	8	16	2.4
Solanaceae	8	15	2.3

Table 10, continued. Top 10 families of the Dead Horse Mountains and the Solitario.

Solitario	Total genera	Total species	% of flora
Asteraceae	49	71	13.4
Poaceae	30	55	10.3
Cactaceae	12	33	6.2
Fabaceae	14	32	6.0
Euphorbiaceae	10	28	5.3
Pteridaceae	7	16	3.0
Malvaceae	8	15	2.8
Brassicaceae	10	14	2.6
Solanaceae	8	14	2.6
Scrophulariaceae	7	14	2.6

parts of the arid Trans-Pecos flora (Table 11). The genus *Dalea* may be undercollected in the Solitario. Also undercollected may be *Opuntia* species (prickly pear) in the DH. The recognition of many of the different taxa is highly dependent on detailed understanding of field habits, which the author does not possess. Many hybrids of prickly pear species are probably also present (Powell & Weedin 2004), confounding attempts at accurate identification.

The similar importance of Euphorbiaceae and Pteridaceae in the Solitario and the DH may reflect a tenacious character of the families, persisting through temperature and precipitation inconsistencies. These species may be more evenly dispersed through the landscape: parallel to the increase in the size of the DH flora, there was an equal increase in species of both Pteridaceae and Euphorbiaceae, maintaining a proportion equal to that in the Solitario. The similarity of the sites is also supported by species restricted in their distributions to the local area. As mentioned previously, the rare *Andrachne arida* (Trans-Pecos maidenbush) occurs at both sites, in addition to the Bullis Gap range, east of the DH about 50 miles (Butterwick & Lott [1977]). *Quercus laceyi* (Lacey oak), found in the DH during the current study, is more normally a central-Texas species (Turner et al. 2003). In 1974 it was found in a side canyon of the Solitario, making that the westernmost locality for the species (Hardy 1997).

Broadening the scope to include BBNP and BGWMA (Table 12), the floras generally hold together well as a cohesive body, which is an encouraging sign that the conclusions drawn are based on a well-founded characterization of the regional flora: the Asteraceae and Poaceae are co-dominant, with many families being similarly important throughout the entire southern Big Bend. Of course, differences exist, and, as discussed

Table 11. Genera with the highest number of species occurring in Texas (Turner et al. 2004).

Genus	Number of Species
Carex	96
Cyperus	56
Quercus	48
Eleocharis	42
Chamaesyce	40
Dalea	39
Muhlenbergia	39
Ipomoea	35
Oenothera	32
Astragalus	32
Juncus	30

Table 12. Comparison of top ten families in terms of proportion of flora, between four floras of the southern Big Bend region of Texas (Solitario: Hardy 1994; BBNP: NPS 1996; Black Gap WMA: Mahler 1971).

Dead Horse Mountains	T/sp	% of flora	Big Bend National Park	T/sp	% of flora	Black Gap WMA	T/sp	% of flora	Solitario	T/sp	% of flora
Asteraceae	80	12.0	Asteraceae	168	13.9	Asteraceae	69	12.2	Asteraceae	71	13.4
Poaceae	75	11.3	Poaceae	148	12.2	Poaceae	57	10.1	Poaceae	55	10.3
Fabaceae	52	7.8	Fabaceae	76	6.3	Cactaceae	47	8.3	Cactaceae	33	6.2
Euphorbiaceae	34	5.1	Cactaceae	63	5.2	Fabaceae	34	6.0	Fabaceae	32	6.0
Cactaceae	31	4.7	Euphorbiaceae	51	4.2	Euphorbiaceae	26	4.6	Euphorbiaceae	28	5.3
Pteridaceae	20	3.0	Solanaceae	34	2.8	Boraginaceae	21	3.7	Pteridaceae	16	3.0
Boraginaceae	20	3.0	Brassicaceae	33	2.7	Brassicaceae	19	3.4	Malvaceae	15	2.8
Brassicaceae	16	2.4	Pteridaceae	29	2.4	Verbenaceae	16	2.8	Brassicaceae	14	2.6
Nyctaginaceae	16	2.4	Nyctaginaceae	27	2.2	Solanaceae	14	2.5	Solanaceae	14	2.6
Solanaceae	15	2.3	Boraginaceae	25	2.1	Nyctaginaceae	12	2.1	Scrophulariaceae	14	2.6

T/sp = total species

above, an increased elevational range may be one factor creating those discrepancies in the importance of a given family between floras. Big Bend National Park includes 2000 more feet (610 m) of elevation than the DH and is 2723 ft (829 m) higher than the Solitario, which creates potential for change in family-level statistics. The Chisos Mountains of BBNP support well-developed pinyon-oak-juniper vegetation as well as more montane forests. In comparison with the DH and the Solitario, the increase of elevation range and inclusion of different vegetation types does not influence the status of the Asteraceae and Poaceae in BBNP as the co-dominant families. The fact that the Solitario has a slightly different composition in its top 10 families may signify that the sample area was too small to adequately represent the flora of the larger region, or it may reflect a difference in local conditions, such as complex geology and, thus, substrate, that could produce changes in the dominant flora.

Black Gap is easily comparable to the other floras, being contiguous to BBNP, containing part of the DH, and having all limestone substrate. It does lack about 3000 ft (914 m) of the higher-elevation habitats and contains 50% less land area than the whole of the DH. Those facts notwithstanding, a provisional account of the Black Gap flora (Mahler 1971) supports the main trends already observed but introduces other differences. The top 10 families are similar, and the regional co-dominance of the Asteraceae and Poaceae is supported. However, the current flora of BGWMA does not support the hypothesis that, due to an increased presence of the Fabaceae, Tamaulipan vegetation has a strong influence on the eastern side of the Big Bend: the proportion of the Fabaceae in BGWMA is more similar to that recorded for BBNP and the more westerly-located Solitario. Perhaps more striking are the high percentage of the

Cactaceae, the omission of the Pteridaceae, and the inclusion of the Verbenaceae within the most important families. All of these differences may be artifacts of a plant list that is out of date.

The BGWMA flora used here for comparison is from 1971 and has not been updated to include the significant contributions made during the Brushy Canyon survey nor any other collecting over the past 35 years. The Cactaceae may be more highly represented in Mahler's (1971) list because they are perennial plants and more obvious, and thus more recorded, members of a flora as opposed to, for example, rain-dependent annuals. Cactaceae numbers may also be high because of the long-standing nomenclatural and systematic complexities surrounding the family, that have only recently been comprehensively treated for the area (Powell and Weedin 2004). Upon review, a few species may be deleted due to nomenclatural tidying, but, ultimately, individual specimens would need review to determine whether the species number is artificially inflated.

Ferns are certainly underrepresented in the Black Gap list. Perhaps Pteridaceae was not of interest to the workers involved in compiling the list. The Fabaceae could be undercollected and could very easily rise in importance with a more complete flora, thus better supporting the argument for the spreading influence of eastern vegetation types. This possibility should certainly be pursued, along with validating and updating the species list for BBNP (NPS 1996). As with the Black Gap flora, the conclusions drawn in the current report with respect to the national park flora should be considered

preliminary; the list dates from 1996, and many inconsistencies and omissions no doubt still exist, despite heavy editing in order to get a more accurate accounting of the park's flora for this analysis.

Finalizing any flora is a difficult process, and, even if brought up to date as much as possible, differences in floras may not necessarily be due to inherent dissimilarities. Collector bias, environmental conditions unconducive to collection, or a host of other variables that may remain inscrutable to science can play a part in preventing a flora from being truly complete. For example, the Boraginaceae have more than twice as many species in the DH, and the family is nearly twice as important in the DH as in the Solitario. The reason for this discrepancy is not clear; the borage family is known to be well represented in desert floras (Takhtajan 1986) and perhaps may simply be undercollected in the Solitario, especially considering that this family is well represented in BBNP and BGWMA. In the greater southwestern United States, the Boraginaceae the represent on average 2.9% of the flora (McLaughlin 1986), which is more consistent with other southern Big Bend numbers. However, comparisons between the Big Bend and the greater Southwest are hardly exact parallels.

Floristic Analysis and Comparsion: Regional level

Based on data from 50 floras throughout the southwestern United States, including western Texas, western New Mexico and Colorado, all of Utah, Nevada, Arizona, and southeastern California, the Southwest (SW) was characterized floristically (McLaughlin 1986). In addition to statistics on taxonomic composition, McLaughlin (1986) calculated similarity indices based on the degree of similarity between all 50 floras. The top three SW families are shared with the DH and BBNP, but the Asteraceae

are clearly the dominant family of SW floras (Table 13). Interestingly, the average number of Asteraceae species per SW flora is equal to the number found in the DH. Without knowing the average area of the SW flora sites used to compile the SW data, it is not possible to correlate these numbers exactly. However, it seems that the reduced importance of the Asteraceae in the southern Big Bend is due to the proportional increase in Poaceae species. This demonstrates the connection to the Great Plains grasslands, moving into Texas through the High and Rolling Plains vegetation zones of the Panhandle region. This relationship is visually apparent when traveling through the Trans-Pecos but is also supported by quantitative methods: similarity indices between a central Arizona flora and surrounding floras were computed and demonstrated a strong graminoid connection among parts of Arizona, western Texas, and the central U.S. (Christie 2006).

The Fabaceae are more important locally in the DH but are also important in the SW. This family comprises a larger percentage of the species of the SW flora than in the DH, yet the DH have more fabaceous species (52) than the average for SW floras (28). This increased diversity at the species level may, again, relate to possible peripheral influences of the Tamaulipan Thornscrub flora. Another family discrepancy involves the Cactaceae. This family is more than twice as important in the southern Big Bend as it is for the entire SW, though, because it is a desert-oriented family, the numbers are not representative of what might occur within, for example, the Sonoran Desert alone. Another great discrepancy involves the Polemoniaceae. This family accounts for only

Table 13. Comparison of family percentages between the southern Big Bend of Texas (BGWMA: Mahler 1971; BBNP: NPS 1996; Solitario: Hardy 1994) and the average of 50 southwestern U.S. floras (McLaughlin 1986).

Family	% of total flora for southern Big Bend region				Family	% of total flora, Southwestern U.S.
	BGWMA	BBNP	Dead Horse Mountains	Solitario		
Asteraceae	12.2	13.9	12.0	13.3	Asteraceae	17.1
Poaceae	10.1	12.2	11.3	10.3	Fabaceae	9.0
Fabaceae	6.0	6.3	7.8	6.0	Poaceae	6.6
Euphorbiaceae	4.6	4.2	5.1	5.3	Scrophulariaceae	5.1
Cactaceae	8.3	5.2	4.7	6.2	Brassicaceae	3.8
Pteridaceae	1.4	2.4	3.0	3.0	Polygonaceae	3.2
Boraginaceae	3.7	2.1	3.0	1.5	Boraginaceae	3.0
Brassicaceae	3.4	2.7	2.4	2.6	Polemoniaceae	2.6
Nyctaginaceae	2.1	2.2	2.4	2.3	Cactaceae	2.0
Solanaceae	2.5	2.8	2.3	2.6	Rosaceae	2.0

0.8% of the DH flora, while it is in the top 10 SW families at 2.6%. This may be a more cosmopolitan family that requires more habitats than the southern Big Bend can offer for increased species diversity.

Diversity is even less aligned at the generic level than at the family level. There are only two genera in common within the top 10 genera of the SW and the DH. Only five DH genera make the SW's top-twenty list, and they do not include *Dalea* (dalea), one of the two dominant genera of the DH. The genera that are shared in common with the SW list have more species present in the DH than, on average, throughout the SW. Although the importance of this would be clearer if the average size of the SW flora sites were known, it does seem clear that the DH flora differs significantly from the average diversity of Southwestern floras. The centers of diversity, perhaps, are shifted, or perhaps it is not appropriate to include the southern Big Bend region with the general SW in terms of their floristics. To further illustrate this, a floristic study done in central Arizona, within a pinyon-juniper vegetation type and including only 1312 ft (400 m) of elevation range (Christie 2006), recorded 85% of the most common SW species (McLaughlin 1986). This compares to only 41% similarity with the DH. The differences continue on a broader scale when comparing relative importance of taxonomic groups (Table 14).

At first glance, the importance of ferns and fern allies seems greater in the SW, but if the entire range of habitats within the Big Bend is considered, the percentages become more equal. The entire BBNP, encompassing 2000 ft (610 m) more elevation than the DH, is home to at least seven pteridophyte families (NPS 1996). This increase in diversity makes floristic comparisons with the Southwest more equal, although the

Table 14. Taxonomic summary of Southwestern floristic areas: number of families and species per taxonomic group and the resulting proportion of the entire area flora. SW= data summary from 50 southwestern U.S. floras (McLaughlin 1986); DH= Dead Horse Mountains, Brewster County, Texas; SOL= the Solitario, Brewster and Presidio Counties, Texas; CDR= Chihuahuan Desert Region (Henrickson and Johnston 2004).

Taxonomic group	Families								Species							
	SW	%	DH	%	SOL	%	CDR	%	SW	%	DH	%	SOL	%	CDR	%
Ferns and Allies	9	7	3	3.3	2	2.3	11	7.3	120	2.2	24	3.6	20	3.8	94	2.9
Gymnosperms	3	2.4	3	3.3	2	2.3	4	0.3	36	0.6	7	1.1	4	0.8	36	1.1
Monocots	10	7.9	10	11	10	11.6	20	13.3	723	13.2	107	16.1	74	13.9	515	15.9
Eudicots	105	82.7	75	82.4	72	83.7	125	83.3	4579	83.9	525	79.2	434	81.6	2588	80

increase in species tallied is due to montane populations that are anomalous relicts in the context of the desert landscape surrounding them. The slightly enhanced proportion of gymnosperms in the DH may be explained by the overlapping ranges of similar species that regionally do not often occur together. It is possible that the two juniper species and the two pinyon pine species reported for this flora may be reduced to only one taxon per genus when the specimens can be further examined by experts. Though *Juniperus coahuilensis* (rose-fruited juniper) is the common grassland species and *Juniperus pinchotii* (red-berry juniper) is more expected on rocky slopes and mountains, they are documented to occur together elsewhere in the southern Big Bend (Powell 1998). The sympatric distributions are thought to have been influenced by population expansions and contractions across present-day Texas and Mexico during the Pleistocene glacial periods (Adams 1975).

The pinyon pine species occur together in few localities in the Big Bend, and, despite previous synonomy, they are currently recognized as distinct taxa. Growth habit and cone morphology are important distinguishing characters but, unfortunately, are not present on enough specimens from the DH to make an easy determination. *Pinus cembroides* (Mexican pinyon) is a mainly Mexican taxon, while *Pinus remota* (papershell pinyon) is, perhaps, the most widespread pinyon in the Trans-Pecos (Powell 1998). That these junipers and pines seem to occur in the same location provides more evidence for the DH as a place where multiple floristic influences can be seen.

In a comparison of the relative proportions of monocots and eudicots between regions, the major anomaly relates to the monocots. At the family level the number of monocot families is, on average, equal in the SW and southern Big Bend, but monocots

comprise a larger percentage of the southern Big Bend floras. At the species level, however, the Solitario is more similar to the SW than are the other southern Big Bend floras. It may be that the Solitario constitutes too small an area to accurately reflect regional characteristics, and when one examines the corresponding taxonomic numbers for the CDR, the regional importance of monocots is clarified. The Chihuahuan Desert has a higher percentage of monocots at the family level than the other areas under consideration and is more equal to the DH, BBNP, and BGWMA at the species level (Table 14). This suggests that monocots as a group are more important in the CDR and, by association, northern Mexico, than in the southwestern US. That the southern Big Bend in general reflects this pattern suggests, perhaps, a purer connection to the CDR rather than to other southwestern areas. Apart from this observation's being convenient because the southern Big Bend is located solidly within the CDR, it also provides an avenue to explore the larger connections at work throughout the southwestern U.S.

Phytogeographic Context

Where do these comparisons with the local and regional flora leave the Dead Horse in a floristic context? Of peripheral vegetational areas, the study area has connections to the Great Plains through its significant graminoid flora, which relates back to the Holocene-era dominance of grasslands. The importance of the Tamaulipan Thornscrub area may be seen in the local importance of the Fabaceae and certainly in the many other resident thornscrub species, including *Aloysia gratissima* (beebrush), *Ziziphus obtusifolia* (lotebush), and *Leucophyllum* spp. (silverleaf). For the few Trans-Pecos individuals of the more Tamaulipan species, *Acacia berlandieri* (guajillo), *Croton*

torreyi (Torrey croton), and *Karwinskia humboltiana* (coyotillo), the Rio Grande corridor has most likely provided a conduit of limited habitat that enabled these species to extend their distributions upriver into generally more arid surroundings.

To the northeast, the Edwards Plateau region is perceived by some to overlap floristically with the Trans-Pecos (Gould 1962; Hatch et al. 1990), which seems a natural connection, according to Johnston (1977). He considered the Edwards Plateau a disjunct piece of the Sierra Madre Oriental, the main eastern mountain range of Mexico and the primary floristic influence for the CDR; the Chihuahuan Desert is not simply an extension of the Sonoran region, as Cronquist (1982) suggests. Rzedowski (1973) notes that both desert areas have several endemic genera (21 Sonoran, 16 CDR), suggesting a long period of isolation and autochthonous development. He goes further and provides evidence through similarity indices that the CDR flora shows more affinity to the southern end of the Sierra Madre Oriental than it does to Baja/Sonoran flora. Still, it is hard to delineate the Chihuahuan Desert exactly.

Due to inconsistencies in climate and vegetation, the boundaries of the CDR are not drawn exactly the same by all workers (Henrickson & Johnston 2004). Because there do not seem to be distinctive topographic limits to northern vegetative expansion (McLaughlin 1989), the limits may be more climatically controlled: CDR flora shows more similarity to coastal Peru than to the Great Basin (Rzedowski 1973). This becomes more significant when realizing that the Great Basin, Sonoran, and Chihuahuan Deserts are linked topographically and geologically as members of the Basin and Range province. Anthropomorphic change is another cause behind the hazy borders of the CDR, with

grazing and deforestation hastening the advance of desert scrub (Henrickson & Johnston 2004). However, debatable floristic extent does not imply lack of a central floristic connection.

The individualistic species concept (Gleason 1926) is well known and certainly is logical on a local scale. Each species undoubtedly responds to the range of environmental conditions available and will exploit those niches that are best suited to its own particular needs, independent of the surrounding vegetation. Individual species' tolerances are probably what drove the paleovegetational changes in response to the changing climate. However, as McLaughlin (1986) points out, that is no reason why, on a larger scale, there cannot be found coherent assemblages of species occurring in non-random patterns. Many floristic regions, delineated as places where the climate acts upon the vegetation (as opposed to more local vegetational areas, using delimiters like soils or geography), have been applied to the Southwest (Dice 1943, Cronquist 1982, Takhtajan 1986, McLaughlin 1986, Bailey 1998). The boundaries of these large-scale, ecological regions can be drawn strictly using climate and gross vegetational features (Bailey 1998), by using centers of endemism to create distinct groupings (Cronquist 1982, Takhtajan 1986), which could be called a "scarceness" model, or the focus could be on the degree of overlap between individual floras throughout a region (McLaughlin 1986, 1989). This particular model does not focus on the dominant or rare taxa; rather, it takes into account all extant species and is a method based on "commonness." To this end, McLaughlin's (1986, 1989) work has provided floristically-based evidence supporting many historical floristic distinctions, intuitive or otherwise.

Considering the commonness of floristic data, the Sonoran and Chihuahuan Deserts are seen to be distinct. Interestingly, the area of southeast Arizona and southwest New Mexico, where Henrickson and Johnston (2004) draw an arbitrary border of the CDR because of its perceived transitional nature, is shown to be part of a distinct floristic area that was intuitively recognized by Dice (1943). There is even an outlying connection of this so-called "Apachian" area to the Davis Mountains of the Big Bend, which Turner (1959) reflected in his floristic interpretation of the area. In support of this connection, the Davis Mountains, based on a subset of its flora (Larke 1989), has a family profile more similar to the Southwest—and is located more closely to the core of the Apachian element—than to floras in the southern Big Bend. As discussed, the Asteraceae dominate the flora of the SW, as opposed to being co-dominant with the Poaceae as in the southern Big Bend. Comparison with floras covering larger areas, such as the entire Davis Mountains region, the entire Big Bend National Park, and the CDR as a whole, would be more informative; further work will be possible once these floras are completed and available for further research. However, at this point these relationships pose interesting questions.

The Apachian floristic element is thought to be autochthonous but allied to the Sierra Madre Occidental (McLaughlin 1989). Perhaps during the expansions and contractions of vegetation communities in response to Pleistocene climate change, this Apachian center extended its influence into the Big Bend. As many as 25 glacial-interglacial periods have affected the southwest (Henrickson & Johnston 2004), allowing more temperate plant species to expand into the Big Bend region from both the north and south. In the Chisos Mountains of BBNP, *Pseudotsuga menzezii* (Douglas-fir) and

Populus tremuloides (quaking aspen) occur with the Mexican montane species *Cupressus arizonica* (Arizona cypress) and what is believed to be *Ponderosa arizonica* (Arizona ponderosa pine; Powell 1998). In the DH, cooler-climate species that may be remnants of glacial expansion include *Achnatherum curvifolium* (Guadalupe ricegrass) from the north and the Mexican pinyons from the south. In warmer times, the desert scrub and more tropical species expanded from the south. These climate fluctuations allowed for speciation through isolation, but there would have been more opportunities for diversification in the southern CDR, away from more extreme climate changes coming from the continental interior (Van Devender 1986).

The California floristic area is suggested by Raven and Axelrod (1978) to have a similar history, with a high center of diversity where speciation was allowed by long-term stable evolution, where "old" species were able to persist, even as bursts of speciation occurred to exploit new niches created by climate change (the uplift of the Sierra Nevada and a shift to Mediterranean climate on the coast). Both long-term species and "neoendemics" were able to persist in California and the southern CDR, creating areas of high endemism and species/genus ratios. Any discussion of speciation must acknowledge that the process is not simply a function of time or climate. Life forms, breeding systems, and genetics are also critical in producing differential speciation abilities (Grant 1958).

The resulting diversity can be measured, in one sense, by the species-per-genus ratio: high for the California floristic area (5.7) and then declining slightly for the Sonoran Desert (3.3), the CDR (3.8), and Texas (3.9), as noted in Raven and Axelrod (1978) and Henrickson and Johnston (2004). The Big Bend ratios are much lower: Davis

Mountains 1.5 (Larke 1989); Solitario 1.8 (Hardy 1997); DH 1.9; and BBNP 2.3 (Worthington 2001). The smaller size of the floras may limit the full expression of this view of diversity, but that, in itself, may be the limiting factor. The areas with high habitat diversity in the Big Bend, which are thus often the focus of floristic research, are centered around mountain ranges, which are highly isolated from each other by large expanses of desert terrain. Where places such as the more equable southern CDR may have benefited from the oscillating climate (in terms of increased speciation), the persistence of diversity in the Big Bend region may have been hindered by the extinction of isolated populations left over from previous expansions and contractions.

Relicts persisting at the highest elevations in the DH hint at the complex history of environmental response to climate change through recent geologic history. The Big Bend region, including the DH, can be seen as a transition area between several floristic regions, with its higher elevations providing habitat for many isolated populations that are much more extensive elsewhere. Instead of providing equable conditions over the long term, which could have allowed for steady progress of evolution in addition to speciation into available niches, extinction may have been a more effective mechanism than speciation in affecting today's floristic diversity in the Big Bend. More floristic study is warranted for the region. Beyond simply improving baseline knowledge of the Trans-Pecos flora, previous floristic work (McLaughlin 1986, 1989) should be revisited and improved by updating the original data, since several Trans-Pecos floras have increased by 40–50% since the 1980s (Worthington 2001, F. Armstrong pers. com.). A forthcoming review of North American floristic relationships may address these changes (McLaughlin 2007). Regionally, similarity index studies similar to those by McLaughlin

(1986, 1989) and, especially, Christie (2006) could be used to elucidate in more detail the floristic influences on the Big Bend region and might help to more concretely identify the distinctions between CDR provinces. The completion of the current Dead Horse Mountains flora is an important step towards a more complete understanding of West Texas regional floristic relationships.

CHAPTER V

LITERATURE CITED

Adams, M.B. 1978. From darkness into light. Pioneer Book Publishers, Seagraves, TX.

Adams, R.P. 1975. Numerical-chemosystematic studies of infraspecific variation in *Juniperus pinchotii*. Biochem. Syst. & Ecol. 3:71–74.

Alex, B.L., A. Leavitt, J. Timmer, and J. Sirotnak. 2006. Final report on the sensitive plant project, Big Bend National Park, Texas, Field Seasons: June 2003–April 2006. Science & Resource Management, Big Bend National Park, Texas. Unpublished report to the National Biological Infrastructure Inventory, U.S. Geological Survey, Washington, D.C.

Alex, T. 1990. Big Bend Archaeology pamphlet. Big Bend Natural History Association, Big Bend National Park, TX.

Amos, B. and D. Giles. 1992. Survey of the vascular plants of Brushy Canyon. Unpublished report to the Nature Conservancy of Texas, Fort Davis.

Anthony, M. 1956. The *Opuntiae* of the Big Bend region of Texas. Amer. Midl. Naturalist 55:225–256.

Arizona Department of Agriculture [AZDA]. 2005. Prohibited, regulated, and restricted noxious weeds website. URL: www.azda.gov/PSD/quarantine5.htm.

Automated National Catalog System [ANCS+]. 2006. The museum collection management system of the National Park Service. Big Bend National Park specimen records. Re:discovery Software, Inc., Charlottesville, VA.

Bailey, R.G. 1998. Ecoregion map of North America. United States Fish and Wildlife Service misc. pub. 1548.

Barneby, R.C. 1977. Daleae imagines. Mem. New York Bot. Gard. 27:1–891.

Bell, G. 1997. Ecology and management of *Arundo donax*, and approaches to riparian habitat restoration in Southern California. In: J.H. Brock, M. Wade, P. Pysek, and D. Green eds. Plant invasions: studies from North America and Europe. Blackhuys Publishers, Leiden, Netherlands.

Bowers, J.E. and S.P. McLaughlin. 1982. Plant species diversity in Arizona. Madroño 29:227–233.

Brown, D.E. (ed). 1994. Biotic communities: southwestern United States and northwestern Mexico. University of Utah Press, Salt Lake City.

Bryson, R.A. and W. Wendland. 1967. Tentative climatic patterns for some late glacial and post-glacial episodes in central North America. In: S.J. Mayer-Oakes, Jr., ed. Life, land, and water, University of Manitoba Press, Winnipeg.

Butterwick, M. and E. Lott. [1977]. A botanical survey of the Bullis Gap range – San Francisco Canyon area, Brewster County, Texas. Unpublished report, Natural Area Survey series, University of Texas, Austin.

Butterwick, M. and S. Strong. 1976. A vegetational survey of the Solitario. In: Lyndon B. Johnson School of Public Affairs. The Solitario: a natural area survey, No. 9. Lyndon B. Johnson School of Public Affairs, University of Texas, Austin.

Carignan, J.M. 1988. Ecological survey and elevational gradient implications of the flora and vertebrate fauna in the northern Del Norte Mountains, Brewster County, Texas. MS Thesis, Sul Ross State University, Alpine, TX.

Christie, K. 2006. Vascular flora and floristic analysis of the lower San Francisco Volcanic Field, Coconino County, Arizona. MS Thesis, Northern Arizona University, Flagstaff.

Clausen, R.T. 1981. Variation of species of *Sedum* of the Mexican cordilleran plateau. Robert T. Clausen, Ithaca, NY.

Clelland, R. 2001. Inventory of vascular flora of the Big Bend National Park. Big Bend Natural History Association, Big Bend National Park, Texas.

Cochran, R.A. and F.L. Rives. 1985. Soil survey of Big Bend National Park, part of Brewster County, Texas. United States Department of Agriculture, Soil Conservation Service, in cooperation with United States Department of Interior, National Park Service, and Texas Agricultural Experiment Station, College Station.

Correll, S. and M. C. Johnston. 1970. Manual of the vascular plants of Texas. University of Texas, Dallas.

Cronquist, A. 1982. Map of the floristic provinces of North America. Brittonia 34:144–145.

Dice, L.R. 1943. The biotic provinces of North America. University of Michigan Press, Ann Arbor.

Fenstermacher, J. 2006. *Seymeria falcata* (Scrophulariaceae), a new record for Texas and the United States. Sida 22:811–812.

Fenstermacher, J., A. Leavitt, J. Sirotnak, and W. Weckesser. 2006. Floristic inventory of proposed mountain bike trail in Big Bend National Park, Texas: Survey 1 – late summer/rainy season. Unpublished report to the Science and Resource Management division, Big Bend National Park, TX.

Flora of North America Editorial Committee (eds.) [FNA]. 2002. Flora of North America north of Mexico, Vol. 26: Magnoliophyta: Liliidae: Liliales and Orchidales. Oxford University Press, New York, NY.

Flora of North America Editorial Committee (eds.) [FNA]. 2003a. Flora of North America north of Mexico, Vol. 4: Magnoliophyta: Caryophyllidae, part 1. Oxford University Press, New York, NY.

Flora of North America Editorial Committee (eds.) [FNA]. 2003b. Flora of North America north of Mexico, Vol. 25: Magnoliophyta: Commelinidae (in part): Poaceae, part 2. Oxford University Press, New York, NY.

Flora of North America Editorial Committee (eds.) [FNA]. 2006. Flora of North America north of Mexico, Vols. 19–21: Magnoliophyta: Asteridae: Asteraceae, parts 1–3. Oxford University Press, New York, NY.

Flora of North America Editorial Committee (eds.) [FNA]. 2007. Flora of North America north of Mexico, Vol. 24: Magnoliophyta: Commelinidae (in part): Poaceae, part 1. Oxford University Press, New York, NY.

Flora of Texas Consortium [FTC]. 2003. Digital flora of Texas herbarium specimen browser, version II. URL: www.texasflora.org/dfthsbbase.htm.

Fulcher, W. 1959. The way I heard it: tales of the Big Bend. University of Texas Press, Austin.

Funk, V.A. and K.S. Richardson. 2002. Systematic data in biodiversity studies: use it or lose it. Sys. Biol. 51:303–316.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bull. Torr. Bot. Club 53:7–26.

Goff, F.G., G.A. Dawson, and J.J. Rochow. 1982. Site examination for threatened and endangered plant species. Environm. Managem. 6:307–316.

Gould, F.W. 1962. Texas plants—a checklist and ecological summary. Texas Agricultural Experiment Station, Texas A&M University, College Station.

Gould, F.W. 1975. The grasses of Texas. Texas A&M University Press, College Station.

Grant, V. 1958. The regulation of recombination in plants. Cold Spring Harbor Symp. Quantit. Biol. 23:337–363.

Hardy, J.E. 1997. Flora and vegetation of the Solitario dome, Brewster and Presidio Counties, Texas. MS Thesis, Sul Ross State University, Alpine, TX.

Hatch, S.L., K.N. Gandhi, and L.E. Brown. 1990. Checklist of the vascular plants of Texas. Miscellaneous Publication 1655, Texas Agricultural Experiment Station, Texas A&M University, College Station.

Haynie, S.D. 2000. A floristic analysis of Fort Davis National Historic Site, Fort Davis, Texas. MS Thesis, Sul Ross State University, Alpine, TX.

Henrickson, J. 2003. Studies in *Glandularia* (Verbenaceae): the *Glandularia quadrangulata* complex. Sida 20:953–967.

Henrickson, J. 2005. A new species of *Leucospora* (Scrophulariaceae) from the Chihuahuan Desert of Mexico. Aliso 24:435–439.

Henrickson, J. and M.C. Johnston. 1986. Vegetation and community types of the Chihuahuan Desert. In: J.C. Barlow, A.M. Powell, and B.N. Timmermann, eds. Second symposium on resources of the Chihuahuan Desert Region, United States and Mexico. Chihuahuan Desert Research Institute, Alpine, TX.

Henrickson, J. and M.C. Johnston. 2004. A Flora of the Chihuahuan Desert Region. Unpublished manuscript, edition 1.5, CD version. University of Texas, Austin.

Howe, W.H. and F.L. Knopf. 1991. On the imminent decline of Rio Grande cottonwoods in central New Mexico. SouthW. Naturalist 36:218–224.

Integrated Taxonomic Information System [ITIS]. 2007. Online database. URL: http://itis.gov.

Johnston, M.C. 1977. Brief resume of botanical, including vegetational, features of the Chihuahuan Desert Region with special emphasis on their uniqueness. In: R.H. Wauer and D.H. Riskind, eds. Transactions of the symposium on the biological resources of the Chihuahuan Desert Region, United States and Mexico. U.S. Department of the Interior, National Park Service transactions and proceedings series, number three.

Langford, J.O. with F. Gipson. 1995. Big Bend, a homesteader's story. University of Texas Press, Austin.

Larke, J.O. 1989. Flora and vegetation of the Forbidden Mountains area, Jeff Davis County, Texas. MS Thesis, Sul Ross State University, Alpine, TX.

Louie, D. 1996. The rare and threatened plant species of Big Bend National Park, Texas. MS Thesis, Sul Ross State University, Alpine, TX.

Mahler, B. 1971. Keys to the vascular plants of the Black Gap Wildlife Management Area, Brewster County, Texas. Privately published by Wm. F. Mahler, Dallas, TX.

Maxwell, R.A. 1979. The Big Bend of the Rio Grande: a guide to the rocks, geologic history, and settlers of the area of Big Bend National Park. The University of Texas at Austin, Bureau of Economic Geology, Guidebook 7.

Maxwell, R.A. 1985. The Big Bend Country: a history of Big Bend National Park. Big Bend Natural History Association, Big Bend National Park, TX.

Maxwell, R.A and J.W. Dietrich. 1965. Geology of the Big Bend area, Texas with road log and papers on the natural history of the area. Fieldtrip guidebook publication 65–51. West Texas Geological Society, Midland.

Maxwell, R.A., F.T. Lonsdale, R.T. Hazzard, and J.A. Wilson. 1967. Geology of Big Bend National Park, Brewster County, Texas. The University of Texas at Austin, Bureau of Economic Geology, pub. no. 6711.

McDougall, W.B. 1936. Special report: preliminary report on the vegetation of the Dead Horse Mountains, Big Bend area of Texas. Unpublished report held by the National Archives and Records Administration, Rocky Mountain Region, Denver, CO.

McLaughlin, S.P. 1986. Floristic analysis of the southwestern United States. Great Basin Naturalist 46:46–65.

McLaughlin, S.P. 1989. Natural floristic areas of the western United States. J. Biogeogr. 16:239–248.

McLaughlin, S.P. 2007. Tundra to tropics: the floristic plant geography of North America. Sida, Bot. Misc. 30. Botanical Research Institute of Texas, Fort Worth.

Missouri Botanical Garden [MBG]. 2007. VAScular Tropicos nomenclatural database, Release 1.5. URL: http://mobot.mobot.org/W3T/Search/vast.html.

Morafka, D.J. 1977. A biogeographical analysis of the Chihuahuan Desert through its herpetofauna. Biogeographica (The Hague) 9. Dr. W. Junk B.V. Publishers, The Hague, Netherlands.

Moustafa, A.R. 1988. Structural geology of the Sierra del Carmen, Trans-Pecos, Texas. Geologic quadrangle map no. 54. Bureau of Economic Geology, University of Texas, Austin.

National Park Service [NPS]. 1996. The vascular flora of Big Bend National Park, Texas. In-house publication prepared by the Science and Resource Management Division.

National Park Service [NPS]. 2003. Archives, administrative history, Big Bend National Park. Chapter 11: discovering nature's way: scientific research and resource protection, 1936. URL: www.nps.gov/archive/bibe/adhi/adhi11b.htm.

National Park Service [NPS]. 2004. Basic park map. URL: www.nps.gov/bibe/planyourvisit/upload/BIBEmap3.pdf.

National Park Service [NPS]. 2006. Web query of the National Park Service Visitor Report, internal website. URL: http://165.83.32.36/mpur/reports.

The Nature Conservancy [TNC]. 2005. The Global Invasive Species Initiative red alert archive: weed alert website: http://tncweeds.ucdavis.edu/alert/alrtcenc.html.

Neibuhr, E. 1936. The Excavation of Chisos 8:2, August 24 to 28, 1936. In: E.K. Reed, ed. Special report of archaeological work in the Big Bend. Unpublished report submitted to the National Park Service, Region Three, Santa Fe.

Neilsen, R.P. 1986. High-resolution climatic analysis and southwest biogeography. Science 232:27–34.

Nesom, G. and B.L. Turner. 1995. Systematics of the *Sedum parvum* group (Crassulaceae) in northeastern Mexico and Texas. Phytologia 79:257–268.

New York Botanical Garden [NYBG]. 2006. New York Botanical Garden international plant science center virtual herbarium website. URL: http://sciweb.nybg.org/science2/hcol/allvasc/index.asp.

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

Pearson, J. (ed). 1990. Hikers guide to the trails of Big Bend National Park. Big Bend Natural History Association, Big Bend National Park, TX.

Pinkava, D.J. 1984. Vegetation and flora of the bolson of Cuatro Cienegas region, Coahuila, Mexico: IV. Summary, endemism and corrected catalogue. J. Arizona-Nevada Acad. Sci. 19:23–47.

Plant Resources Center, University of Texas at Austin [PRC]. 2006. Flora of Texas TEX-LL database. URL: http://129.116.69.198:427/Tex.html.

Plumb, G.A. 1991. Assessing vegetation types of Big Bend National Park, Texas for image-based mapping. Vegetatio 94:115–124.

Plumb, G.A. 1992. Vegetation classification of Big Bend National Park, Texas. Texas J. Sci. 44:375–387.

Poole, J.M., J.R. Singhurst, D.M. Price, and W.R. Carr. 2007. A list of the rare plants of Texas, January 2007 edition. Wildlife Diversity Program, Texas Parks and Wildlife Department and the Nature Conservancy of Texas, Austin and San Antonio.

Poole, J.M., W.R. Carr, D.M. Price, and J.R. Singhurst. [in press.] Rare plants of Texas: a field guide. Texas A&M University Press, College Station.

Powell, A.M. 1998. Trees and shrubs of Trans-Pecos Texas. University of Texas Press, Austin.

Powell, A.M. 2000. Grasses of the Trans-Pecos and adjacent areas. Iron Mountain Press, Marathon, TX.

Powell, A.M. [in prep.] Flowering plants of the Trans-Pecos and adjacent areas: Eudicots. Sul Ross State University, Alpine, TX.

Powell, A.M. and R.A. Hilsenbeck. 1995. A floristic overview of the Chihuahuan Desert Region. Chihuahuan Desert Disc. Winter/Spring. Chihuahuan Desert Research Institute, Alpine, TX.

Powell, A.M. and B.L. Turner. 1977. Aspects of the plant biology of the gypsum outcrops of the Chihuahuan Desert. In: R.H. Wauer and D.H. Riskind, eds. Transactions of the symposium on the biological resources of the Chihuahuan Desert Region, United States and Mexico. U.S. Department of the Interior, National Park Service transactions and proceedings series, No. three.

Powell, A.M. and J.F. Weedin. 2004. Cacti of the Trans-Pecos and adjacent areas. Texas Tech University Press, Lubbock.

Powell, A. M., S. C. Yarborough, and S. D. Jones. [in ms.]. Flowering plants of the Trans-Pecos and adjacent areas: Monocots, excluding the grasses: cat-tails, sedges, and rushes to lilies, agaves, and orchids. Sul Ross State University, Alpine, Texas.

Pulling Together Initiative [PTI]. 2006. Texas invasive plant database. URL: www.texasinvasives.org/Invasives_Database/Invasives.html.

Ralston, B.E. 1987. A biosystematic study of the *Opuntia schottii* complex (Cactaceae) in Texas. M.S. Thesis, Sul Ross State University, Alpine, TX.

Ralston, B.E. and R.A. Hilsenbeck. 1989. Taxonomy of the *Opuntia schottii* complex (Cactaceae) in Texas. Madroño 36:221–231.

Ralston, B.E. and R.A. Hilsenbeck. 1992. *Opuntia densispina* (Cactaceae): a new club cholla from the Big Bend region of Texas. Madroño 39:281–284.

Raven, P.H. and D.I. Axelrod. 1978. Origin and relationships of California flora. Univ. Calif. Publ. Bot. 72. University of California Press, Berkeley.

Raven, P.H., R.F. Evert, and S.E. Eichhorn. 2003. Biology of plants. W.H. Freeman, New York, NY.

Rogers, T.D. 1964. Biological observations with emphasis on the vegetation of the Black Gap Wildlife Management Area, Brewster County, Texas. MS Thesis, Sul Ross State University, Alpine, TX.

Rzedowski, J. 1973. Geographical relationships of the flora of Mexican dry regions. In: A. Graham, ed. Vegetation and vegetational history of northern Latin America. Elsevier, New York, NY.

Saltonstall, K. 2003. Microsatellite variation within and among North American lineages of *Phragmites australis*. Mol. Ecol. 12:1689–1702.

Schmidt, R.H., Jr. 1979. A climatic delineation of the 'real' Chihuahuan Desert. J. Arid Environm. 2:243–250.

Schmidt, R.H., Jr. 1986. Chihuahuan climate. In: J.C. Barlow, A.M. Powell, and B.N. Timmermann, eds. Second symposium on resources of the Chihuahuan Desert Region, United States and Mexico. Chihuahuan Desert Research Institute, Alpine, Texas.

Shreve, F. 1942. The desert vegetation of North America. Bot. Rev. 8:195–246.

Sikes, S. and J. Smith. 1973. Victorio Canyon, a vegetational survey. In: Lyndon B. Johnson School of Public Affairs. Victorio Canyon: a natural area survey, Part IV of IV. University of Texas, Austin.

Smith, V.J. 1924. How Dead Horse Canyon got its name. In: J.F. Dobie, ed. Legends of Texas. Publications of the Texas Folklore Society, Number III. Held by the Archives of the Big Bend, Alpine, TX.

Takhtajan, A. 1986. Floristic regions of the world. University of California Press, Berkeley.

Terrell, E.E. 1996. Taxonomic notes on Texan and Mexican species of *Hedyotis* and *Houstonia* (Rubiaceae). Phytologia 81:108–114.

Terrell, E.E. 2001. Taxonomy of *Stenaria* (Rubiaceae: Hedyotidae), a new genus including *Hedyotis nigricans*. Sida 19:591–614.

Texas A&M Bioinformatics Working Group [TAM-BWG]. 2006. Texas Endemics: checklist of all endemics. URL: www.csdl.tamu.edu/FLORA/endemics/ endemics2.htm.

Texas Parks and Wildlife Department [TPWD]. 2006. Rare and threatened species of Texas by county. URL: www.tpwd.state.tx.us/landwater/land/maps/gis/ ris/endangered_ species.phtml.

Turner, A.J. 1977. Soil Survey of Jeff Davis County, Texas. United States Department of Agriculture, Soil Conservation Service in Cooperation with the Texas Agricultural Experiment Station, College Station.

Turner, B.L. 1959. The legumes of Texas. University of Texas Press, Austin.

Turner, B.L. 1997. Turner's rebuttal to Terrell's taxonomic notes on Turner's treatment of Texan and Mexican *Hedyotis*. Phytologia 82:82–85.

Turner, B.L., H. Nichols, G. Denny, and O. Doron. 2003. Atlas of the vascular plants of Texas. Sida, Bot. Misc. 24. BRIT Press, Fort Worth, Texas.

Turner, B.L. and A.M. Powell. 2005. Chromosome numbers of *Glandularia* (Verbenaceae) from central and Trans-Pecos, Texas. Sida 21:1657–1661.

Tyler, R.C. 1975. The Big Bend: a history of the last Texas frontier. National Park Service, Washington, D.C.

United States Department of Agriculture [USDA]. 2006. Natural Resources Conservation Service soils website. URL: www.soils.usda.gov.

United States Department of Agriculture [USDA]. 2007. Natural Resources Conservation Service PLANTS Database website. URL: http://plants.usda.gov/.

Van Devender, T.R. 1986. Pleistocene climates and endemism in the Chihuahuan Desert. Quatern. Res. 15:278–290.

Van Devender, T.R. 1990. Late quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico. In: J.L. Betancourt, T.R. Van Devender, and P.S. Martin, eds. Packrat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson.

Van Devender, T.R., R.S Thompson, and J.L. Betancourt. 1987. Vegetation history of the deserts of southwestern North America; the nature and timing of the Late Wisconsin-Holocene transition. In: W.F. Ruddiman and H.E. Wright, Jr., eds. North America and adjacent oceans during the last deglaciation, The Geology of North America Vol. K–3. The Geological Society of America, Boulder, CO.

Warnock, B.H. 1946. The vegetation of the Glass Mountains, Texas. PhD Dissertation, University of Texas, Austin.

Warnock, B.H. 1970. Wildflowers of the Big Bend country, Texas. Sul Ross State University, Alpine, TX.

Warnock, B.H. 1974. Wildflowers of the Guadalupe Mountains and the sand dune country, Texas. Sul Ross State University, Alpine, TX.

Warnock, B. H. 1977. Wildflowers of the Davis Mountains and the Marathon Basin, Texas. Sul Ross State University, Alpine, TX.

Weckesser, W. [in prep.] Vascular flora of Reed's Plateau, Brewster County, Texas. MS Thesis, Sul Ross State University, Alpine, TX.

Wells, P.V. 1965. Vegetation of the Dead Horse Mountains, Brewster County, Texas. SouthW. Naturalist 10:256–260.

Wells, P.V. 1966. Late Pleistocene vegetation and degree of pluvial climatic change in the Chihuahuan Desert. Science 153:970–975.

Wood, S., G. Harper, E. Muldavin, and P. Neville. 1999. Final report: vegetation map of the Sierra del Carmen, U.S.A. and Mexico. Unpublished report to the National Park Service, Big Bend National Park, TX.

World Wildlife Fund [WWF]. 2001. Tamaulipan mezquital ecoregion (NA1312) full scientific report. URL: www.worldwildlife.org/science/ecoregions/ nearctic.cfm.

Worthington, R.D. 1995. A floral inventory of the Big Bend Ranch State Natural Area, Presidio and Brewster Counties, Texas. Unpublished report, University of Texas, El Paso.

Worthington, R.D. 2001. Inventory of the flora of Big Bend National Park, Brewster County, Texas: first working draft. Floristic inventories of the southwest program, University of Texas, El Paso.

Yarborough, S. C. and A. M. Powell. 2002. Fern and fern allies of the Trans-Pecos and adjacent areas. Texas Tech University Press, Lubbock.