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DYNAMICS OF THE SHRUB DESERT FORMATION-  
SUCCULENT DESERT FORMATION TRANSITION  
IN BIG BEND NATIONAL PARK, TEXAS

A DISSERTATION  
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DYNAMICS OF THE SHRUB DESERT FORMATION-  
SUCCULENT DESERT FORMATION TRANSITION  
IN BIG BEND NATIONAL PARK, TEXAS

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DYNAMICS OF THE SHRUB DESERT FORMATION-  
SUCCULENT DESERT FORMATION TRANSITION  
IN BIG BEND NATIONAL PARK, TEXAS

CHAPTER I

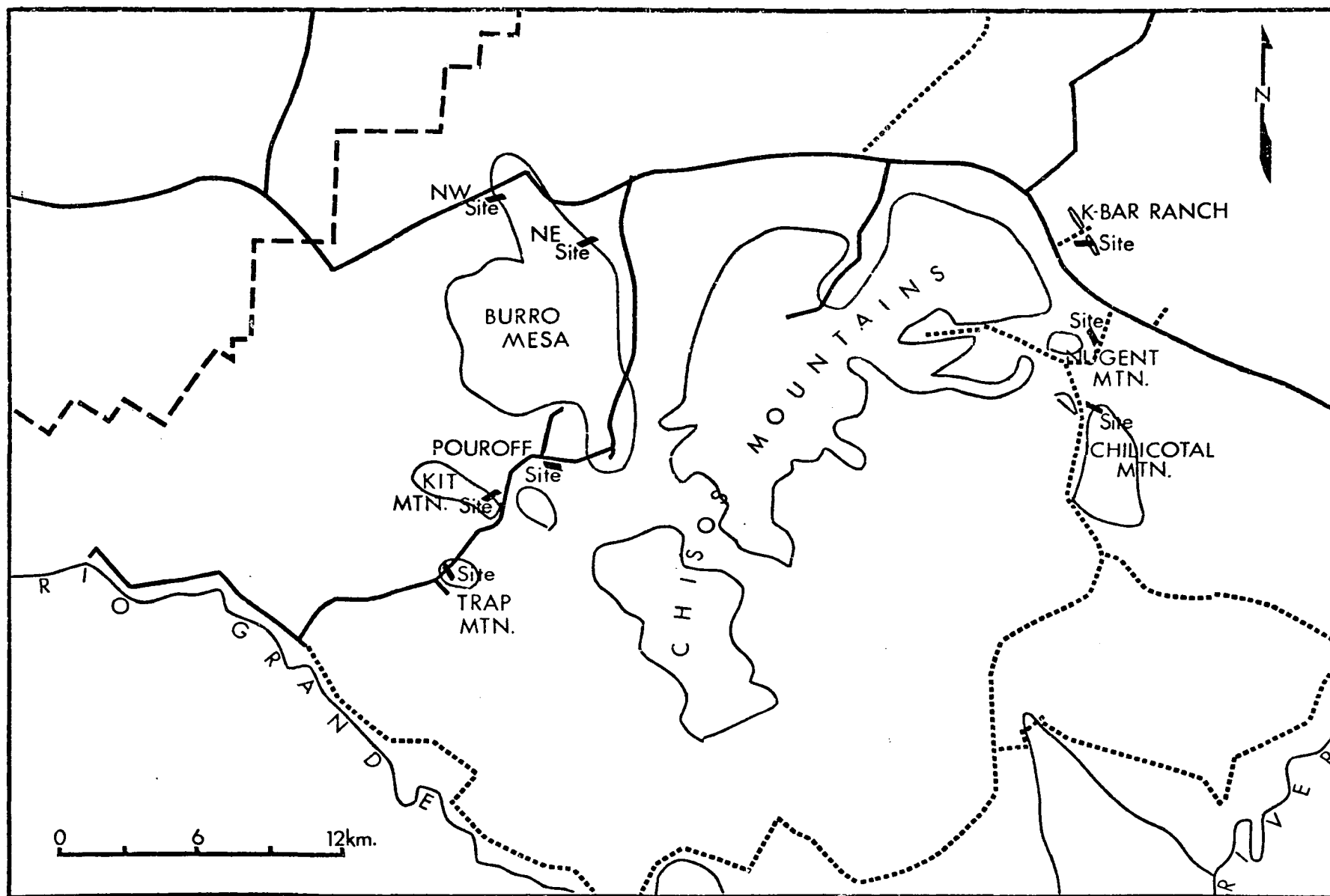
INTRODUCTION

The fundamental tenets of desert vegetation dynamics are based on Forrest Shreve's (1925; 1929; Shreve and Hinckley, 1937) early work conducted in the Sonoran Desert. Basically the tenets are "there is no evidence of successional change" and "the species and even the individuals which are pioneers in the revegetation of cleared areas remain as final components of the vegetation" (Shreve, 1929). Muller (1940), Gible (1950), and Murray (1959) presented more recent evidence to support Shreve's concepts. All studies except Muller's utilized the resampling of permanent plots established by Spalding and Shreve on the grounds of the Desert Botanical Laboratory of the Carnegie Institute at Tucson, Arizona. Muller confined his study to the description of the vegetation stages in the erosion cycle of the Larrea-Flourensia climax in West Texas in an area now within the confines of Big Bend National Park.

Lowe (1958-59) reaffirmed the concepts of Shreve and implemented the terms development for the direct replacement of vegetation without succession and change for the alteration of vegetational composition through time by climatic variation. Both of these are embodied in his genetic climax, which he exemplified by two distinct vegetation types contiguously located under the same macroclimate, adaptively selected for vegetation composition, and not related successionally to each other.

Whereas the above studies were primarily confined to the dynamics of the dominant species in seemingly mature and stable Larrea divaricata vegetation, the purpose of this study was to investigate the mechanism of Larrea vegetation development and change emphasizing the subordinate species. A less stable vegetation was chosen in order to delineate invasion mechanisms and to monitor environmental factors pertinent to vegetation dynamics. Specifically, the sharp contact boundaries of the Shrub Desert Formation and the Succulent Desert Formation (Gehlbach, 1967) in Big Bend National Park, Texas, were utilized (Fig. 1). The dynamic behavior of pertinent species with respect to both biotic and edaphic factors along the transition was investigated. Special emphasis was given to the following species: Larrea divaricata, Erioneuron pulchellum, Cathastecum erectum, Agave lecheguilla, and Bouteloua breviseta.

Figure 1. Distribution of the study sites within  
Big Bend National Park, Texas.



The two vegetation formations utilized in this study are widespread in the Chihuahuan Desert of western Texas, southern New Mexico, and northern Mexico. Gehlbach (1967) recently suggested that the same formations occur in the Sonoran Desert, but with different species. The Shrub Desert Formation is more xerophytic and is generally dominated by Larrea, a shrub widely distributed in a rather uniform vegetation throughout southwestern United States and northern Mexico. The more mesophytic Succulent Desert Formation is an exceedingly more complex vegetation dominated by grasses (Bouteloua, Hilaria, etc.) and succulents (Agave, Dasyllirion, Opuntia, etc.). Occasionally shrubs may assume dominance in some localities.

## CHAPTER II

### PHYSIOGRAPHY, GEOLOGY AND CLIMATE

Big Bend National Park, Brewster County, Texas, lies within the southern Chisos Biotic District (Denyes, 1956), which is physiographically dominated by broad, flat basins interrupted by resistant sedimentary or igneous ranges. Rising to varying heights, the resistant ranges reach their maximum in the Chisos Mountains (2388 m). The Chisos Mountains and many of the outlying hills are composed of extensive layers of Eocene and Oligocene lavas and basalts which cap older Cretaceous and Tertiary intrusive and extrusive igneous rock (Maxwell et al., 1967).

The resistant formations are commonly flanked by long, gently sloping bajadas dissected by numerous arroyos and composed of consolidated Quaternary terrace and valley-fill gravels and silt in addition to large expanses of recent unconsolidated alluvium. Desert pavement with larrea vegetation predominates on these bajadas which range in elevation from 1067-1372 m at the base of the Chisos Mountains to 579-701 m at the Park's southern boundary, the Rio Grande.

The regional climate is seasonally influenced by the spring-summer, southerly, tropical maritime masses laden

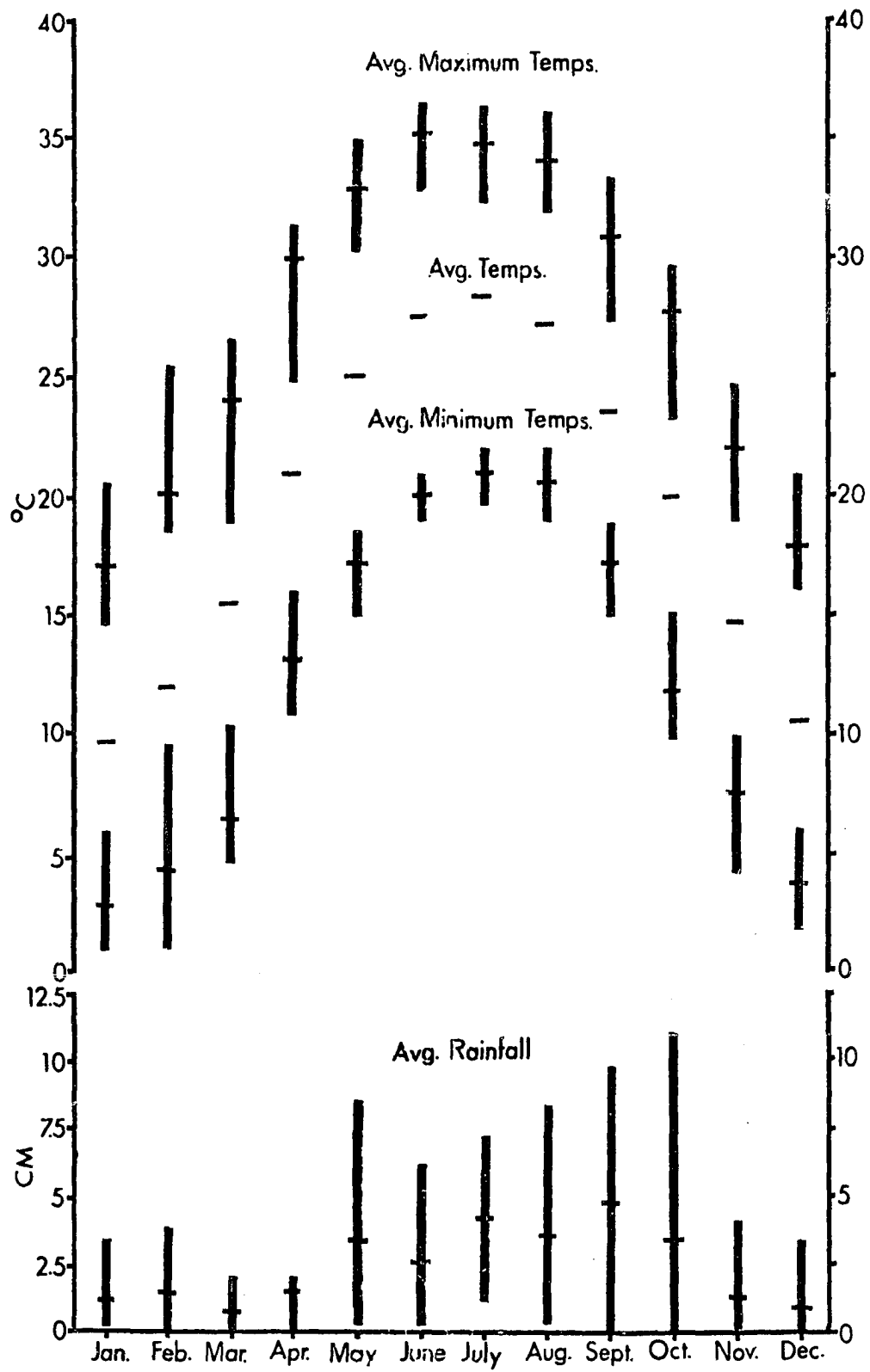


with moisture from the Gulf of Mexico and the fall-winter polar continental and arctic cold air fronts from the north and northwest (Orton, 1964). The annual seasonal weather pattern is characterized by high summer and early fall temperatures and rainfall, whereas lower temperatures and rainfall are recorded in the winter and spring (Fig. 2). Fig. 2, a thirteen year summary (April 1955-October 1968), most likely includes the extremes encountered at each of the study sites, although data utilized were for Panther Junction (USDC, Climatological Summaries: Texas, 1955-68), Park Headquarters, situated on the northern lower bajada of the Chisos Mountains at 1060 m elevation.

It is during the period from May-October that 2/3 of the annual precipitation is received in the form of sporadic, convective rainfall. The thirteen year annual average rainfall is 30.5 cm with a low of 21.0 cm recorded in 1956 and a high of 46.7 cm in 1966.

The highest average maximum temperature is reached in June; however, the highest average minimum is not reached until July, when the average overall temperature is at its maximum. During this period and into September the extremes become higher, but the more frequent convective rainstorms cause fluctuating temperatures for a day or two, thus decreasing the averages. The most severe cold-waves persist for several days at a time from December through March bringing less than 20 mm annual average snowfall to the desert region.

Figure 2. Thirteen year average annual weather summary for Panther Junction, Big Bend National Park, Texas.



## CHAPTER 111

### STUDY SITES

Widely separated sites (Fig. 1) were selected in order to include substantial edaphic, climatic, and vegetational variation. All sites were located on foothills beyond the main Chisos Mountain bajadas where less human and grazing impact is present. All ranching activities were permanently terminated on Park lands in 1944 after a history of goat, sheep, and cattle grazing and browsing since the early 1800's (Casey, 1968; Utley, 1962). The earliest and heaviest ranching activities were in the western section of the Park as is exemplified at the Burro Mesa Junction sites. The effects are exceedingly less evident at the other western and eastern sites, although remnants of goat and/or sheep corrals are evident at the K-Bar Ranch and Chilicotal Mountain sites.

Several criteria were employed in selecting the eight study sites. Those sites chosen possessed a distinct line of demarcation separating the two formations, with the change or transition usually on a gentle slope (Table 1) within a distance of 2-4 m. The sites exhibited the Succulent Desert Formation vegetation on the upper slope and the

Table 1. Characteristics of eight Shrub Desert Formation-Succulent Desert Formation transition sites studied in Big Bend National Park.

Site	Eleva- tion	Expo- sure	Slope	Parent Materials <sup>1</sup>
Chilicotal Mountain	975	W	3-15°	Alluvium; bentonitic clays
Nugent Mountain	1036	E	2-15°	Alluvium; porphyritic alkalic microgranite sill
K-Bar Ranch	1036	W	1-5°	Alluvium; riebeckite granophyre dike
Northwest Burro Mesa	975	W	2-20°	Alluvium; undifferenti- ated lavas overlayed by Tule Mtn. trachyandesite
Northeast Burro Mesa	1036	NE	3-20°	Same as above
Burro Mesa Pour- off Junction	1036	W E	2-25° 0-25°	Alluvium; porphyritic, Ash Spring basalt
Kil Mountain	975	NE	2-20°	Alluvium; undifferenti- ated lavas overlayed by Bee Mtn. basalt
Trap Mountain	945	NW	3-20°	Same as above

<sup>1</sup> Derived from Maxwell et al., 1967.

Shrub Desert Formation vegetation below. Because the slopes were so gentle any exposure was usually accepted, although at the Burro Mesa Pouroff Junction site opposing exposures demonstrated marked differences. Every attempt was made to avoid known disturbances such as erosional paths or human influence, with two exceptions. One exception was the Trap Mountain site with a newly paved highway, 1965, dissecting the transects. At least 9 m buffer zone was permitted on either side of the pavement to allow disturbance influences to diminish. The second exception, the Nugent Mountain site, had two small dirt roads dissecting the transects and was chosen to determine their influence upon the Shrub Desert Formation vegetation.

The sites extended from Chilicotal Mountain on the east to Trap Mountain on the west, an aerial distance of 28 km, with the high Chisos Mountains between. All sites occurred within an elevational belt of 91 m, from 945 m at Trap Mountain to 1036 m at several sites (Table 1). At all sites the Shrub Desert Formation occurred on the younger alluvium and the Succulent Desert Formation on the older igneous-derived parental material (Table 1).

The major soil series of the Park were described by Carter (1928), but only the Reeves and Brewster series are of importance in the study areas. The Reeves series, a gravelly loam, low in humus and basic in reaction, supports predominately Larrea and associated shrubs. The igneous

mountains and hills support the Brewster series, a very shallow loamy soil sometimes rich in humus, sustaining lechuguilla-grass associations at lower elevations or woodland vegetation on the higher Chisos Mountain slopes.

## CHAPTER IV

### VEGETATION

The vegetation of Big Bend National Park was studied with special reference to vegetation dynamics by Muller (1940) and Whitson (1965, 1970). Muller developed the Super-Climax concept, similar to that of Shreve, from his study of the vegetational stages of the Larrea-Flourensia climax associated with the erosional sequences of the Tornillo clays in the northern region of the Park. Whitson (1965) reported on the dynamics of the woodland vegetation of Boot Canyon in the Chisos Mountains and more recently (1970) updated these results for permanent plots and presented the dynamic pattern of the vegetation in the Chisos Basin where the desert vegetation contacts the Evergreen Woodland Formation. This study of the relationship between vegetation and soils was the first since the early work of Carter and Cory (1930-31).

#### Shrub Desert Formation

The Larrea dominated vegetation of the Big Bend region and the Park has been classified in various manners: Mexican Greasewood Formation (Bray, 1901), extreme arid



Lower Sonoran Zone (Bailey, 1905), Southern Desert Shrub (Shantz and Zon, 1924), Chihuahuan Desert (Shreve, 1939), Desert Plains Grassland (Whitfield and Anderson, 1938), and Chihuahuan Desert Shrub (Muller, 1947). Denyes (1956) included three creosotebush associations in the treatment of her Desert Plains Life Belt: Creosote-Tarbrush, Creosote-Mesquite, and Creosote-Tasajillo.

The recent classification of Gehlbach (1967) is used in this report as he presents quantitative comparisons for similar vegetation throughout the southwest including the Park. Since a thorough study of the Park vegetation is not available, dominance types or associations will not be considered at this point.

The open appearance of the shrubs and the lack of vegetative ground cover make the Shrub Desert Formation very distinct from other vegetation types in the Park. This sparse cover readily reveals the smooth, pebble-strewn desert pavement with its paucity of plant duff. Numerous acres of this physiognomy occur in the Park, where Larrea is rivaled by no shrub or succulent, and only scattered succulents, forbs, or perennial grasses are present.

Several shrubs may rival Larrea for physiognomic control in specific areas. On the shallow soils of the bajadas extending northward from the Chisos Mountains Flourensia is a common associate as are Viguiera stenoloba and Parthenium incanum (Gehlbach, 1967). Adjacent to

arroyos, on deep clay loams Prosopis glandulosa and Opuntia leptocaulis are frequent associates (Anthony, 1954).

Fouquieria splendens frequently contributes to the physiognomy on low rocky outcrops or old rocky outwashes.

The most common associate of Larrea on the intermediate to upper bajadas extending from the Chisos Mountains is Agave lecheguilla. This extensive transition association is especially common on the eastern and southern bajadas extending from the mountains. A frequent associate of these is Jatropha dioica, a significant contributor to ground cover.

#### Succulent Desert Formation

This formation has been classified as the Mixed Cactus, Yucca, and Agave Formation and the Lechuguilla and Sotol Formation (Bray, 1901), Grassland Transition (Muller, 1947), Chihuahuan Desert Formation (Gehlbach, 1966) and the Succulent Desert Formation (Gehlbach, 1967). Bailey (1905) and Shreve (1939) did not distinguish this vegetation from the former. Denyes (1956) cited four associations of the Foothills Life Belt which occurred in the Park: the Sotol-Lecheguilla, Creosote-Lecheguilla, and the Sotol-Sachauiste being the three most pertinent.

The major distinguishing characteristics of the Succulent Desert Formation are the succulence of many species and the lowness and density of the vegetation. The density

and cover frequently obscure the shallow, rocky soil and large amounts of plant duff. This vegetation, dominated by Agave, Dasyllirion leiophyllum, and several grasses, controls the physiognomy of the foothills.

In specific areas at lower elevations Agave is commonly associated with Larrea, but on the upper bajadas or isolated foothills Larrea is replaced by Bouteloua breviseta, Bouteloua eriopoda, Bouteloua hirsuta, Hilaria mutica or other grasses. Frequently Dasyllirion accompanies the grasses and Agave on northern exposures, even to the extent that the grasses and Dasyllirion predominate. On the upper limits of the bajadas small Juniperus pinchoti shrubs, Nolina erumpens, and other shrubs may accompany the Agave and Dasyllirion. These associations, primarily situated on igneous or gravel derived substrates, are significantly different from those described by Wells (1965) for limestone substrates in the Park.

## CHAPTER V

### METHODS

#### Vegetation Sampling

At each of the eight sites two transects were established to sample the vegetation for composition, density, and cover and to obtain soil samples across the formation boundaries. The two parallel transects were approximately 30 m apart, and each was established by selecting the point of vegetation contact and running a string into both formations at right angles to the contact zone. At 15.24 m (measurements originally in ft, hence the decimals) intervals into each formation a stake was positioned to hold the string and demarcate the corner of four contiguous plots, and a 3.05 m long guide stick was used to delimit the outer boundary of the vegetation on both sides of the string. This provided two adjacent plots 15.24 m long and 3.05 m wide. The transects were usually 76.2 m long, providing three contiguous plot pairs in the Larrea dominated Shrub Desert Formation and two contiguous plot pairs in the Agave-Bouteloua dominated Succulent Desert Formation. Longer transects were utilized at Trap Mountain (91.4 m) and Northeast Burro Mesa (121.9 m) sites as the vegetation change

was more gradual and relative vegetation stability was not achieved in the usual transect length.

Every vascular plant within the plots was measured for maximum diameter cover to the nearest even centimeter. In the case of Jatropha dioica each individual stem was not recorded; instead, the total clump was measured as an individual to reduce figures and time. Sites possessing the grass Cathastecum erectum required the total percentage cover to be estimated and the area covered measured in order that total plot coverage could be calculated later. The number of individuals was then determined by dividing the total plot cover by 81.07 sq cm, the average cover of a given rooted individual. Whenever possible the cover for each rooted individual was recorded and it was from these values that the average cover value was determined.

All vegetation sampling was conducted during the summer (June-August) 1967. Voucher specimens from the study are deposited in the Bebb Herbarium, University of Oklahoma, and all nomenclature in the report follows Gould (1969).

#### Soil Collection

During the summer of 1967 soil samples were obtained at the point of formation contact and at both ends of the transect for each site transect. At each collection point samples were taken from the 0-15 cm and 15-30 cm depths using a rock pick to excavate a soil cylinder 20-30 cm in

diameter. As the soils were exceedingly rocky they were immediately sieved through a 2 mm wire screen into paper bags, air-dried for two days, and transferred to plastic bags for transport.

A second and similar sized excavation was made at both depths and all materials removed were separated by sieve pan and screen into three particle categories: >22 mm, 22-2 mm, and <2 mm. These categories were weighed separately by a tension spring scale in the field and the values used to obtain relative weight percentages.

During late April-early May in 1968 soil moisture and field capacity determinations were made at the ends of both transects at each site. Duplicate soil samples for determining soil moisture were collected at both depths. Each sample was immediately placed in a pre-weighed jar, and the total weight recorded. After flooded sites within covered retaining dams were allowed to infiltrate 48 hours, duplicate soil samples were collected at the 0-15 cm depths for field capacity determination. The samples were immediately placed in pre-weighed jars, and the total weights recorded.

Water infiltration rates of the soils within 3 m of the ends of both transects at each site were determined during late April and early May. Infiltration was measured by determining the number of seconds required for  $3\frac{1}{4}$  cc of water to penetrate the soil. The water was poured into a

6 cm diameter cylinder which had been carefully pushed into the soil to a depth of 1-1.5 cm. A stopwatch was used to record the time for water disappearance for 10 trials at each sampling point.

A Delmhorst electrical resistance gypsum block system was employed to obtain soil moisture at near weekly intervals during the summer of 1967. The gypsum blocks were calibrated and installed along both transects at 15 and 30 cm depths at contact of the formations and at both ends of the transect. Moisture readings were recorded between 8:00 and 8:30 am to reduce extreme temperature variation. The sensitivity of the system in dry desert soils proved to be inadequate, but the system was employed for the summer. No block gave readings the following spring even after the sites were artificially flooded.

#### Soil Analyses

Upon return to the laboratory, the soils were sieved through a 2 mm screen and any remaining plant debris removed before the soils were stored in air-tight jars. Small duplicate aliquots were oven-dried at 100-102°C for 24 hours, allowed to cool in desiccators, and weighed to determine air-dry equivalent values which were used in all analyses. The pH was determined on duplicate samples by the glass electrode method of Piper (1942), and calcium carbonate on triplicates by the gasometric procedure of Jackson (1958).

The latter method was modified by the insertion of a graduated burette into the reaction flask rather than the small vial to deliver the acid. The acid was added at a drop per second rate or less with consistent results. Total phosphorus was determined on duplicate samples by the method of Shelton and Harper (1941) after the soil had been ground in a Wiley mill.

Before the soils were analyzed for texture, organic carbon, and total nitrogen, carbonates were removed with a pH 5 NaOAc buffer solution and procedure described by Grossman and Millet (1961). The soils, in dialysis bags, were leached for 96 hours in the buffer and kneaded frequently to expel the carbon dioxide bubbles. The soils were then desalted in running tap-water for 144 hours and air-dried in ethyl alcohol and air-dry equivalents established. Textural analysis was determined by the hydrometer method of Bouyoucos (1936). The remaining leached soils were ground in the Wiley mill and used to determine organic carbon on duplicate samples by the chromic acid digestion method of Piper (1942) and total nitrogen by the macro-Kjeldahl method as modified from Noggle and Wynd (1941). Occasional duplicates were analyzed for texture and nitrogen to verify procedural consistency.



## CHAPTER VI

### RESULTS OF VEGETATIONAL ANALYSES

Analysis of the vegetational transition along the Shrub Desert Formation and the Succulent Desert Formation contact indicates a variable vegetational composition and complex pattern of vegetation dynamics. Much of the variation is due to the broad distribution of the sites in the Park and the local changes which can occur over even short distances. Even though the transects at each site were generally 30 m apart, the variation between the two transects with respect to quantitative characteristics prevented the summation of equivalent plots for special patterns of dynamics. In both formations, but more particularly in the Shrub Desert Formation, the smaller plots on either side of the centerline varied too greatly to obtain variation along the transect. Throughout the study a plot refers to the summation of the two adjacent plots in a transect and represent 93 sq m.

The two formations were physiognomically distinct with different life forms predominating in each (Table 2). Floristically, the Succulent Desert Formation was the richer formation with a greater number of species occurring in the

Table 2. Vegetation summary of Shrub Desert and Succulent Desert Formations sampled in Big Bend National Park.

Characteristic	Shrub Desert Formation	Succulent Desert Formation
Species encountered	75	85
Species exclusive	9	19
Shrubs	22	22
Succulents	10	14
Grasses	14	15
Forbs	29	34
Species per plot (Mean No.) <sup>1</sup>	13 (4-27)	18 (10-25)
Density per plot <sup>1</sup>	332 (48-1069)	1842 (361-4875)
Shrubs <sup>2</sup>	23	4
Succulents <sup>2</sup>	13	20
Grasses <sup>2</sup>	54	70
Forbs <sup>2</sup>	10	6
Mean percent cover per plot <sup>1</sup>	28 (15-56)	43 (27-59)
Shrubs <sup>2</sup>	78	27
Succulents <sup>2</sup>	11	22
Grasses <sup>2</sup>	6	46
Forbs <sup>2</sup>	5	5

<sup>1</sup> Range of values in parentheses

<sup>2</sup> Relative values

plots and more species exclusive to the formation. The various life forms were represented by a similar number in each formation, with 66 of the 94 species encountered in the study shared by both formations. Forbs and shrubs contributed the greatest number of species, but did not similarly contribute to the physiognomy quantitatively. It is in the comparison of these quantitative characteristics that the formations differ greatly.

The Succulent Desert Formation had nearly a six-fold greater density and a two-fold greater cover per plot than the Shrub Desert Formation. Of significant physiognomic importance was the 78% relative cover of shrubs for the Shrub Desert Formation dominated by Larrea versus a 27% relative shrub cover in the Succulent Desert Formation. On the other hand, the succulents and grasses had a combined relative cover of 68% in the Succulent Desert Formation and only 17% in the Shrub Desert Formation. These values indicate a difference in predominant life form between the two formations and demonstrate the greater sensitivity of cover rather than density for detecting the quantitative dissimilarities.

A summary of the dominant vegetation is presented in Figures 3-11 for a single transect at each site. The data used to compile the graphs were the Importance Percentages (IP = relative density + relative cover) of the two dominant species at each plot along the transect. When a species

Figure 3. Importance percentage value distribution of dominant species for Chilicotal Mountain (South) site. Solid triangle on abscissa indicates transition from Shrub Desert Formation (on left) to Succulent Desert Formation.

Figure 4. Importance percentage value distribution of dominant species for Nugent Mountain (East) site.

Figure 5. Importance percentage value distribution of dominant species for K-Bar Ranch (South) site.

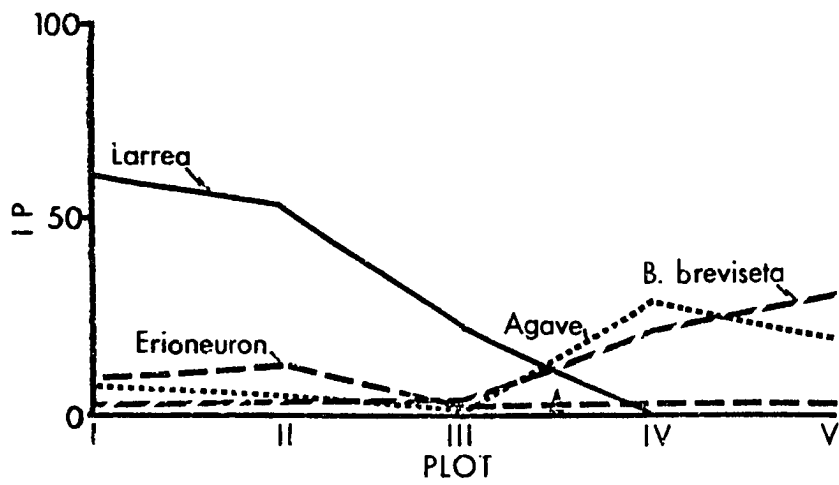
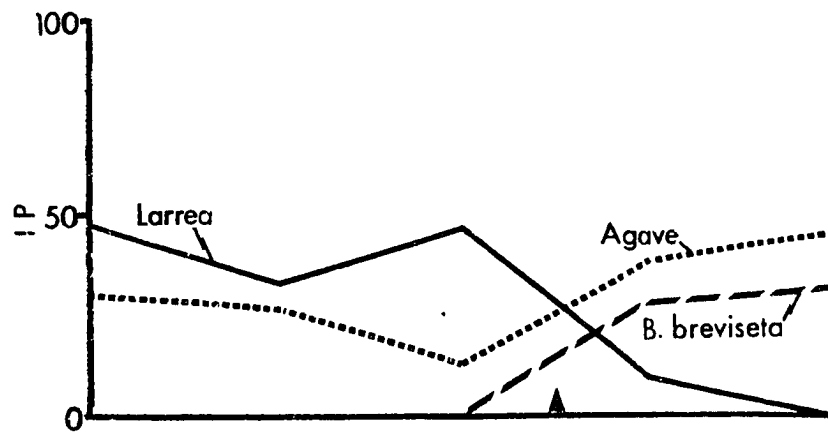
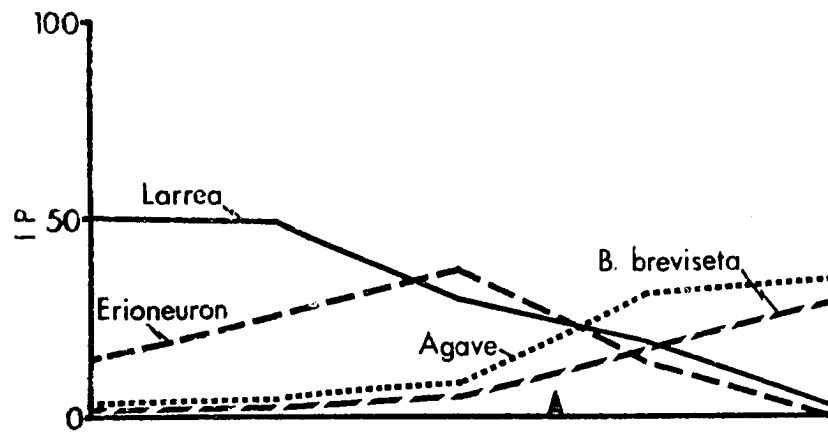


Figure 6. Importance percentage value distribution of dominant species for Northwest Burro Mesa (East) site.

Figure 7. Importance percentage value distribution of dominant species for Burro Mesa Pourroff Junction (East) site.

Figure 8. Importance percentage value distribution of dominant species for Burro Mesa Pourroff Junction (West) site.

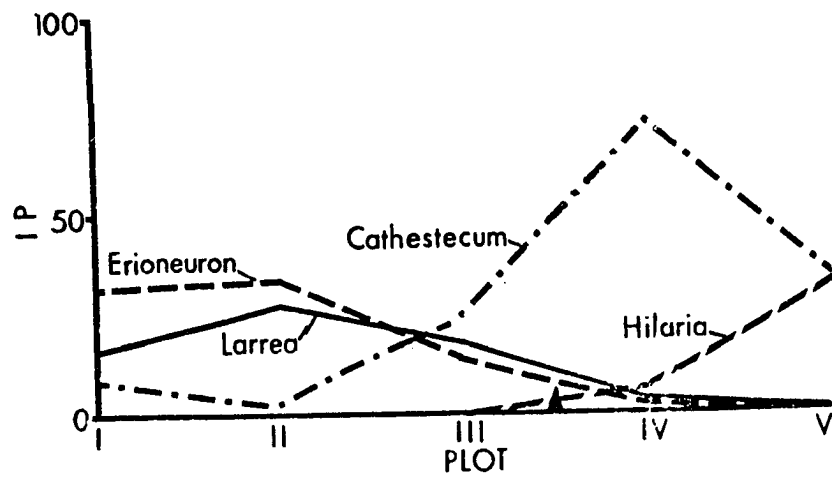
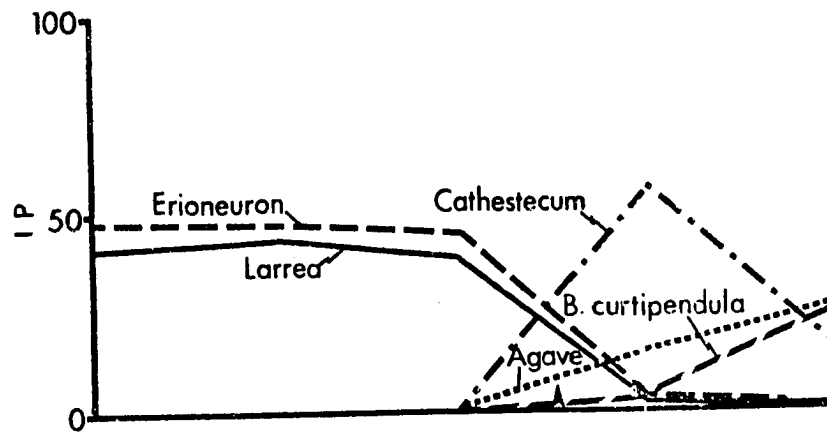
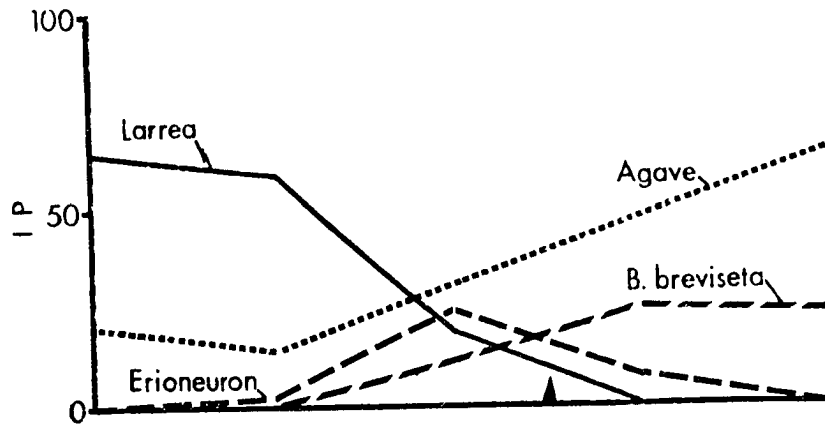


Figure 9. Importance percentage value distribution of dominant species for Kit Mountain (North) site.



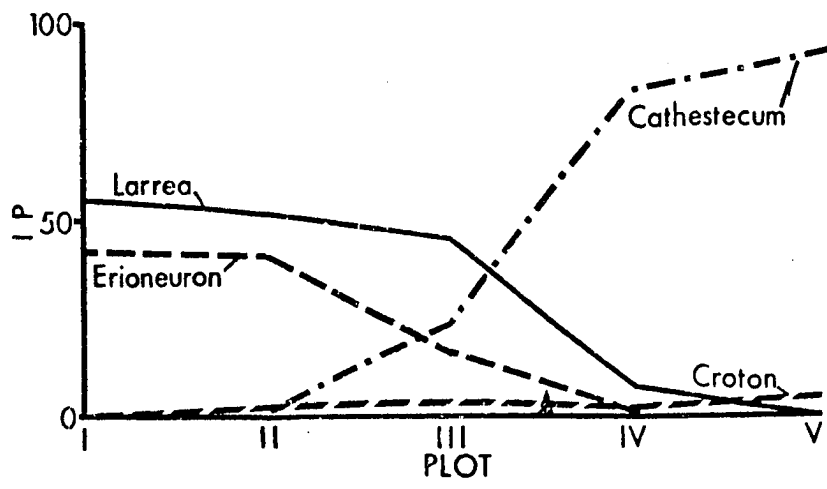
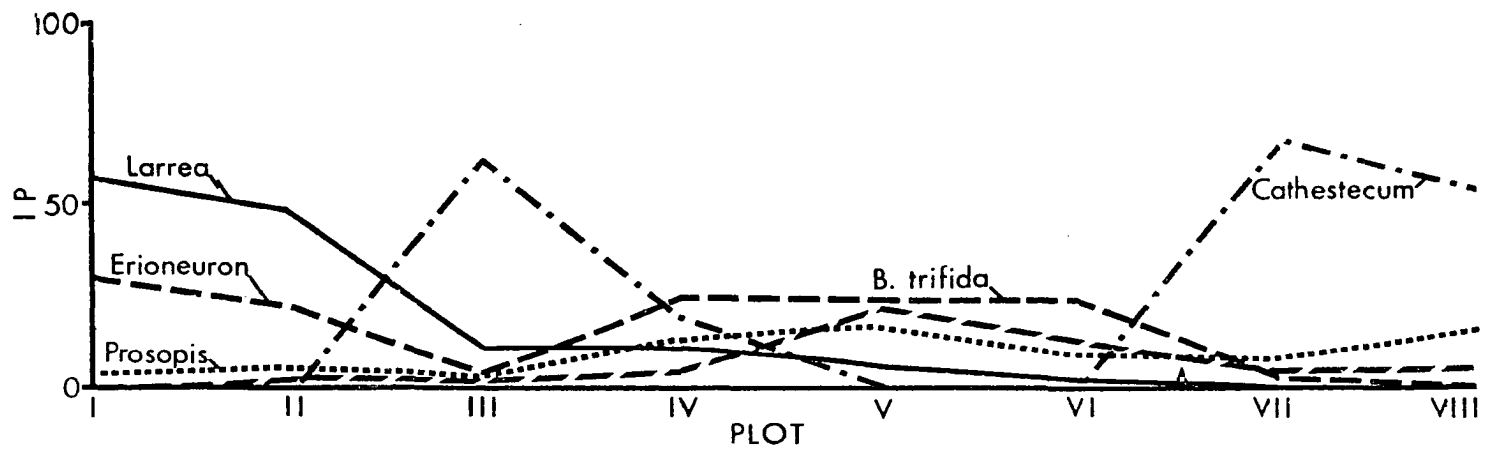
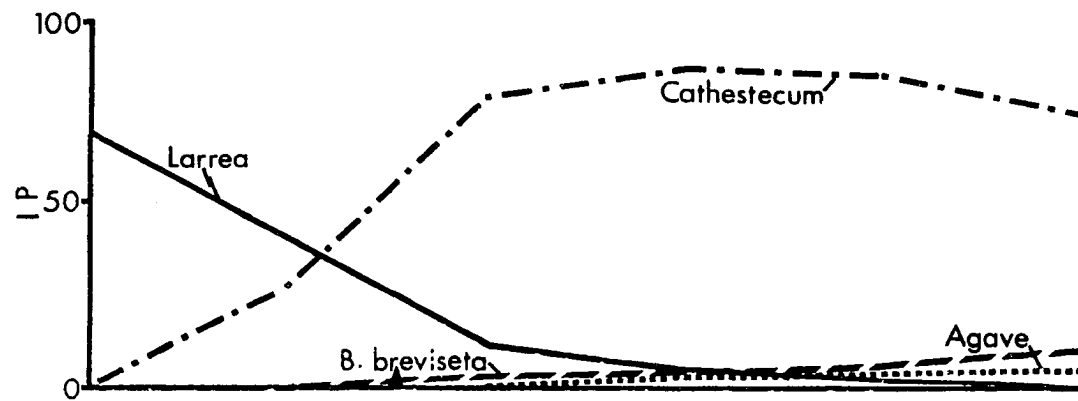


Figure 10. Importance percentage value distribution of dominant species for Trap Mountain (West) site. Transect is one plot (VI) longer than usual length.

Figure 11. Importance percentage value distribution of dominant species for Northeast Burro Mesa (East) sites. Transect is three plots (VI, VII, VIII) longer than usual length.



was dominant in only a single plot in the transect, its value was omitted to reduce figure confusion. At Burro Mesa Pourroff Junction the vegetation varied greatly enough to warrant a separate graph for each transect. The IP best portrays the Succulent Desert Formation since density and cover are most closely correlated, but this is not the case for the Shrub Desert Formation. Here, the high density of Erioneuron skews the pattern, although it probably does not greatly control or influence the community as Larrea does.

In addition to the two distinct vegetation types at each site, the eight sites can be divided into two distinct site types. The first group exhibits a sharp line of demarcation separating the Larrea dominated vegetation from the Agave-Bouteloua dominated vegetation and the second group has an ecotonal zone of Cathastecum separating the two vegetation types.

Chilicotal Mountain, Nugent Mountain, K-Bar Ranch, and Northwest Burro Mesa comprise the first group (Fig. 3-6). At these sites the 1 m high Larrea vegetation abruptly changes to the lower 30-40 cm high Agave-Bouteloua vegetation with scattered shrubs which break the lower, dense ground cover. Frequently a few Larrea individuals extend into the Succulent Desert Formation and create an overlapping effect in the physiognomy as at Chilicotal and Nugent Mountains (Fig. 3-4).

The second group composed of Northeast Burro Mesa, Burro Mesa Pouroff Junction, Kit Mountain, and Trap Mountain exhibit the Cathestecum ecotone (Fig. 7-11). The prostrate, dense carpet of grass separates the Shrub Desert Formation from the typical Succulent Desert Formation. The zone may be narrow as at Burro Mesa Pouroff Junction (East) where the zone is between 16-20 m broad or as wide as at Kit Mountain where it extends far beyond the 46 m transect end before it contacts the typical succulent-grass vegetation. The boundary of the zone is more obscure at the Agave-Bouteloua contact because of the absence of a distinct desert pavement.

#### Shrub Desert Formation

The Shrub Desert Formation is a sparsely vegetated community and varies little floristically from site to site (Fig. 3-11). Only Prosopis glandulosa and Bouteloua trifida ranked as additional dominants in the formation along with Larrea and Erioneuron. This occurred at Northeast Burro Mesa (Fig. 11) and at the K-Bar Ranch (Plots IV and V, North) sites. The figures also show that Agave and B. breviseta contribute to the Larrea vegetation significantly more in the eastern sites (Fig. 3-5) than in the western sites, with the exception of Northwest Burro Mesa. Cathestecum, on the other hand, contributes more to the Larrea vegetation in the western sites. A few Cathestecum

individuals were encountered at K-Bar Ranch, the only occurrence of this species in the eastern sites.

Associated with the four dominants were several species exclusively sampled in the Shrub Desert Formation plots. These were: Dyssodia pentachaeta, Coldenia mexicana, Janusia gracilis, Condalia lycioides, Condalia spathulata, Selinocarpus angustifolius, and Mammillaria heyderi. These species are not strictly confined to the Shrub Desert Formation, but were only sampled in the plots so categorized. Accompanying these were a number of species recorded in disturbed and small isolated areas of desert pavement in the Succulent Desert Formation, but more commonly associated with the Shrub Desert Formation. This list included: Cassia durangensis, Nerisyrenia camporum, Polygala scoparioides, Baileya multiradiata, Iva ambrosiifolia, Flourensia cernua, Yucca torreyi, Fouquieria splendens, Opuntia grahamii, Opuntia leptocaulis, and Echinocactus horizontalis.

As the study progressed, variation in areal species distribution became evident within the Shrub Desert Formation. At the eastern sites the shrubs Leucophyllum violaceum, Flourensia and Condalia lycioides accompanied by the forbs Jatropha, Polygala macrodenia, and Heliotropium confertifolium were more frequently encountered, although all except Condalia lycioides were recorded in the Succulent Desert Formation. In the Larrea vegetation of the western sites,

succulents Opuntia grahamii, and O. leptocaulis were more frequently encountered as was Fouquieria.

The quantitative variation of the Shrub Desert Formation with respect to the various species is shown in Fig. 3-II, as well as the values depicting general formation characteristics (Table 2). Because Larrea is the characteristic species of the formation and probably controls the community biologically, as will be demonstrated later, a discussion of other quantitative aspects of Larrea follows.

Although the relative density of Larrea in the formation was low, 20%, compared to that of Erioneuron, 50%, the relative cover of the shrub, 77% of the plot vegetation, enhances its importance. Density and cover data for Larrea in the Shrub Desert Formation are presented in Table 3. The values represent plot means with respect to density; however, cover values represent means of individuals per plot. The means are based upon all plots in both transects or the end and transition plots of both. The end plot is most distant in the Shrub Desert Formation (I on all figures) while the transition plot is nearest the Succulent Desert Formation (II, III, or VI).

The mean cover of a Larrea individual was 0.57 sq m while the mean density was 28 per plot, with a mean distance of 2 m between Larrea individuals. Because great variation apparently exists between sites, their respective values were included. Several points stand out with respect to

Table 3. Density and cover of Larrea in the Shrub Desert Formation plots. A is mean density per 93 sq m plot and B is mean cover of individual plant (sq m).

Site	Transition						
	Site Value		End Plot		Plot		Mean Distance <sup>1</sup>
	A	B	A	B	A	B	
Chilicotal	25	0.53	37	0.44	12	0.71	2.1
Nugent	36	.38	31	.40	35	.35	1.8
K-Bar	39	.49	37	.53	34	.46	1.7
NW Burro Mesa	21	.71	25	.66	15	.79	2.3
NE Burro Mesa	21	.84	28	.82	10	1.19	2.3
Burro Pourouff	20	.71	27	.50	13	.92	2.4
Kit	38	.70	16	1.58	43	.48	1.7
Trap	53	.26	57	.28	50	.24	1.5
Grand Mean	28	.57	33	.55	27	.49	2.0

<sup>1</sup>Mean distance (m) between Larrea individuals for the site



comparison of these values. At the three sites having the lowest number of Larrea per plot, the Larrea had the largest cover. A comparison of the end and transition plots suggests a similar trend, but it is not as regular. If the high and low densities are compared with their respective cover in both plots, the correlation is the same. This correlation will be considered again under Interactions of Larrea With Other Species.

The reduced number of Larrea individuals in the transition plots versus the end plots was consistent also except at Nugent Mountain where there was a greater than two-fold increase. A 2-3 fold reduction was generally established except at K-Bar and Trap Mountain where there was just a slight reduction. These last two sites also deviated from the regular pattern of reduced density-increased cover when comparing the end and transition plots. For both sites a decrease in density accompanies a decrease in cover. These four plots will be more closely reviewed under Interactions of Larrea With Other Species as their deviations suggest recent invasion or reduced growth through interference.

One factor of the dynamics of the Shrub Desert Formation vegetation was the response of certain species to natural disturbances. At both Burro Mesa Pouroff Junction transects small erosion paths dissected the end plots of the desert pavement and created a suitable habitat for an

abundance of Erioneuron in and along the paths and the smaller more shallow side branches which extended into the adjacent plots. Accompanying Erioneuron along the west transect was Bouteloua trifida, lower in density and overall importance. A similar path diagonally cut across Plot V at Northeast Burro Mesa site (Fig. 11), creating a similar species response pattern. These situations were unavoidable when establishing the transects as the transects were so extensive; however, their results have provided insight into species responses to natural disturbances.

#### Succulent Desert Formation

The Succulent Desert Formation is a floristically more complex and heavily vegetated community than the Shrub Desert Formation and varies greatly from site to site. The major complexity arises from the different associations which are encountered and the distinct ecotone which separates the two formations. In this report the ecotone is considered an association of the Succulent Desert Formation, and because of its distinct physiognomy and dynamics will be discussed below in a separate section.

Six species were recorded as having dominant roles in the Succulent Desert Formation; however, only Cathastecum, Agave, and B. breviseta were of widespread importance. Hilaria mutica, Parthenium incanum, and Acacia greggii were of only local importance, the latter two being important at

the K-Bar site and the first at Burro Mesa Pouroff (West).

Several species were sampled exclusively in the Succulent Desert Formation plots in association with the above dominants. These were: Dalea aurea, Polygala obscura, Boerhaavia sp., Froelichia sp., Euphorbia simulans, Euphorbia eriantha, Machaeranthera pinnatifida, Dyssodia acerosa, Verbena neomexicana, Acleisanthes longiflora, Xanthocephalum sarothrae, Hilaria mutica, Calliandra conferta, Mimosa borealis, Dasyllirion leiophyllum, Echinocactus hamatacanthus, Echinocactus intertextus var. dasycanthus, Echinocactus intertextus, and Mammillaria tuberculosa. These species are not strictly confined to the Succulent Desert Formation, but were only sampled there. Accompanying these species are those species which occurred in the small isolated areas of Succulent Desert Formation within the Shrub Desert Formation. They are, however, more commonly associated with the Succulent Desert Formation. This list included: Ayenia microphylla, Allionia incarnata, Ruellia parryi, Trixis californica, Hibiscus denudata, Menodora longiflora, Menodora decemfida, Polygala macrodenia, Jatropha dioica, Bouteloua curtipendula, Setaria macrostachya, Panicum halli, Aristida glauca, Digitaria californica, Heteropogon contortus, Zexmenia brevifolia, Lycium pallidum, Lantana macropoda, Coldenia greggii, Portieria angustifolia, Opuntia imbricata, and Echinocereus viridiflorus.

The distribution of several important species of the Succulent Desert Formation can be discerned in Fig. 3-11. In addition to Cathestecum (at the western sites), Hilaria and B. curtispindula were also important (Fig. 8-9). The eastern sites had better developed and more typical succulent-grass vegetation. Trends were established at all western sites but did not appear as dominant in all the figures. At Burro Mesa Pouroff (West) Agave importance was low at plot V. Both Agave and B. breviseta occurred in plot VIII and V respectively at Northeast Burro Mesa and Kit Mountain, indicating a trend toward typical succulent-grass vegetation.

Floristically, the Succulent Desert Formation had four different associations as sampled: the Agave lecheguilla-Bouteloua breviseta (lechuguilla-chinograss) Assoc., Agave lecheguilla-Bouteloua curtispindula (lechuguilla-sideoats grama) Assoc., Agave lecheguilla-Hilaria mutica (lechuguilla-tobosa grass) Assoc., and the Cathestecum erectum (false-grama) Assoc. The first three associations are similar in physiognomy and quantitative characteristics, the last is distinct in both (Table 4). The major differences between the two physiognomic types are lower density of the Agave-Bouteloua vegetation, especially grasses, and a closer similarity of the Agave-Bouteloua cover and density values for succulents and grasses.

Table 4. Comparison of vegetative characteristics of two association types of the Succulent Desert Formation.

Characteristic	<u>Cathestecum</u> ecotone	<u>Agave-</u> <u>Bouteloua</u>
Species encountered	61	73
Species exclusive	6	10
Shrubs	16	17
Succulents	12	13
Grasses	13	15
Forbs	20	28
Species per plot (Mean No.) <sup>1</sup>	17 (9-23)	19 (14-25)
Density per plot <sup>1</sup>	3024 (592-4875)	540 (361-846)
Shrubs <sup>2</sup>	2	6
Succulents <sup>2</sup>	3	37
Grasses <sup>2</sup>	91	48
Forbs <sup>2</sup>	3	9
Mean percent cover per plot <sup>1</sup>	46 (31-57)	39 (27-59)
Shrubs <sup>2</sup>	25	29
Succulents <sup>2</sup>	13	33
Grasses <sup>2</sup>	58	33
Forbs <sup>2</sup>	3	5

<sup>1</sup> Range of values in parentheses

<sup>2</sup> Relative values

The contribution of the dominant species to relative density and cover presents a better understanding of their roles. Agave contributed 36% to succulent density and 25% to cover, whereas Bouteloua and Hilaria contributed 23% to grass density and 31% to grass cover. Cathestecum contributed 88% to the grass density and 51% to the grass cover of the ecotone.

An important factor of vegetation dynamics of the Succulent Desert Formation is the response of species to disturbance. B. trifida and Erioneuron are the most frequent inhabitants of disturbed areas, although Aristida glauca is a third associate. This response was most evident at the K-Bar (North) transect where it was observed that javelina frequented the last two plots to root and use a small erosion site which dissected plot V as a path. In this treaded area, B. trifida, A. glauca, and Erioneuron were important. In addition to the grasses in the treaded area several small established Larrea seedlings were present.

Another such rooting site was observed adjacent to the west transect at Northeast Burro Mesa. Here the area where the Agave was rooted by the animals was covered by Cathestecum within five months time. The stoloniferous grass exhibited rapid growth in response to the late summer and early fall showers which frequented the region. Where the grass is not present, the disturbed area probably follows the preceding pattern.

A small erosion pathway dissecting the last plot (V) of the Chilicotal (South) transect had an abundance of Polygala macrodenia and Heliotropium confertifolium individuals. After the main course left the plot, a small branch coursed down the transect into the Shrub Desert Formation plots where both species maintained rather high importance (IP = 1-10).

#### Cathestecum Ecotone

The Cathestecum ecotone community is complex due to its position between the two typical formations and its hybrid species composition. The ecotone is physiognomically different from all other vegetation types in the region, most closely resembling the extensive Buchloe dactyloides vegetation of the Central Plains short-grasslands. The prostrate, stoloniferous Cathestecum densely covers the soil surface, while species from the other two vegetation types provide additional cover and physiognomic character. The zone varies greatly in width and seems to play an important role in mediating the interactions between the two formations.

The ecotone vegetation was found to be most prevalent in the western section of the Park and covered long, narrow bands or irregular patches on flat, gravelly surfaces or gentle gravelly slopes. It did not occur in extensive expanses or on steep, rocky slopes where species of Bouteloua

and other grasses occurred. The stoloniferous means of vegetative reproduction may account for the more stable types of site occupied.

The ecotone varied in width from 16-20 m at Burro Mesa Pourroff (East) to beyond the 46 m transect end at Kit Mountain. The zone at Trap Mountain was approximately 107-122 m wide as the highway dissected the transects and accounted for the additional 30 m of cover. The zone had rather continuous cover at all sites except Northeast Burro Mesa (Fig. 11) where large areas of desert pavement interrupted the continuous pattern of cover. At all sites small areas 1-3 m in diameter broke the pattern also.

Within these small bare areas were located the many Shrub Desert Formation species and those which frequented erosion paths in the Succulent Desert Formation, such as Erioneuron, Aristida, B. trifida, and Larrea. Without exception the smallest established seedlings of Larrea occurring in this zone were in these small bare areas. In the adjacent covered areas the older Larrea shrubs may be completely surrounded by Cathestecum, even to the extent that the grass stolons become entwined in the numerous arising branches of the shrubs. On the other hand, the older Larrea individuals would have what appeared to be a maintained bare area surrounding their base. Generally, the area on slopes is elliptical with the greatest bareness



downslope from the caudex. Within this bare area Erioneuron, Aristida, and B. trifida were prevalent.

The Larrea individuals and bare areas are located near the Shrub Desert Formation boundary contact, whereas on the upper half of the ecotonal zone similar bare areas contain Agave, Bouteloua, or Hilaria. Again, Cathestecum may become entwined in the older Agave and grasses.

Several species were encountered which were only sampled in the ecotone. They were: Polygala obscura, Euphorbia simulans, Euphorbia eriantha, Machaeranthera pinnatifida, Echinocactus intertextus, and Calliandra conferta. The last four species occurred only at the Trap Mountain site, whereas the first species occurred only at Burro Mesa Pouroff (East). Euphorbia simulans was sampled at both Kit and Trap Mountains. Other species which most frequently occurred in the ecotone were: Ayenia microphylla, Zexmenia brevifolia, and Psilostrophe tagetina.

In the ecotone zone Larrea contributed 1.1% to the relative shrub density and 17% to relative shrub cover, whereas Cathestecum contributed 88% to relative grass density and 51% to relative grass cover (Table 4). These two species were the major contributions to the composition and physiognomy of the ecotone.

Species Behavior

One purpose of the study was to evaluate the possibility of the existence of species associates in community development and invasion of other vegetation. Since Larrea is the dominant plant of the Shrub Desert Formation and has received attention as a recent invader (Gardner, 1951; Branscomb, 1958; Humphrey and Mehrhoff, 1958; Yang, 1961; Buffington and Herbel, 1965; York and Dick-Peddie, 1969; Barbour, 1969b), the species associated with it are of major interest.

Table 5 represents a generalized transect which incorporates all 88 plots of the 16 transects and provides the species associated with Larrea in a theoretical transect spanning from "pure" Larrea to the complete absence of Larrea. All plots are ranked according to their percentage of relative Larrea cover and each species having a frequency of 50% or greater in each category has its relative cover percentage recorded. To demonstrate the actual variation obtained at the sites, the plots which lacked Larrea were divided into two categories: those dominated by Cathestecum ( $O^1$ ) and those dominated by Agave, Bouteloua, or Hilaria ( $O^2$ ).

Striking distribution and association patterns develop as Larrea cover decreases. Agave, B. breviseta, and Cathestecum cover increases significantly as Larrea cover decreases to 20-40%, however, Agave and B. breviseta

Table 5. Comparative relative cover values of species which have frequencies exceeding 50% with different plot cover percentages of Larrea.

Species	Relative Cover of <u>Larrea</u>						
	80-100	60-80	40-60	20-40	1-20	0 <sup>1</sup>	0 <sup>2</sup>
<i>Bouteloua breviseta</i>	1.0	1.7	4.0	7.3	15.0	3.4	28.2
<i>Erioneuron pulchellum</i>	.8	1.0	1.4	1.9	.8	.3	.9
<i>Bahia absinthifolia</i>	.3	.5	.4	.4	.2		.3
<i>Agave lecheguilla</i>		5.1	7.8	13.3	14.0	7.5	27.1
<i>Bouteloua trifida</i>		.1	1.1	1.0		3.0	.5
<i>Iva ambrosiaefolia</i>		.7	.1	.2			
<i>Opuntia engelmannii</i>			19.2	9.8	3.3	10.5	2.7
<i>Argythamnia neomexicana</i>			.4	.2	.2		
<i>Aristida glauca</i>			1.5	.9		1.8	1.2
<i>Prosopis glandulosa</i>			8.0	11.1			2.4
<i>Jatropha dioica</i>			6.1				7.2

Table 5 (Continued)

Species	Relative Cover of <u>Larrea</u>						
	80-100	60-80	40-60	20-40	1-20	0 <sup>1</sup>	0 <sup>2</sup>
<i>Opuntia macrocentra</i>				2.2	3.3	2.1	5.8
<i>Cathestecum erectum</i>				22.8	58.2	47.8	
<i>Krameria glandulosa</i>				4.1			
<i>Croton pottsii</i>					.9	2.1	
<i>Viguiera stenoloba</i>					4.1		4.6
<i>Coldenia greggii</i>						7.0	
<i>Aristida ternipes</i>						.8	
<i>Porlieria angustifolia</i>							5.6
<i>Echinocereus viridiflorus</i>							.1
Total Cover Percent	92.1	79.1	100.0	105.2	110.0	88.3	86.6
Number of plots	16	18	8	13	18	7	8

<sup>1</sup> *Cathestecum* dominant

<sup>2</sup> *Agave*, *Bouteloua*, *Hilaria* dominant

are low in the Cathastecum plots which lacked Larrea. The 20-40% cover category represents the last plots dominated by Larrea in actual site sequence and the 1-40% categories are the beginning of the Succulent Desert Formation vegetation which reaches maximum development in the areas where Larrea is absent. Several species exhibit a tendency for greater frequency and cover in areas with 20-60% Larrea cover, where the species which dominate the Succulent Desert Formation first occur or increase more in cover. Erioneuron, B. trifida, Opuntia engelmannii, Argythamnia neomexicana, A. glauca, Prosopis, Jatropha, and Krameria suggest this trend most strongly. Bahia and Iva usually have greater frequency and cover in the Larrea vegetation, whereas Croton, Coldenia, and A. ternipes are more important in the Cathastecum area. Porlieria and Echinocereus had greater frequency and cover in the Agave, Bouteloua, and Hilaria plots.

Even though the frequency criterion excluded many species and their respective cover percentages, the ranking procedure still gave a close approximation of 100% total relative cover for the sum of Larrea and the other species. Three categories had decreased cover totals due to low frequencies. In the 60-80% category Prosopis, O. engelmannii, and Opuntia leptocaulis accounted for 24% additional cover. Muhlenbergia porteri and Calliandra conferta had a combined cover of 10% which would increase the 0<sup>1</sup> category total. Two

species, Parthenium incanum and Cathestecum, would add 15% to category  $O^2$  with a lowered frequency criterion.

Several species which reached their greatest cover in the lower Larrea cover categories frequent disturbed areas in both formations, indicating that the transition zone is a zone of tension or community instability. To test this hypothesis further and relate transition species to Larrea, Table 6 was compiled. The species presented are those with transition position tendencies and occur in transects shown in Fig. 3-9. These transects were utilized as each had five plots and known disturbances could be omitted in the species cover calculations. The differences between the species values in plots I (stable Larrea vegetation) and III (transition vegetation) demonstrate their variable relationship to Larrea. As the cover values are actual means, the increased species values in the transition plots support their significance as indicators of community instability and early development and further substantiate the tension zone concept. All species except Bahia exhibited a four or more fold increase at the transition with respect to stable plots. Cover values of these species and the associated species provide insight into community development and succession. The associated species such as Agave, B. breviseta, Cathestecum, and other species more restricted to  $O^1$  and  $O^2$  would be replaced by other species where the transition borders on another vegetational dominance type. However,

Table 6. Mean cover (sq dm) for important transition species which occurred with Larrea in the site transects having five plots.

Species	I	II	III	IV	V
<i>Erioneuron pulchellum</i>	8.4	26.0	31.6	15.8	
<i>Bouteloua trifida</i>	.5	8.4	12.1	10.2	
<i>Bahia absinthifolia</i>	11.1	15.8	13.9	13.9	12.1
<i>Iva ambrosiaefolia</i>	.9	1.8	6.5	.5	
<i>Euphorbia</i> spp.	11.1	3.7	78.0	75.2	43.6
<i>Aristida glauca</i>	2.8	3.7	28.8	27.9	34.4
<i>Prosopis glandulosa</i>		153.3	189.5	203.4	61.3

no quantitative Larrea factor correlated with these species associations other than those suggested by the trends in Table 3.

The Cathestecum ecotone per se is not the transition just presented, but instead is an indicator species of the Succulent Desert Formation which may be present. The species (Table 6) were also present with increased importance where the Cathestecum ecotone contacted the Larrea vegetation. Many transition species occurred in the Cathestecum zone as well (Table 5). Discontinuous areas of Cathestecum and the other transition species can be indicators of the transition as demonstrated at Northeast Burro Mesa (Fig. 11). The increase of Erioneuron importance in the transition is also demonstrated in Fig. 3 and 6.

A series of species pairs may also be useful in relating developmental direction to the community. Coldenia greggii-Coldenia canescens, Hibiscus denudata-Hibiscus coulteri, and Dyssodia acerosa-Dyssodia pentachaeta are three such combinations which appeared in this study. The first species listed of each pair are most common in the Succulent Desert Formation and the last one of the pair is more confined to the Shrub Desert Formation. Increased information of this nature can contribute to differentiation of other subordinate species associates which aid in community development analysis.



## CHAPTER VII

### RESULTS OF SOIL ANALYSES

The percentage of rock ( $>22$  mm) was significantly greater at both soil depths in the Succulent Desert Formation than in the Shrub Desert Formation (Table 7). Reciprocally, the percentage of gravel (2-22 mm) and sand-silt-clay ( $<2$  mm) was significantly greater at both depths in the Shrub Desert Formation. These differences were seemingly correlated with the type of parental material. The Succulent Desert Formation is dominant on the eroding igneous derived soils supported by igneous parent materials, whereas the Shrub Desert Formation is dominant on the recent alluvial soils. Significant differences in the basic textural components were not found, although silt and clay percentages were higher in the Succulent Desert Formation.

The infiltration rate was significantly higher in the Succulent Desert Formation than the Shrub Desert Formation, indicating more non-capillary pore space in the former. Field capacity was significantly higher in the Succulent Desert Formation, and soil moisture was higher at both levels in April based on a gravimetric procedure. Soils with a high infiltration rate would generally have

Table 7. Mean values of selected soil factors for formations and transition zone. A, 0-15 cm depth; B, 15-30 cm depth.

Soil Factor	Shrub Desert Formation		Transition Zone		Succulent Desert Formation	
	A	B	A	B	A	B
<b>Particles (%)</b>						
Rock (>22 mm)	19.0 <sup>a</sup>	29.0 <sup>b</sup>			44.0 <sup>a</sup>	55.0 <sup>b</sup>
Gravel (2-22 mm)	50.0 <sup>a</sup>	43.0 <sup>b</sup>			37.0 <sup>a</sup>	29.0 <sup>b</sup>
Sand-Silt-Clay (<2 mm)	31.0 <sup>a</sup>	28.0 <sup>b</sup>			19.0 <sup>a</sup>	16.0 <sup>b</sup>
<b>Texture (%)</b>						
Sand (2.0-0.02 mm)	73.0	68.0	73.0	66.0	68.0	63.0
Silt (0.02-0.002 mm)	10.0	11.0	9.0	11.0	10.0	13.0
Clay (<0.002 mm)	17.0	21.0	18.0	23.0	21.0	24.0
pH	8.7	8.6	8.6	8.6	8.1	8.3
Calcium carbonate (%)	6.0 <sup>c</sup>	9.9 <sup>c</sup>	5.8 <sup>d</sup>	10.0 <sup>d</sup>	4.5 <sup>e</sup>	9.3 <sup>e</sup>
Organic carbon (%)	0.44 <sup>a</sup>	0.47 <sup>b</sup>	0.52	0.52	0.87 <sup>a</sup>	0.81 <sup>b</sup>

Table 7 (Continued)

Soil Factor	Shrub Desert		Transition		Succulent Desert	
	Formation		Zone		Formation	
	A	B	A	B	A	B
Total nitrogen (%)	0.065 <sup>a</sup>	0.063 <sup>b</sup>	0.071	0.074	0.097 <sup>a</sup>	0.094 <sup>b</sup>
Total phosphorus (%)	0.034	0.028	0.052	0.039	0.044	0.036
Infiltration (sec)	52.5 <sup>a</sup>				24.6 <sup>a</sup>	
Field capacity (%)	10.3 <sup>a</sup>				12.4 <sup>a</sup>	
Moisture (%-April 1968)	6.1	6.6			7.1	8.2
Delmhorst Blocks	3.0	3.3	2.9	2.5	1.9	1.9
(bars-Summer 1967)						

a,b,c Significant difference ( 0.01) between same superscript of same soil factor

d,e Significant difference ( 0.05) between same superscript of same soil factor

considerably more available water in an arid area since most of the rain falls in a torrential fashion as in Big Bend.

Total carbon was significantly higher in the Succulent Desert Formation at both soil depths and nearly double the amounts in the Shrub Desert Formation. Total nitrogen was significantly higher in the Succulent Desert Formation also. The values in the transition zone were intermediate for both elements. Total phosphorus was higher at both levels in the Succulent Desert Formation than in the Shrub Desert Formation, but amounts in the transition zone were higher than in either formation. Erosion may account for the higher amount of phosphorus in this zone. Soil analyses of both formations demonstrated the effects of the arid soil building climate with significantly greater calcium carbonate in the 15-30 cm depth than in the 0-15 cm depth. The amount of carbonate was greater at both depths in the Shrub Desert Formation than in the Succulent Desert Formation. Even though the pH was not significantly different in the two formations the trend corresponded with the carbonate levels.

Larrea is the only plant which controls the physiognomy of the Shrub Desert Formation, but this is not the case with the Succulent Desert Formation as the soils support four different association types (Table 8). Statistical analyses are not available for the characteristics, but sound trends seem established for the associations. The most variant physical characteristics were found in both the

Table 8. Comparison of soil factors supporting vegetation associations of the Succulent Desert Formation.

Soil Factor		<u>Agave-</u> <u>B. brevi-</u> <u>seta</u>	<u>Cathestecum</u> <u>erectum</u>	<u>Agave-</u> <u>B. curti-</u> <u>pendula</u>	<u>Agave-</u> <u>Hilaria</u>
Particles:					
Rock	A <sup>1</sup>	55.0	44.0	82.0	35.0
	B <sup>2</sup>	65.0	50.0	70.0	72.0
Gravel	A	36.0	37.0	12.0	44.0
	B	28.0	33.0	21.0	8.0
Sand, etc.	A	19.0	19.0	6.0	21.0
	B	14.0	17.0	9.0	20.0
Texture:					
Sand	A	70.2	71.5	57.9	44.6
	B	63.0	67.3	56.9	34.9
Silt	A	11.9	7.8	15.1	10.4
	B	13.4	12.7	15.7	11.7
Clay	A	17.8	19.9	27.0	45.0
	B	23.6	20.0	27.4	53.4
pH	A	8.4	8.3	7.2	9.7
	B	8.4	8.4	7.6	10.0

Table 8 (Continued)

Soil Factor		<u>Agave-</u> <u>B. brevi-</u> <u>seta</u>	<u>Cathestecum</u> <u>erectum</u>	<u>Agave-</u> <u>B. curti-</u> <u>pendula</u>	<u>Agave-</u> <u>Hilaria</u>
Calcium	A	6.7	3.1	0.5	10.7
carbonate	B	11.9	7.5	1.1	15.3
Organic	A	1.01	0.66	1.48	0.17
carbon	B	1.03	0.62	1.05	0.43
Total	A	0.115	0.078	0.122	0.052
nitrogen	B	0.118	0.073	0.087	0.052
Total	A	0.031	0.038	0.104	0.100
phosphorus	B	0.027	0.037	0.065	0.050
Infiltration	A	22.6	25.1	36.0	16.0
Field capacity	A	11.7	11.3	13.4	23.0
Percent	A	5.8	7.1	11.1	11.2
moisture	B	7.0	7.4	12.7	19.5

<sup>1</sup> 0-15 cm depth

<sup>2</sup> 15-30 cm depth

Agave-Hilaria and Agave-B. curtipendula associations. The Agave-B. curtipendula Assoc. had the highest rock percentage for the entire study at the 0-15 cm depth, while the Agave-Hilaria Assoc. had the highest at the 15-30 cm depth. Only the soils of the Agave-B. curtipendula Assoc. and a Larrea dominated site at K-Bar approached the high clay values of the Agave-Hilaria Assoc.

The Agave-Hilaria and Agave-B. curtipendula Assoc. differed the most with respect to chemical characteristics also. The highest pH values for the study were recorded in the former association while the lowest were recorded in the latter. The calcium carbonate levels were high and low respectively for the two formations, but do not represent extreme values for the study. The highest values were recorded for the Agave-B. breviseta Assoc. at the Chilicotal Mountain site. Both the Agave-Hilaria and the Agave-B. curtipendula Assoc. had high phosphorus values, with the highest values for the study recorded in the 0-15 cm depth at the transition zone of both transects. Organic carbon and nitrogen values were comparatively lower in the Agave-Hilaria Assoc., but carbon was comparatively higher in the Agave-B. curtipendula Assoc.

The Agave-Hilaria and Agave-B. curtipendula vegetation both had soil types with varied soil moisture characteristics. The Agave-B. curtipendula Assoc. had the slowest infiltration rate of the formation, but the rate was still

more rapid than in the Larrea formation. The Agave-Hilaria Assoc. on the other hand had a much more rapid infiltration rate than other Succulent Desert Formation associations. The high clay content of the Agave-Hilaria Assoc. soil was again revealed in the high field capacity which was the highest recorded in the study and nearly double the next highest value (13.7) recorded for a Larrea site at K-Bar. The moisture percent in the Agave-Hilaria Assoc. was also the highest recorded for the study with the Agave-B. curtipendula value second. Only a Larrea dominated site at K-Bar with a high field capacity rivaled the two values.



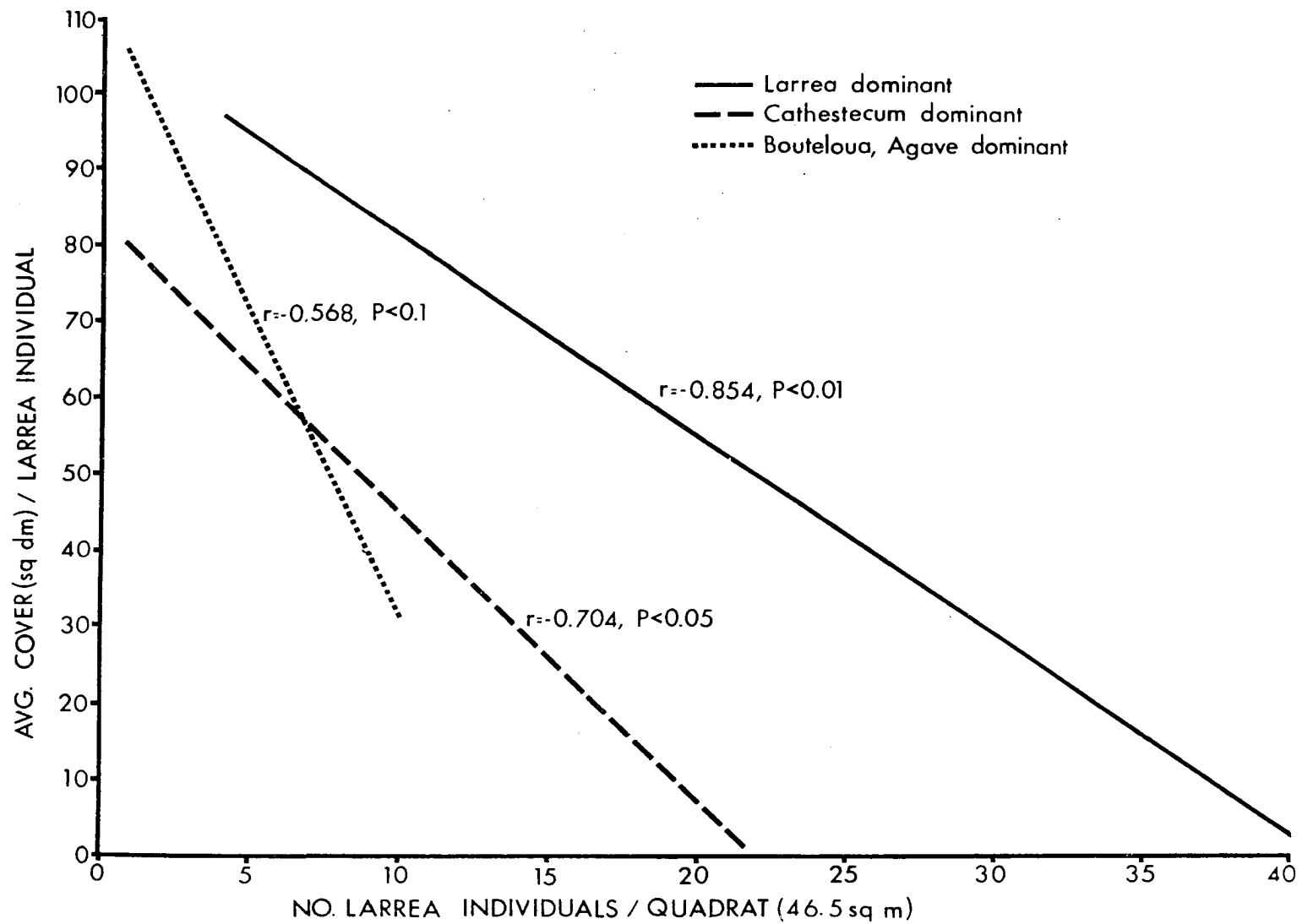
## CHAPTER VIII

### INTERACTIONS OF LARREA WITH OTHER SPECIES

The distribution and establishment of Larrea in Big Bend National Park suggests a keen interaction between Larrea and the other vegetation at a competitive or other biological level superimposed on basic substrate differences.

In an attempt to test this hypothesis, all 176 subplots or quadrats in the study were ranked according to the number of Larrea individuals per quadrat with their respective average cover per individual. Correlation coefficients were calculated for the Larrea of the three major dominant vegetation types and their regression lines were plotted (Fig. 12). It is evident that one or more of three hypotheses may account for the smaller size of the Larrea in the non-Larrea dominated vegetation if one assumes that the substrate conditions for the growth of Larrea were equal to or better than in areas where it is dominant. The three major hypotheses are the plants are smaller because of: 1) their younger age, 2) competitive or allelopathic interference from other species, and 3) genetic differences (ecotypic variation). The last

Figure 12. Regression lines correlating number of Larrea individuals per quadrat (subplot) with average cover per individual of Larrea for three vegetation types possessing that species.



hypothesis cannot be approached at this time since data concerning this form of variation are not available. The first two are suspected to be the chief differences.

Twenty-six Larrea individuals taken from the Succulent Desert Formation vegetation at all sites except Trap and Chilicotal Mountains were scored as to the number of caudex rings they possessed and correlated with their respective cover diameters (Fig. 13). There was a strong positive correlation between cover class and the age (ring number of caudex). The number of rings produced per year is not known for the Larrea of this region, however, Chew and Chew (1965) reported that a single ring was produced by Larrea in southern New Mexico, based upon known established individuals.

The 1648 Larrea individuals sampled in the study were divided into cover classes of 15.2 cm intervals to a diameter of 152.4 cm and the last class, 11, for those individuals greater than 152.4 cm in cover. The Cathestecum vegetation had a greater percentage of its Larrea population in the smaller or younger categories than did the other vegetation types (Fig. 14). It had 68% of its Larrea population in the 1-5 cover class, while Bouteloua and Larrea had 59% and 57% respectively. The Cathestecum population of Larrea dropped sharply after the 6<sup>th</sup> cover class and maintained low cover class percentages, whereas the larrea population in the Bouteloua vegetation maintained

Figure 13. Regression line correlating number of Larrea caudex rings with its diameter cover classes. Each class is a 15.2 cm diameter interval.

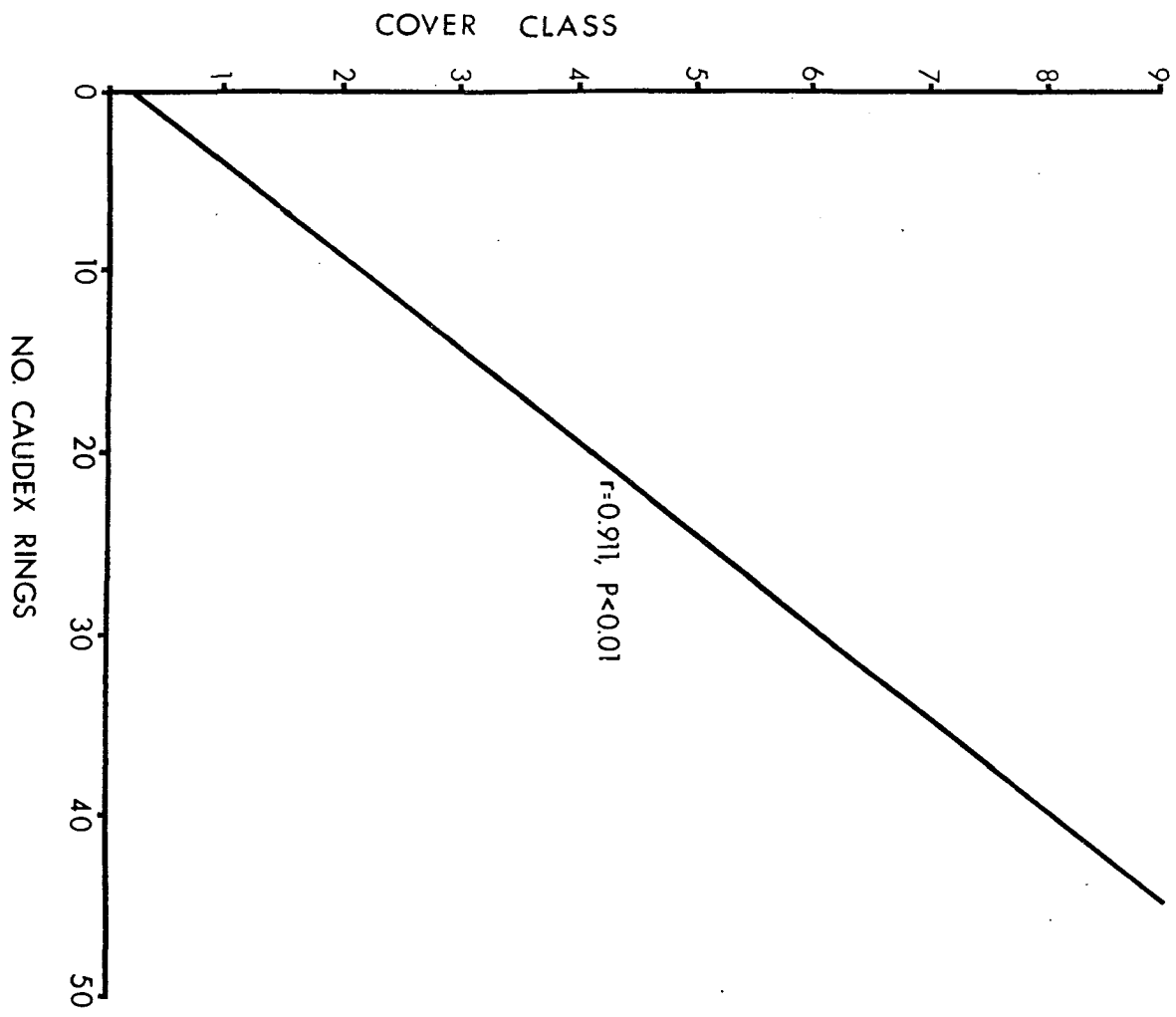
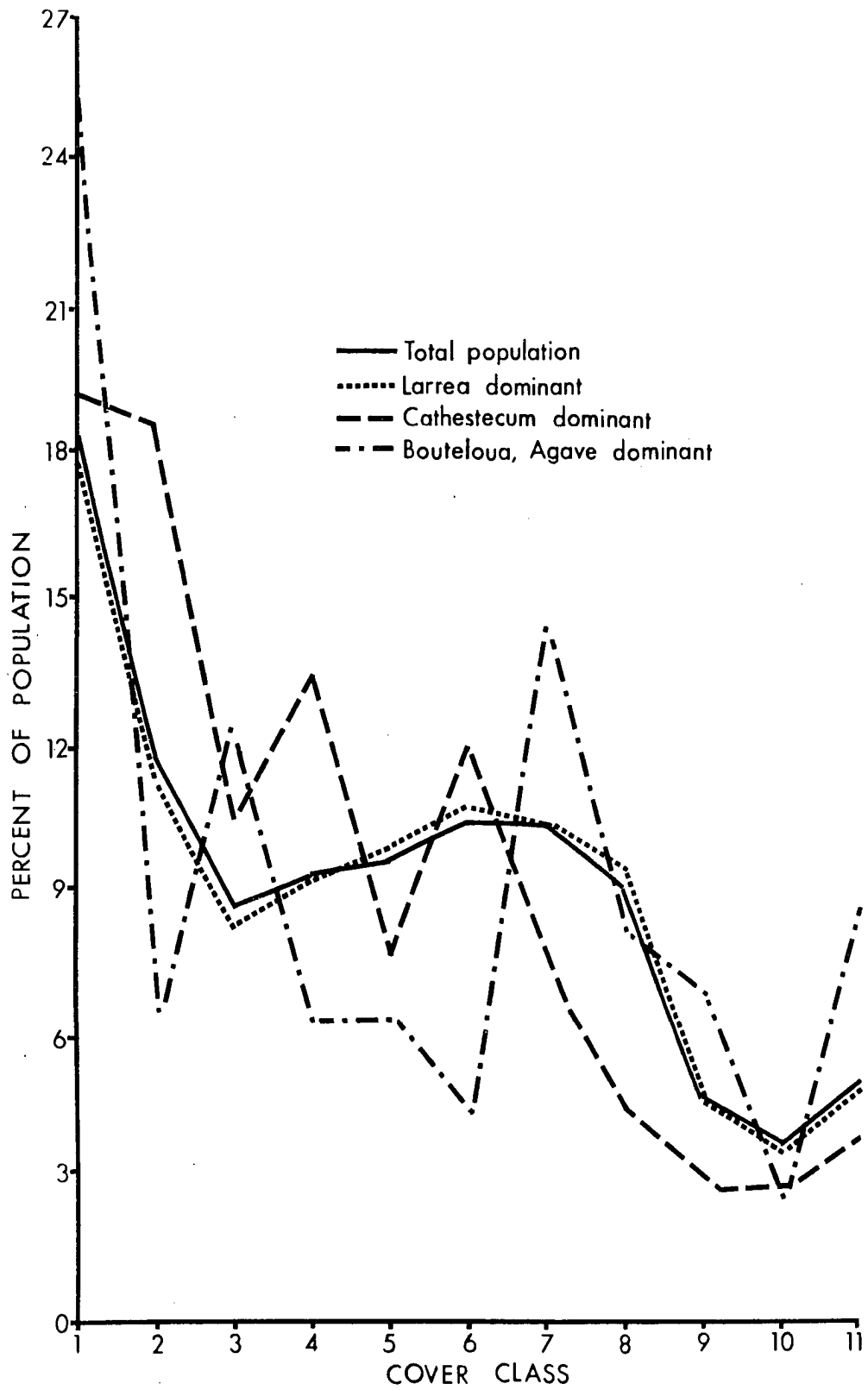


Figure 14. Larrea population cover class distributions for three vegetation types possessing that species.





higher percentages of larger class size, indicating a bimodal curve of cover class distribution.

These population structures suggest that the establishment of Larrea has not been at a uniform rate in the Cathastecum and Bouteloua vegetation, assuming that Larrea growth rates have been relatively uniform. Figure 12 suggests the contrary, but the degree of interaction between the vegetation of the Succulent Desert Formation and Larrea growth is not available. The isolated peaks and lows suggest different group invasion times with relatively uniform sized individuals within the group. If such a dynamic scheme is real, growth behavior of Cathastecum could account for such Larrea establishment groups.

In the Cathastecum ecotone Larrea plants of size class 1 and the majority of class 2 were not recorded or observed in the dense Cathastecum cover, but were instead established in the open desert pavement areas of the ecotone. This suggested that a form of "interference exclusion" was functioning in Larrea seedling establishment, but once the seedling is established it can tolerate Cathastecum cover. The same mechanism could be operative in the Bouteloua-Agave vegetation also.

Cover class distributions of Larrea were plotted for the sites to further test the vegetative exclusion mechanism (Fig. 15, 16). Only Trap, Kit, and Nugent

Figure 15. Larrea population cover class distributions at three sites suggesting recent Larrea establishment.

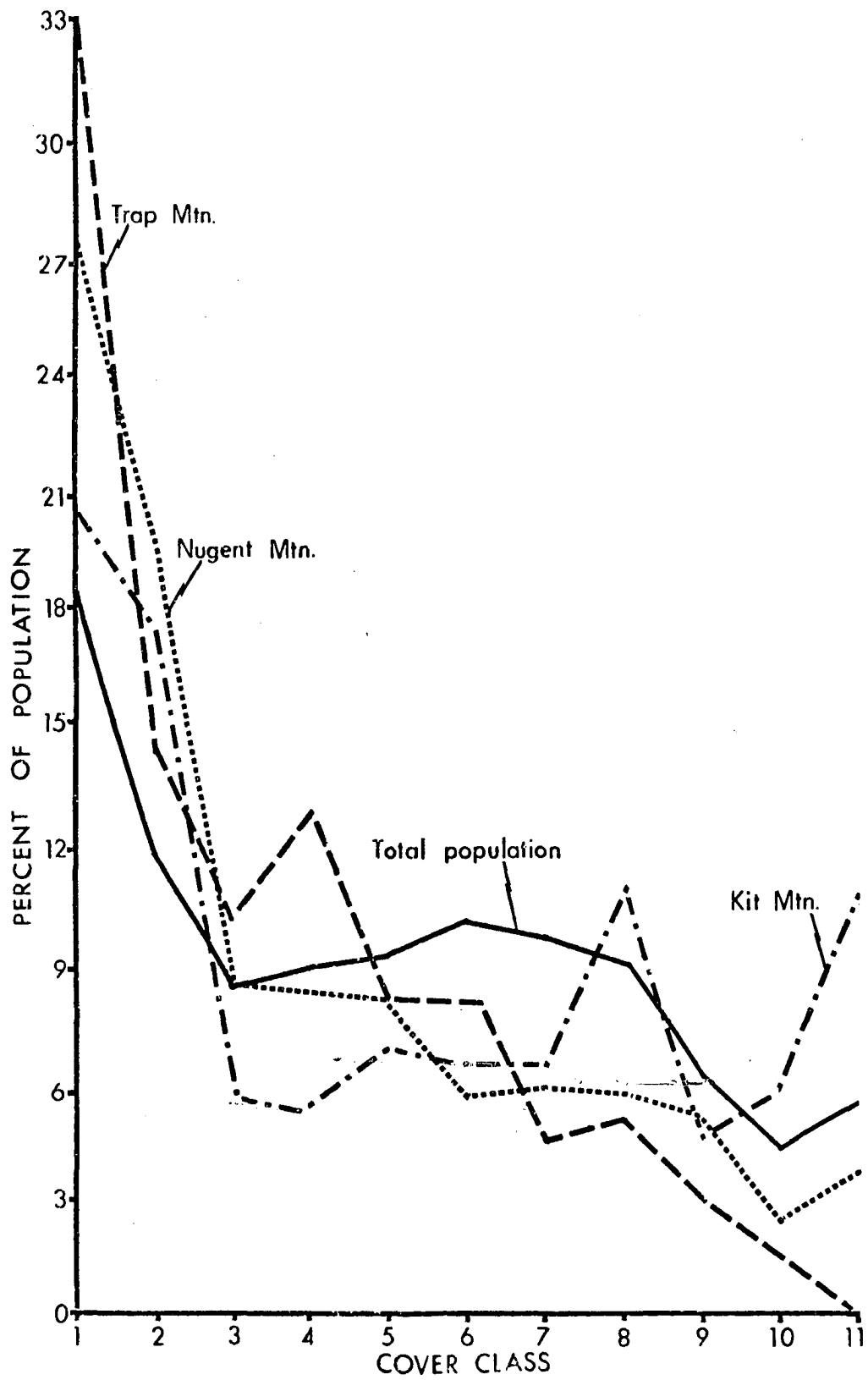
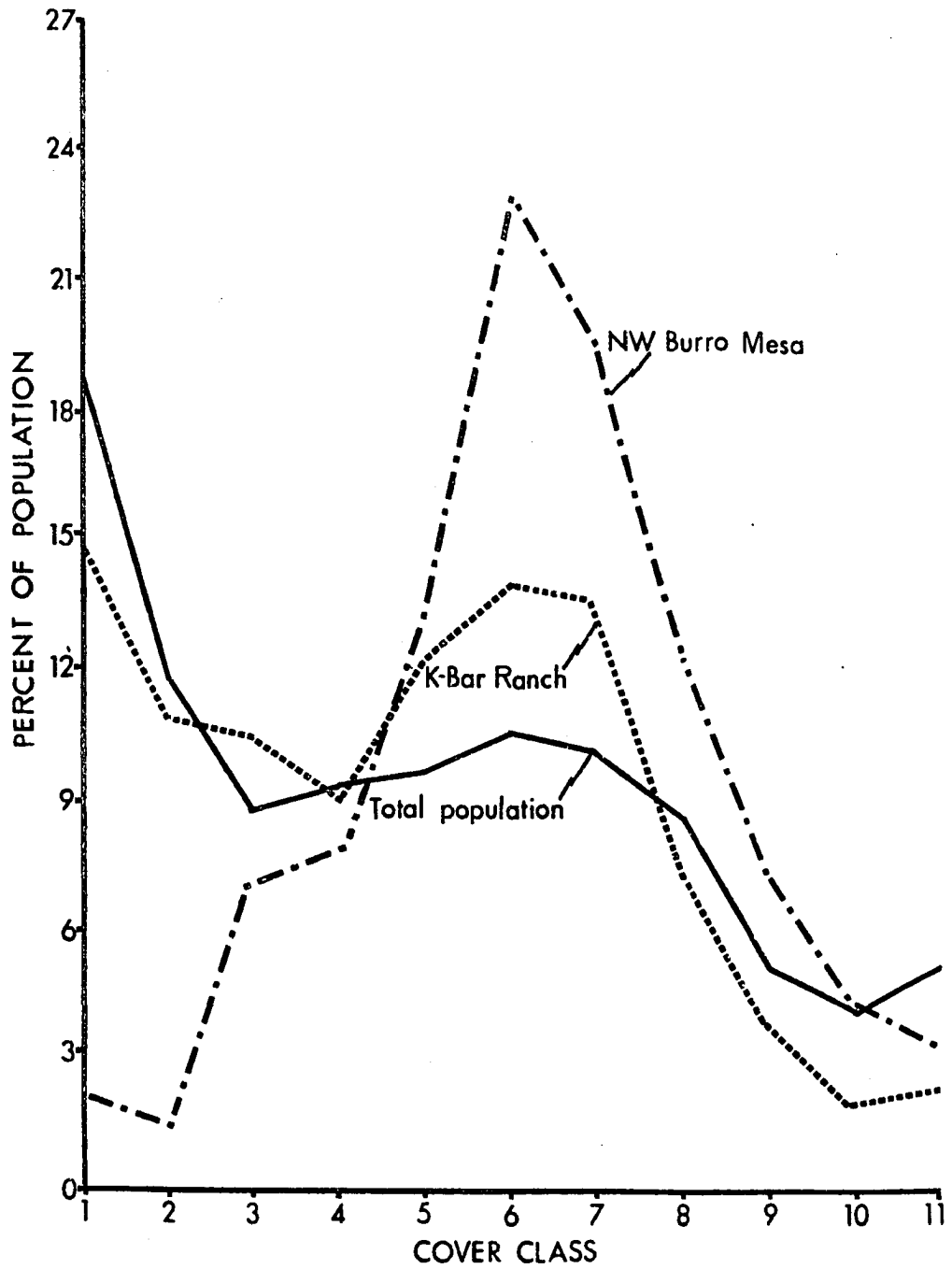


Figure 16. Larrea population cover class distributions for two sites suggesting no major recent Larrea establishment.



Mountain sites displayed a recent Larrea population expansion above that of the Total Population. At these sites the recent large establishments deviated greatly from sites like Northwest Burro Mesa and Burro Mesa Pour-off Junction which had bell-shaped cover class distributions and from Chilicotal, K-Bar, and Northeast Burro Mesa which had more even cover class distributions.

Of interest in the site cover class curves are those belonging to the first group; both Trap and Kit Mountain sites had broad Cathestecum ecotones. The Nugent site, selected as a test for method sensitivity, had two small dirt roads which dissected the Larrea vegetation and provided known disturbances in the study plots which accentuated Larrea establishment.

The Larrea cover class distributions of the three most dynamic sites were considered further with respect to their position along the transects (Table 9). The total number of Larrea individuals in each cover class for both transects at each site were placed in their respective numbered plots. The Larrea dominated plots (I-II or I-III) were summed, however, to reduce complexity. Based upon the number of individuals within a class size, Larrea establishment groups existed in both the Larrea and non-Larrea dominated vegetation. In non-Larrea dominated vegetation (III-V or IV-V), for example, several individuals occurred in the 1-3 and 8-10 cover classes at Nugent Mountain,

2.

[illegible]

but few or no individuals occurred in the intermediate cover classes. This suggests that Larrea establishment was extremely low for 25 ring growth seasons in plot IV and above 40 for plot V with extrapolations from Fig. 13. The number of cover classes and Larrea individuals within them decreased markedly as the plot distance increased from the transition.

These evidences demonstrate that Larrea establishment is possible in the Cathestecum and Bouteloua-Agave dominated vegetation, but that an interference exclusion mechanism is functionally operative in limiting reproductive pressure exerted by Larrea along the Shrub Desert Formation boundary. These small more isolated groups suggest that Cathestecum has retreated to variable distances in the past and left bare pavement for Larrea establishment.



## CHAPTER IX

### DISCUSSION AND CONCLUSIONS

#### Factors Promoting Sharp Vegetation Delineation

Edaphic factors: The sharp line of vegetation demarcation along the Shrub Desert Formation and Succulent Desert Formation transition in Big Bend National Park appears to be presently determined by substrate materials and those edaphic factors which are altered or controlled by the resident vegetation. Abrupt vegetation changes cited by Shreve (1922, 1925), Fosberg (1940), and Waterfall (1946) for Larrea and adjacent vegetation in various parts of its North American range have also been attributed to substrate changes.

A major factor of substrate contribution in Big Bend is the increased percentage of igneous particle sizes above the basic textural range in the Succulent Desert Formation. These large particles or rocks effectively contribute to increased infiltration and soil moisture by reducing runoff and erosion with their damming effect. In addition to damming smaller soil particles and rainfall runoff, large quantities of organic matter are stabilized and incorporated into the soil improving both moisture

capacity and mineral levels. The more mesic succulent-grass vegetation type is supported by these edaphic factors, whereas the Larrea dominated vegetation is supported by the drier, finer soils.

Superimposed upon the basic substrate differences are the ameliorating effects which the vegetation contributes to edaphic factor variation. The more extensive cover of the Succulent Desert Formation reduces isolation at ground level and provides a greater number of microclimates to support various species. Not to be excluded are the extensive root systems of the grasses which assist in increasing moisture and mineral levels upon decay.

The Agave-Hilaria and Agave-B. curtispindula associations of the Succulent Desert Formation had the most restricted edaphic factors, although Agave occurred at nearly every factor range in the study. The Agave-Hilaria site edaphic factors were similar to a Hilaria site east of Alpine, Texas, on deep, heavy, basic clay soils (Cottle, 1931). An Arizona Hilaria site was comparable (Johnson, 1961), as were soil descriptions for southern New Mexico (Gardner, 1951) and far West Texas (Williams, 1970). Soil moisture characteristics of the Agave-Hilaria and Agave-B. curtispindula association soils were higher than those of other vegetation types encountered.

The Agave-B. curtispindula site factors of this study were similar to an Arizona site (Johnson, 1961),

although the soil texture and pH values were respectively finer and lower there. Great variation could be expected as the species is widely distributed even within the Park (Whitson, 1970). Comparative data are not available for the Agave-B. breviseta Assoc. sites, although Waterfall (1946) reported B. breviseta as a gypsophile in his western Texas-New Mexico study. A site supporting both species on limestone in the Chisos Basin (Whitson, 1970) had a recorded carbonate value of 58%, but this study indicates that igneous substrates are also dominated by the two species.

A similar lack of comparative data exists for Cathestecum with only Harvard's (1885) citation of its first notice in the United States. He sighted it frequently on the bluffs of the Rio Grande from El Paso to the Great Cañon (Santa Elena) in the present Park. The soil factor ranges are similar to those occupied by Larrea, but the flat or gentle slope of the habitat is specific.

Edaphic site values for Larrea vegetation are comparable to the ranges reported by Mallery (1935), Yang (1950), and Johnson (1961) for Arizona and Giles (1961) for New Mexico. Only the values reported by Valentine and Norris (1964) for New Mexico Larrea sites on gypsum differed appreciably. Because Larrea vegetation approaches a single species community rather than a group of species, the community site factors are much broader and approach

the variation of a single species distribution. The recent reports by Yang (1967a; 1967b; 1970; Yang and Lowe, 1968) and Barbour (1969a) of ecotypic variation in Larrea for the North American deserts substantiate the plastic nature of the species and indicate that divergence has occurred within the species to form physiological and morphological races.

Succulent Desert Formation Interference: A second contribution to the sharp line of demarcation between the two vegetation types is postulated to be the presence of the Succulent Desert Formation vegetation and the alteration of the edaphic factors to exceed the tolerances of the Larrea vegetation type. Because the individual species of both formations frequently occurred on both ends of the transects and the substrate changes were not always closely accompanied by a sharper vegetation change, it was hypothesized that the vegetation and the associated edaphic factors promote a form of interference exclusion. This extends Gause's (1934) "competitive exclusion" concept to communities rather than species. Wells (1960) elaborates on this concept for plant communities and suggests that the width of an ecotone between two plant communities is inversely proportional to the differences in physiognomy and physiology which render them incompatible. The vegetation studied demonstrated great physiognomic differences, although specific physiological implications

are lacking. Buffington and Herbel (1965), York and Dick-Peddie (1969), and Gardner (1951) have postulated that the dense grass cover with its compact root systems act as barriers excluding Larrea. Similar reports by Miller, Parker, and Wolff as cited by Ellison (1938) suggest grasses as limiting barriers against juniper encroachment. These concepts suggest that the physiognomy must also be extended to subsurface physiognomy in addition to the areal aspects.

The Cathastecum ecotone exemplifies a very distinct physiognomic and dynamic zone or population which effectively separates and limits the two typical formation types. Although the ecology of the species is poorly known, the role the species plays in covering bare desert pavement and limiting Larrea and succulent-grass distribution is extremely effective. A utilization of the dynamic behavior of this species may be effective in rehabilitating or halting Larrea encroachment sites.

Shrub Desert Formation Interference: An interference mechanism which possibly contributes to the sharp line of vegetation demarcation is the effect of Larrea upon the sites it invades or controls. A uniform characteristic of the Larrea community is the bare pavement which appears to be the result of Larrea presence and not a feature of the areas invaded by Larrea (Gardner, 1951). Larrea invasion into grasslands of southern New Mexico

(Gardner, 1951) often demonstrates rather sharp lines of vegetation demarcation on the same substrate, a situation like the bare pavement areas within the Cathestecum ecotone in Big Bend which possess Larrea on uniform substrates and soils.

A factor consistent in this study was the dense, compact surface layer of desert pavement soil which could assist in the limitation of the succulent-grass vegetation species in the Larrea dominated vegetation. The compact layer was noticed most when the cylinder for recording infiltration rates was forced into the soil supporting the Larrea vegetation. The layer varied in thickness in the two formations, but was consistently denser and thicker in the Larrea community. Several environmental factors could contribute to the crustal layer such as rainfall compaction, wind, and erosive forces, but the possible effects of Larrea cannot be excluded.

As Knipe and Herbel (1966) reported in their laboratory experiments, extracts of Larrea material reduced water infiltration, a factor also found reduced in natural habitats. No mechanism was offered to account for the phenomenon, which they strongly suspected accounted for the reduced test plant growth rather than possible toxic substances within the extract. A substance that I suspect to be important in explaining their results and also in contributing to or causing the observed soil crust is the

sticky resin which gives Larrea its characteristic odor (Runyon, 1934). Duisberg (1952) reported that 29-35% of the leaf dry weight is resin, whereas the phenolic compound nordihydroguaiaretic acid ranged from 6-10%.

Field experience revealed that the sticky resin functions as an excellent adhesive substance and cements small soil particles together or to other plant materials. Because the resin hardens with age (Runyon, 1934), it could theoretically seal the upper soil surface after years of falling leaves and twigs have increased the build-up of the relatively water insoluble substance. This could be extremely important in limiting the infiltration of water into the soil. Since the substance is not correlated with physiological drought resistance (Duisberg, 1952), a mechanical mechanism of drought resistance, reduced competition through mechanical manipulation of edaphic factors, has apparently evolved in Larrea community dynamics. Only disturbance of the crust can permit further invasion of Larrea or other species, and large quantities of rainfall are required to saturate the soils to effectively support additional plants in the community.

#### Factors Promoting Larrea Establishment

The major mechanism which promotes the invasion and establishment of Larrea is denudation or disturbance as was pointed out by Shreve (1942) and later reemphasized by Lowe (1958-9). The important point is that the

disturbance need only be a small area for the establishment of a single pioneer plant, which may then promote a population (Gardner, 1951). The disturbance appears to disrupt the multiple factor exclusion barrier allowing Larrea establishment. The recent areas of Larrea establishment or replacement in Big Bend National Park are areas which have been mechanically denuded by man or more naturally disturbed by domestic and native animals such as javelina or by the forces of erosion. The effects of grazing and human activities in reducing grass cover and assisting Larrea establishment were documented by Gardner (1951), Humphrey and Mehrhoff (1958), Branscomb (1958), Buffington and Herbel (1965), and York and Dick-Peddie (1969) in the southwest. Maxwell (1968) and Whitson (1970) cited such establishment effects for the Park. This reduction mechanism was cited for Prosopis or Flourensia expansion by these authors also.

In addition to the rooting areas of javelina which create bare areas, studies by Greene and Murphy (1932) and Greene and Reynard (1932) indicate the rodents Dipodomys spectabilis (Kangaroo rat) and Neotoma albigula (Pack rat) contribute to higher nitrogen, phosphorus, and soil moisture capacity in their disturbed burrowing areas. These edaphic effects in addition to the carpel husking and caching behavior of Dipodomys merriami could promote germination and establishment of Larrea (Chew and Chew, 1970).



Another mechanism which may contribute to a denudation process to promote Larrea establishment is that of chemical interactions between plants. The presumed interactions are the allelopathic effects of Euphorbia capitellata upon the vegetation pattern at Burrow Mesa Pourouff (West). In plots III and IV (Fig. 8) the herb was extremely abundant in both living and dead or decaying condition. The vegetation pattern relates primarily to the lack of Cathestecum in the irregularly shaped areas of Euphorbia occurrence. In these areas, Agave and Jatropha individuals were discolored and appeared in poor condition when compared with others in adjacent areas, although Larrea was judged unaffected by the Euphorbia. Also present in the areas, but in greater abundance, were Bahia and Erioneuron. Investigations on related species of Euphorbia (E. corollata, E. supina, and E. marginata) in Oklahoma by Rice (1965a, 1965b), Brown (1968), and Blum and Rice (1969) indicate inhibitory effects upon native and test plant species grown in soils from under Euphorbia and leachates or extracts of living or dead Euphorbia material. Gallic acid and gallotannins were reported by Rice (1965a, 1965b) as inhibitory compounds isolated from the Oklahoma species of Euphorbia. The interaction of plants in creating bare areas or reducing vegetation cover has received renewed emphasis recently (Muller, 1966; Rice, 1967).

Larrea Community Development and Change

Development: Several species were associated with Larrea invasion and early community development or disturbance within the mature Larrea community. The most firmly established species in this study were Erioneuron, B. trifida, Euphorbia spp., Argythamnia, Iva, and Prosopis. Data reported by Johnson (1961) demonstrated similar species associations with Larrea for a transect spanning several vegetation communities in southeastern Arizona. Along the transect Erioneuron frequency increased greatly from a Larrea community (8%) through a Larrea-Parthenium community (24%), to a Larrea-Bouteloua ecotone (52%) and dropped sharply in the Bouteloua eriopoda community (2%). He also stated that many small Larrea plants were established in the ecotone which suggests recent Larrea encroachment into the Bouteloua community. Accompanying Erioneuron with similar frequency distribution patterns were Croton texensis, Menodora scabra, and Krameria glandulosa.

A distinct characteristic of the mature Larrea community is the reduced number of species. Johnson (1961) and Buffington and Herbel (1965) all demonstrated associated species reduction in Larrea controlled sites.

Change: Several species were associated with Larrea which signify community change with time and correlate with the vegetation Larrea may have originally invaded. Agave, B. breviseta, and Cathestecum were the most distinctive.

Since the dynamic pattern is frequently unknown, the direction of change--Larrea invasion or associated species reinvasion--is difficult to assess, but Larrea age and the degree of desert pavement development may be used as additional evidence. Because many years are required to change from one vegetation dominance type to another, site use and climatic effects alter the associated species patterns.

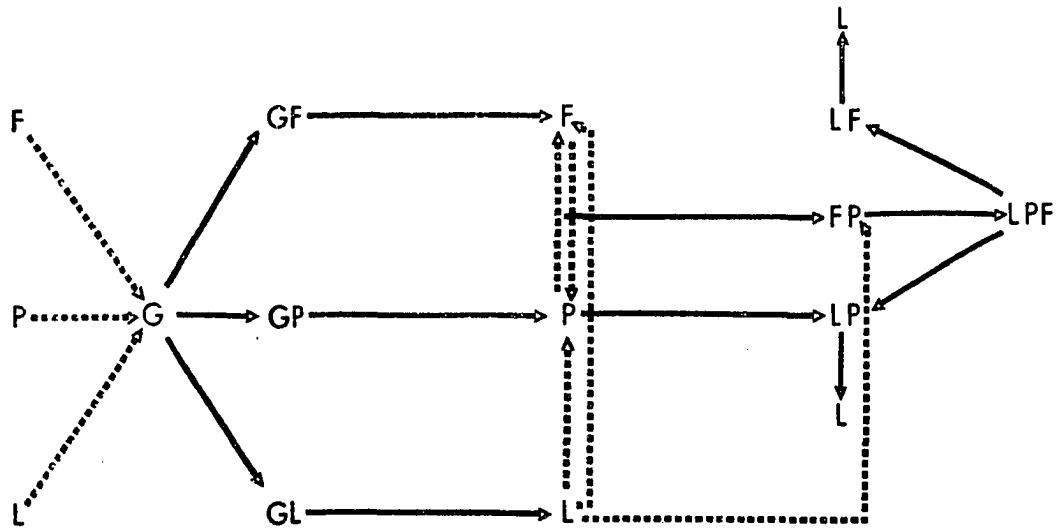
The permanent plot studies of Arizona report substantial data for Larrea community analysis. As Shreve and Hinckley (1937) reported, the greatest change with time in the community occurs in the small-sized and short-lived species groups such as grasses and half-shrubs. Near steady increases in frequency and cover of the shrubs Fraseria deltoidea, Krameria grayi, and Krameria parvifolia were reported by Shreve and Hinckley (1937) and Murray (1959) after 8 and 29 years respectively for the same permanent sites (Area B). Shreve and Hinckley (1937) and Gible (1950) reported similar species increases for other Larrea community plots of 30 and 19 years duration. The plot changes trend toward greater density, cover, and species composition, with the Larrea population increasing in numbers (Area B), but decreasing in average individual cover.

Successional patterns of vegetation change can be derived from Buffington and Herbel (1965), York and

Dick-Peddie (1969), Gardner (1951), Muller (1940), and Branscomb (1958) for the northern Chihuahuan Desert vegetation. Buffington and Herbel (1965) reported that since 1858 numerous acres, earlier dominated by Flourensia and Flourensia-Prosopis, have been invaded by Larrea. In both areas little or no reproduction of Flourensia and Prosopis occurred as Larrea gained greater control of the area. Since both species are invaders of the regional grasslands, both are important associates of Larrea in successional stages. In less than a century known grasslands are controlled in physiognomy by one or a combination of the three shrubs. A sequence of such changes is presented in Figure 17, all stages separately or in part are derived from the authors cited above. The sequence suggests that Larrea is the final single inhabitant of the area, although intermediate stages may be arrested for many years.

The transition importance of Prosopis in the Big Bend sites suggests that Prosopis predates Larrea along the transition and represents an earlier invasion of the retreating grassland. The cover values in Table 6 strongly suggest the early invasion and demonstrate that the invasion of the grassland by Prosopis is still in progress just as by Larrea at three sites. No reproduction or small Prosopis individuals were recorded in the Larrea dominated area, following the pattern cited by Buffington and Herbel. The sequence in Figure 17 suggests that

Figure 17. Major patterns of change in dominant shrub vegetation of northern Chihuahuan Desert.



G = Grass  
 F = Flourensia  
 P = Prosopis  
 L = Larrea  
 ....> invades  
 --> results

Whitfield and Anderson (1938), who reported the northern shrub dominated Chihuahuan Desert to be a disturbed and overgrazed grassland, were accurate in their interpretation of the vegetation dynamics as presently viewed.

Larrea probably had a tropical origin and with associated Madro-Tertiary flora shrubs, did not attain dominance until Miocene times (Barbour, 1969a). This suggests that the northeastward Larrea advancement is relatively recent. Larrea was not present in Big Bend Neotoma middens ranging in age from 36,600-4,200 years BP (Wells, 1966), although numerous other woodland and Succulent Desert Formation species were present (e.g., Agave, Dasyllirion, Yucca, Acacia, Ephedra, etc.). These results suggest Larrea is relatively recent in the region, although vegetation associates predate its occurrence. In addition to advancing aridity, man and his activities have assisted Larrea advancement since the middle of the nineteenth century, and it is presently restricted only at sharp substrate changes possessing well-developed vegetation in the Big Bend region.

## CHAPTER X

### SUMMARY

Vegetation and soils were sampled across the Shrub Desert Formation-Succulent Desert Formation transition in Big Bend National Park and analyzed for composition, density, cover, and several physical and chemical factors respectively. The Succulent Desert Formation vegetation occupied igneous substrates with organic carbon, total nitrogen, infiltration, field capacity, and percentage rock significantly greater than for the Shrub Desert Formation which occupied alluvial substrates. It appears that the usually abrupt change in infiltration rate with resultant differences in available moisture may be primarily responsible for the sudden shift in vegetation across the transition.

Floristically, the Succulent Desert Formation was more complex with four distinct associations: Agave lecheguilla-Bouteloua breviseta, Agave lecheguilla-Bouteloua curtipendula, Agave lecheguilla-Hilaria mutica, and Cathestecum erectum. Each association occupied soils with distinct characteristics, the second and third with higher moisture characteristics. Sharp lines of vegetation demarcation



separated the Shrub Desert Formation, dominated by widely spaced Larrea divaricata from the densely succulent-grass vegetated Succulent Desert Formation at four sites. At the remaining four sites a low prostrate, stoloniferous Cathestecum erectum ecotone of varied width separated the two typical formation types.

The mechanisms of Larrea establishment, occurrence of variously aged Larrea establishment groups in the ecotone and succulent-grass vegetation, and individual species distribution of both formations suggested in conjunction with the substrate differences that a mechanism of interference exclusion also contributes to the sharp line of vegetation demarcation. An allelopathic mechanism promoted by Larrea resin is hypothesized to be of possible importance.

Dynamics analyses indicated that Erioneuron pulchellum, Bouteloua trifida, Argythamnia neomexicana, Euphorbia spp., Iva ambrosiaefolia, and Prosopis glandulosa are closely associated with Larrea community establishment, development, and instability. These species are also common in disturbed areas of the region and decrease in importance as community change occurs. Agave lecheguilla, Bouteloua breviseta, and Cathestecum erectum are species most commonly associated with Larrea as the community changes or approaches stability over a long period of time.

#### LITERATURE CITED

- Anthony, M. A. 1954. Ecology of the Opuntiae in the Big Bend Region of Texas. Ecology 35:334-347.
- Bailey, V. 1905. Biological survey of Texas, U. S. Dept. Agr., N. Amer. Fauna 25:1-222.
- Barbour, M. G. 1969a. Patterns of genetic similarity between Larrea divaricata of North and South America. Amer. Midl. Nat. 81:54-67.
- \_\_\_\_\_. 1969b. Age and space distribution of the desert shrub Larrea divaricata. Ecology 50:679-685.
- Blum, U. and E. L. Rice. 1969. Inhibition of symbiotic nitrogen-fixation by gallic and tannic acid, and possible roles in old-field succession. Bull. Torrey Bot. Club 96:531-544.
- Bouyoucos, G. J. 1936. Direction for making mechanical analysis of soils by the hydrometer method. Soil Sci. 42:225-229.
- Branscomb, G. L. 1958. Shrub invasion of a southern New Mexico desert grassland range. J. Range Manage. 11:129-132.
- Bray, W. L. 1901. The ecological relations of the vegetation of western Texas. Bot. Gaz. 32:99-123, 195-217, 262-291.

- Brown, D. D. 1968. The possible ecological significance of inhibition by Euphorbia supina. M.S. Thesis, University of Oklahoma, Norman, 19 p.
- Buffington, L. C. and C. H. Herbel. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecol. Monogr.* 35:139-164.
- Carter, W. T. 1928. Soil survey (reconnaissance) of the Trans-Pecos area, Texas. *Bull. Univ. Tex. Sci. Ser.* 35:1-66.
- \_\_\_\_\_, and V. L. Cory. 1930-31. Soils of the Trans-Pecos, Texas and some of their vegetative relations. *Trans. Tex. Acad. Sci.* 15:19-37.
- Casey, C. B. 1968. Ranching in the Big Bend. Typescript. (Big Bend Natl. Park Library).
- Chew, R. M. and A. E. Chew. 1965. The primary productivity of a desert shrub (Larrea tridentata) community. *Ecol. Monogr.* 35:355-375.
- \_\_\_\_\_. 1970. Energy relationships of the mammals of a desert shrub (Larrea tridentata) community. *Ecol. Monogr.* 40:1-21.
- Cottle, H. J. 1931. Studies in the vegetation of southwestern Texas. *Ecology* 12:105-155.
- Denyes, H. A. 1956. Natural terrestrial communities of Brewster County, Texas, with special reference to the distribution of the mammals. *Amer. Midl. Nat.* 55:289-320.

- Duisberg, P. C. 1952. Some relationships between xerophytism and the content of resin, nordihydroguaiaretic acid and proteins of Larrea divaricata Cav. Plant Physiol. 27:769-777.
- Ellison, L. 1938. Influence of grazing on plant succession of range lands. Bot. Rev. 26:1-78.
- Fosberg, F. R. 1940. The aestival flora of the Mesilla Valley region, New Mexico. Amer. Midl. Nat. 23: 573-593.
- Gardner, J. L. 1951. Vegetation of the creosotebush area of the Rio Grande Valley in New Mexico. Ecol. Monogr. 21:379-403.
- Gause, G. F. 1934. Struggle for Existence. Williams and Wilkins, Baltimore, Md. 163 p.
- Gehlbach, F. R. 1966. Plant formations in the natural history interpretation of southwestern desert regions. Nat. Parks Mag. 40:16-18.
- \_\_\_\_\_. 1967. Vegetation of the Guadalupe Escarpment, New Mexico-Texas. Ecology 48:404-419.
- Gibble, W. P. 1950. Nineteen years of vegetational change in a desert habitat. M.S. Thesis, University of Arizona, Tuscon. 20 p.
- Giles, L. H. 1961. A classification of Ca horizons in soils of a desert region. Dona Ana County, New Mexico. Soil Sci. Soc. Am. Proc. 25:52-61.
- Gould, F. W. 1969. Texas plants: a checklist and

- ecological summary. MP-585/Revised. Tex. Agri. Exp. Sta., College Station, Texas. 121 p.
- Greene, R. A. and C. Reynard. 1932. The influence of two burrowing rodents, Dipodomys spectabilis (Kangaroo rat) and Neotoma albigula albigula (Pack rat) on desert soils in Arizona. Ecology 13:73-80.
- \_\_\_\_\_, and G. H. Murphy. 1932. The influence of two burrowing rodents, Dipodomys spectabilis (Kangaroo rat) and Neotoma albigula albigula (Pack rat) on desert soils in Arizona. II. Physical effects. Ecology 13:359-363.
- Grossman, R. B. and J. L. Millet. 1961. Carbonate removal from soils by a modification of the acetate buffer method. Soil Sci. Soc. Am. Proc. 25:325-326.
- Havard, V. 1885. Report of the flora of western and southern Texas. Proc. U. S. Nat. Mus. 8:449-533.
- Humphrey, R. R. and L. A. Mehrhoff. 1958. Vegetation changes on a southern Arizona grassland range. Ecology 39:720-726.
- Jackson, M. L. 1958. Soil chemical analysis. Prentice-Hall, Inc., Englewood Cliffs, N. J. 498 p.
- Johnson, D. E. 1961. Edaphic factors affecting the distribution of creosotebush Larrea tridentata (DC.) Cov. in desert grassland sites of southern Arizona. M.S. Thesis, University of Arizona, Tucson. 58 p.
- Knipe, D. and C. H. Herbel. 1966. Germination and growth

of some semidesert grassland species treated with aqueous extract from creosotebush. *Ecology* 47: 775-781.

Lowe, C. H. 1958-59. Contemporary biota of the Sonoran Desert: Problems. pp. 54-74. In *Arid Lands Colloquia*, University of Arizona, Tucson. 92 p.

Mallery, T. D. 1935. Changes in the osmotic value of the expressed sap of leaves and small twigs of Larrea tridentata as influenced by environmental conditions. *Ecol. Monogr.* 5:1-35.

Maxwell, R. A. 1968. The Big Bend of the Rio Grande. Guidebook 7. Bur. Econ. Geol., University of Texas, Austin. 138 p.

\_\_\_\_\_, J. T. Lonsdale, R. T. Hazzard, and J. A. Wilson. 1967. The geology of Big Bend National Park, Brewster County, Texas. University of Texas Publ. 6711, 320 p.

Muller, C. H. 1940. Plant succession in the Larrea-Flourensia climax. *Ecology* 21:206-212.

\_\_\_\_\_. 1947. Vegetation and climate of Coahuila, Mexico. *Madroño* 9:33-57.

\_\_\_\_\_. 1966. The role of chemical inhibition (allelopathy) in vegetational composition. *Bull. Torrey Bot. Club* 93:332-351.

Murray, A. V. 1959. An analysis of change in Sonoran Desert vegetation for the years 1928-1957. M.S.

- Thesis, University of Arizona, Tucson. 146 p.
- Noggle, G. R. and F. L. Wynd. 1941. The determination of selected chemical characteristics of soil which affect the growth and composition of plants. *Plant Physiol.* 16:30-60.
- Orton, R. B. 1964. The climate of Texas and the adjacent Gulf waters. U.S. Dept. Com., Weather Bur., Washington, D.C. 195 p.
- Piper, C. S. 1942. Soil and plant analysis. The University of Adelaide, Adelaide, Australia. 368 p.
- Rice, E. L. 1965a. Inhibition of nitrogen-fixing and nitrifying bacteria by seed plants. II. Characterization and identification of inhibitors. *Physiol. Plant.* 18:255-268.
- \_\_\_\_\_. 1965b. Inhibition of nitrogen-fixing and nitrifying bacteria by seed plants. III. Comparison of three species of Euphorbia. *Proc. Okla. Acad. Sci.* 45:43-44.
- \_\_\_\_\_. 1967. Chemical warfare between plants. *Bios.* 38:67-74.
- Runyon, R. H. 1934. The organization of the creosote bush with respect to drought. *Ecology* 15:128-138.
- Shantz, H. L. and R. Zon. 1924. Natural vegetation. U.S. Dept. Agri., Atlas of Amer. Agri. Pt.1, Sec. E. Washington, D.C.
- Shelton, W. R. and H. J. Harper. 1941. A rapid method

for the determination of total phosphorus in soil and plant material. Iowa State Coll. J. Sci. 15: 408-413.

Shreve, F. 1922. Conditions indirectly affecting vertical distribution on desert mountains. Ecology 3:269-274.

\_\_\_\_\_. 1925. Ecological aspects of the deserts of California. Ecology 6:93-103.

\_\_\_\_\_. 1929. Changes in desert vegetation. Ecology 10:364-373.

\_\_\_\_\_. 1939. Observations on the vegetation of Chihuahua. Madrono 5:1-13.

\_\_\_\_\_. 1942. The desert vegetation of North America. Bot. Rev. 8:195-246.

\_\_\_\_\_, and A. L. Hinckley. 1937. Thirty years of change in desert vegetation. Ecology 18:463-478.

U.S. Dept. of Commerce. 1955-68. Climatological Summaries: Texas.

Utley, R. M. 1962. Longhorns of the Big Bend. Nat. Park Ser. Spec. Report.

Valentine, K. A. and J. J. Norris. 1964. A comparative study of soils of selected creosotebush sites in southern New Mexico. J. Range Manage. 17:23-32.

Waterfall, U. T. 1946. Observations on the desert gypsum flora of southwestern Texas and adjacent New Mexico. Amer. Midl. Nat. 36:456-466.



- Wells, P. V. 1960. Physiognomic intergradation of vegetation on the Pine Valley Mountains in southwestern Utah. *Ecology* 41:553-556.
- \_\_\_\_\_. 1965. Vegetation of the Dead Horse Mountains, Brewster County, Texas. *SW Nat.* 10:256-260.
- \_\_\_\_\_. 1966. Late Pleistocene vegetation and degree of pluvial climatic change in the Chihuahuan Desert. *Science* 153:970-975.
- Whitfield, C. J. and H. L. Anderson. 1938. Secondary succession in the Desert Plains Grassland. *Ecology* 19:171-180.
- Whitson, P. D. 1965. Phytocoenology of Boot Canyon woodland, Chisos Mountains, Big Bend National Park, Texas. M.S. Thesis, Baylor University, Waco, Texas. 45 p.
- \_\_\_\_\_. 1970. The impact of human use upon the Chisos Basin and adjacent lands. U.S. Dept. Inter., Nat. Park Ser. 120 p.
- Williams, J. S. 1970. Postclimax grasses on rubble-clay strata of the Mesilla Valley of Texas. *Tex. J. Sci.* 21:308-310.
- Yang, T. W. 1950. Distribution of Larrea tridentata in the Tucson area as determined by certain physical and chemical factors in the habitat. M.S. Thesis, University of Arizona, Tucson.
- \_\_\_\_\_. 1961. The recent expansion of creosotebush

- (Larrea divaricata) in the North American Desert.  
Western Reserve Nat. His. Mus. Spec. Pub. 1.
- Yang, T. W. 1967a. Chromosome numbers in populations of creosotebush (Larrea divaricata) in the Chihuahuan and Sonoran subdivisions of the North American Desert. J. Ariz. Acad. Sci. 4:183-184.
- \_\_\_\_\_. 1967b. Ecotypic variation in Larrea divaricata. Amer. J. Bot. 54:1041-1044.
- \_\_\_\_\_. 1970. Major chromosome races of Larrea divaricata in North America. J. Ariz. Acad. Sci. 6:41-45.
- \_\_\_\_\_, and C. H. Lowe. 1968. Chromosome variation in ecotypes of Larrea divaricata in the North American Desert. Madrono 19:161-164.
- York, J. C. and W. A. Dick-Peddie. 1969. Vegetation changes in southern New Mexico during the past hundred years. pp. 157-166. In Arid Lands in Perspective. Am. Assoc. Ad. Sci., University of Arizona Press, Tucson.