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DURO CANYON, WEST TEXAS.

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THE UNIVERSITY OF OKLAHOMA
GRADUATE COLLEGE

VEGETATION-ENVIRONMENT RELATIONSHIPS IN PALO DURO CANYON, WEST TEXAS

A DISSERTATION
SUBMITTED TO THE GRADUATE FACULTY
in partial fulfillment of the requirements for the
degree of
DOCTOR OF PHILOSOPHY

by
DAVID B. ADAMS
Norman, Oklahoma
1979

VEGETATION-ENVIRONMENT RELATIONSHIPS IN PALO DURO CANYON, WEST TEXAS

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TABLE OF CONTENTS

TABLE OF CONTENTS (Concluded)

LIST OF FIGURES

LIST OF FIGURES (Concluded)

LIST OF TABLES

LIST OF TABLES (Concluded)

ABSTRACT

This study involved a vegetational gradient analysis of a 240-m deep, 70-km long re-entrant canyon on the eastern edge of the high plains of the Texas Panhandle. In contrast to the surrounding grassy plain, the canyon offers a great deal of topographic and edaphic variety and supports comparatively luxurious cove and riparian woodlands.

The vegetation of the canyon, which consists mainly of shrubland dominated by _Juniperus_ spp. or _Prosopis glandulosa_, was sampled in 29 stands selected to represent the range of environmental variation.

The most useful method of data analysis involved the construction of graphs which related cover by species to annual insolation and elevation. Further analysis involving polar ordination, step-wise multiple regression, and principal components analysis confirmed the importance of insolation (a synthetic, integrative measure of exposure) as a causal factor and also implicated frequency of surface rock as a possibly important factor. In

general, exposure appears to be of overriding importance in determining vegetational variation in the canyon.

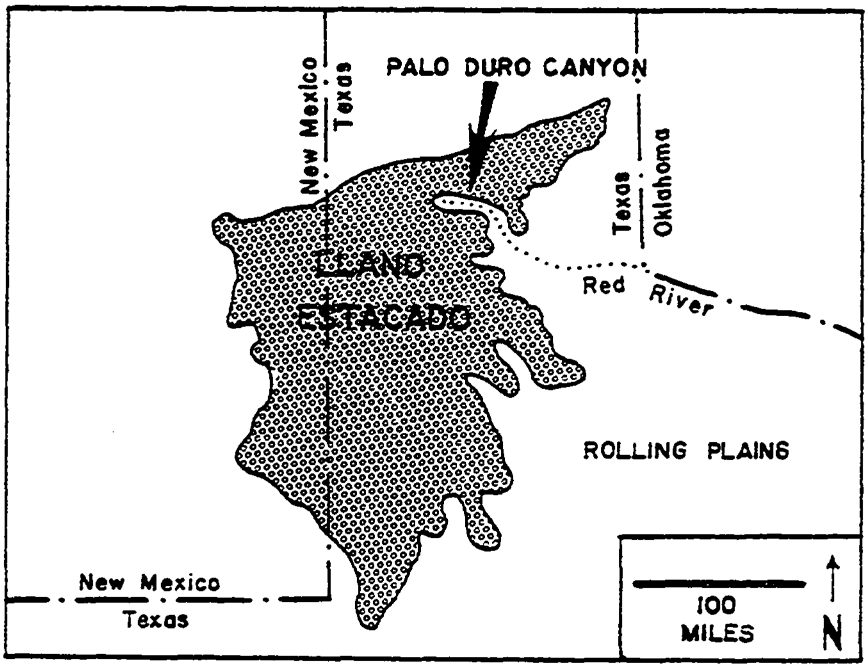
VEGETATION-ENVIRONMENT RELATIONSHIPS IN PALO DURO CANYON, WEST TEXAS

CHAPTER I

INTRODUCTION

The portion of the Great Plains physiographic province lying south of the Canadian River in eastern New Mexico and adjoining Texas is known as the Llano Estacado or "Staked Plains" (Fenneman, 1931). Its boundary is marked by a distinct scarp on the north, west, and east, but on the south it merges gradually with the Edwards Plateau. The surface of the plain is extremely flat and almost untouched by water erosion except along the edges of the escarpment, where short re-entrant canyons extend several kilometers into the plain (Lotspeich and Coover, 1962). The longest and deepest of these is Palo Duro Canyon, which extends for about 70 km into the eastern edge of the escarpment (Fig. 1), and exposes geological formations as old as the Permian.

Figure 1. Llano Estacado and Palo Duro Canyon
(After Lotspeich and Coover, 1962).


PALO DURO CANYON
New Mexico
Texas
Texas
Oklahoma
LLANO ESTACADO
Red River
ROLLING PLAINS
New Mexico
Texas
100 MILES
N

In contrast to the relatively uniform environment of the surrounding plain, Palo Duro Canyon offers a great deal of topographic and edaphic variety. The plain supports -- or did before settlement -- a fairly homogeneous and virtually treeless cover of mid- and short-grasses (Weaver and Albertson, 1956), whereas the vegetation of the canyon varies from steep, exposed, totally barren slopes to comparatively luxurious cove and riparian woodlands with numerous woody species and with trees to 1 m in diameter.

The remarkable contrast between the vegetation of the plain and that of the canyon inspired the study reported here. The purpose of the study was to describe the vegetation of the canyon and relate its variations to soil and exposure gradients in the canyon. Other studies have indicated that factors affecting the supply of available moisture usually have the greatest influence on the vegetation (Johnson and Risser, 1972), and the _a priori_ assumption of this study was that exposure, as the primary determinant of soil moisture, was the major source of vegetational variation in the canyon.

Considerable research has been done on the segregation of vegetation in response to changes in slope exposure (e.g., Cantlon, 1953; Whittaker, 1967; Mowbray and

Oosting, 1968). In a brief review, Cantlon (1953) found that various environmental differences have been correlated with exposure-induced vegetational differences. For example, north-facing slopes generally differ from adjoining south-facing slopes in soil and air temperature, soil and atmospheric moisture, light intensity, and wind velocity. These differences in microclimate are due primarily and ultimately to differences in the insolation-radiation balance for the two slopes (Cantlon, 1953).

CHAPTER II

DESCRIPTION OF THE STUDY AREA

The study was made in Randall County in the 6,000-ha Palo Duro Canyon State Park, 25 km SSE of Amarillo. The park was selected for study because of its accessibility, representativeness, and protection from cattle grazing for many years.

The cultural history of the canyon has been outlined by Emory (1944) and Matthews (1969). Aborigines inhabitated the canyon as early as 10,000 B.C. In historic times, various tribes of Plains Indians lived in the canyon until 1874, when the last of the Comanches were defeated by the U.S. Army. Two years later, Goodnight drove 10,000 buffalo from the canyon, replaced them with 1,600 head of cattle, and established the first ranch in the Texas Panhandle (Haley, 1953). The park acreage was grazed until purchased by the state in 1933. Since then it has become one of the largest parks in Texas and receives more than 300,000 visitors a year.

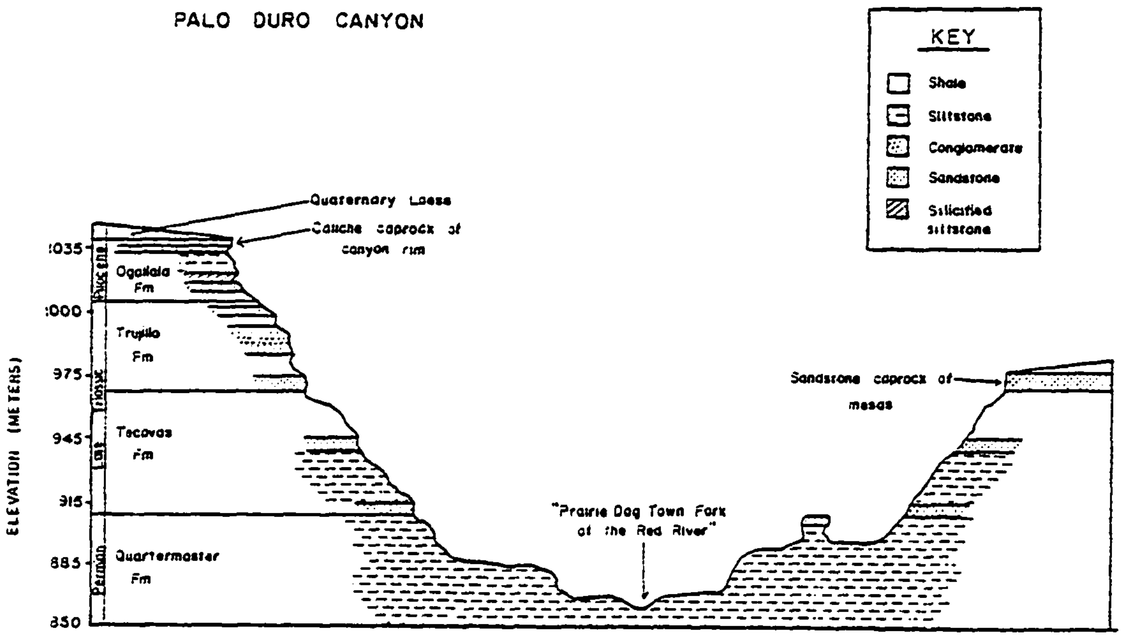
General descriptions of the study area have been prepared by R. Wright (1973), Hughes and Harbour (1972), Matthews (1969), Hall and Carr (1968), Russell (1935), Palmer (1920), Clothier (1904), and Marcy (1853). The first three papers collectively offer the most thorough introduction to the area, and the following material is primarily a restatement of their work.

Geology

The formation of the canyon began in the Pleistocene, when the Red River began cutting headward into the Llano Estacado, deepening and widening the canyon as it progressed (Hughes and Harbour, 1972). The canyon is presently about 70 km long, 25 km wide at its mouth, and as much as 240 m deep.

Strata from four different geological periods are visible in the canyon: the Permian, Triassic, Tertiary, and Quaternary (Fig. 2). The oldest formation exposed is the Quartermaster Formation, of Permian age. It is composed primarily of brick-red to vermilion shales which are interbedded with lenses of gray shales, clays, mudstones, and gypsum. The Quartermaster averages about 20 m thick and forms the floor, footslopes, and lower walls of the

Figure 2. A generalized cross-section of Palo Duro Canyon (cf. Hughes and Harbour, 1972; Matthews, 1969).


PALO DURO CANYON
KEY
Shale
Siltstone
Conglomerate
Sandstone
Silicified siltstone
Quaternary Loess
Caliche caprock of canyon rim
Sandstone caprock of mesas
"Prairie Dog Town Fork of the Red River"
ELEVATION (METERS)
1035
1000
975
945
915
885
850
Pliocene
Triassic
Late
Permian
Ogallala Fm
Trujillo Fm
Tecovas Fm
Quartermaster Fm

canyon (Fig. 2). The Quartermaster tends to form cliffs or steep gullied slopes of red and white banded shales which in some cases erode so rapidly that they are devoid of vegetation.

The Tecovas Formation, of Triassic age, overlies the Quartermaster (Fig. 2). An unconformity exists between these two formations: part of the Late Permian and all of the Early and Middle Triassic records are missing. The Tecovas has a total thickness of about 60 m and consists largely of multicolored shales. Also present are thin layers of soft sandstone, which are disseminated throughout the shales, and a more prominent bed of white sandstone, which marks the middle of the formation (Matthews, 1969). The Tecovas Formation forms relatively smooth, steep slopes, which are also frequently bare of vegetation.

The Trujillo Formation, about 40 m thick, overlies the Tecovas and is separated from it by the massive-bedded, cliff-forming Trujillo sandstone. This sandstone is one of the most conspicuous rock units in the canyon and caps many of its prominent benches and mesas. A middle sandstone unit in the Trujillo is also a conspicuous ledge- and cliff-forming rock, and this is overlain by red and green shales which mark the uppermost limits of the formation (Matthews, 1969).

The Ogallala Formation of Pliocene age overlies uncomformably the Trujillo Formation. Most of the Ogallala Formation, which is about 30 m thick, consists of a mixture of diverse rock types, including conglomerates, sandstone, siltstone, clay, and marl. The upper part of the formation is characterized by thick caliche deposits which form the caprock rim of the canyon (Matthews, 1969). The Ogallala is an important aquifer and occasional seeps and springs occur at its base.

Overlying the Ogallala caliche at most points along the canyon's rim are loose strata of sand and silt which were deposited during the Pleistocene. The same materials have been deposited along streams on the floor of the canyon (Matthews, 1969).

Soils

The soils of the canyon and surrounding plains have been described by Russell (1935), Lotspeich and Coover (1962), Lotspeich and Everhart (1962), and Jacquot et al. (1970), and summarized by R. Wright (1973). The surrounding plain is nearly level to gently rolling and covered with a mantle of calcareous loess that has given rise to deep soils with a clay loam surface and a clay subsoil. Near the canyon these deep soils grade into shallow, grayish-brown, gravelly loam soils overlying the caliche of the Ogallala Formation. The soils of the canyon walls are extremely complex and generally are classed as rough broken land (Jacquot et al., 1970). This land consists of jagged caliche escarpments of the Ogallala, colorful sandstone ledges and bluffs and steep talus slopes of the Trujillo and Tecovas, and highly dissected red-bed plains of the Quartermaster. Below the escarpment there is a mixture of colluvial and alluvial soils. The soils of the colluvial footslopes grade from a grayish-brown sandy loam into a brown loam. The lower, gently sloping footslopes and the nearly level floodplain support deep, calcareous alluvium derived from the uplands. Soils of the canyon floor are generally a red or reddish brown, very fine sandy loam. In some areas, the floodplain soils are of such variable texture and depth that they are classed only as broken alluvial land (Jacquot et al., 1970). These soils are usually loamy, but sand deposits resulting from flooding are not uncommon (R. Wright, 1973; Hughes and Harbour 1972; Jacquot et al., 1970).

Vegetation

The deep soils of the Llano Estacado support a fairly uniform growth of short grasses, especially Boute-

loua gracilis and *Buchloë dactyloides*. In overgrazed areas, *Prosopis glandulosa*, *Opuntia polyacantha*, *Yucca angustifolia*, and other invaders become important. In the shallow soils near the edge of the caprock, the short grasses decrease in relative abundance while midgrasses increase, especially *Schizachyrium scoparium* and *Bouteloua curtipendula*. In this area shrubs become conspicuous, particularly *Juniperus* spp. (R. Wright, 1973).

On the steeper canyon slopes geological erosion removes soil material so rapidly that few plants can become established. On the less steep areas occur scarp woodlands composed mainly of *Juniperus monosperma*, *Rhus aromatica*, and *R. microphylla*. In protected areas, such as small canyons, the environment is mesic enough to support *Juniperus virginiana*, *Celtis reticulata*, *Vitis arizonica*, *Forestiera pubescens*, and others (R. Wright, 1973).

Most of the plants of the plains and escarpment are also found on the canyon floor. The junipers, *Rhus* spp., and *Prosopis glandulosa* are common, and *Populus deltoides*, *Tamarix gallica* and *Salix* spp. occur along the stream (R. Wright, 1973).

There is little agreement on juniper taxonomy in the canyon. Clothier (1904), whose observations in the canyon were fairly extensive, reported *Juniperus monosperma*, *J. scopulorum*, and *J. pinchotii*, while Palmer's (1920) cursory survey mentioned only *J. monosperma* and *J. pinchotii*. Russell (1935) listed *J. scopulorum*, *J. virginiana*, and *J. monosperma*. In the early 1970's, R. Wright (1973) mentioned *J. monosperma* and *J. virginiana*, and J. Wright (1974) listed *J. ashei*, *J. monosperma*, and *J. pinchotii*.

None of these studies was intended to be comprehensive with regard to the canyon's juniper flora, and comparisons are made primarily to illustrate the taxonomic complexity of junipers in the canyon, a subject which has been examined in detail by Hall and Carr (1968).

Hall and Carr (1968) concluded that the canyon's junipers consist of two overlapping species complexes, the *J. monosperma* - *J. pinchotii* complex and the *J. scopulorum* - *J. virginiana* complex. No good specimens of *J. virginiana* in the canyon were found, and they believed the individuals resembling this species were more closely related to *J. scopulorum*. They found most of the junipers in the canyon to belong to the *J. monosperma* - *J. pinchotii* complex, which predominates in all but the most mesic stands; *J. scopulorum* was found only in mesic stands. On the basis of their study, they concluded that *J. monosperma* is more important in xeric sites than *J. pinchotii*, while the reverse is true in more mesic sites. The junipers in this complex vary continuously in certain morphological characteristics, from individuals most like *J. monosperma* to those most like *J. pinchotii*. Complicating this situation still further is the suggestion that *J. pinchotii* is itself a stabilized *hybrid* between *J. monosperma* and *J. deppeana* (Hall and Carr, 1968), although Adams (1972) found strong linkage between *J. pinchotii* and *J. scopulorum* in trans-Pecos Texas.

Climate

The climate is cool temperate and has been classified as steppe or semi-arid by Trewartha (1968). The average annual precipitation is 50 cm. Precipitation is low in winter, high in spring, low in mid-summer and high in late summer and fall. Rainfall occurs most frequently in thunderstorms rather than in general rain. In most years the soil is not wetted below 7 to 8 cm, and the deeper solid layers are wetted only during abnormally wet years. Humidity is low, averaging 38% at 6 p.m. and 72% at 6 a.m. Almost constantly blowing wind is characteristic of the area, and the average speed of the wind is high because the surface of the county offers little resistance. Prevailing winds are usually southerly from May to September and southwesterly during the remainder of the year. The average wind at nearby Amarillo is 11.3 km/hr. The winds and low humidity result in high evaporation rates. Annual class "A" pan evaporation is 226 cm, and the average precipitation/evaporation ratio is 0.22. Average monthly temperatures range from 3.5 C in January to 25.4 C in July. The average length of freeze-free period is 200 days, generally from mid-April to early November (R. Wright, 1973; Orton, 1969; Dougherty, 1975).

CHAPTER III

METHODS

The orientation of the study is gradient analysis, the study of plant communities along environmental gradients (Whittaker, 1967). Accordingly, 29 1- to 5-ha stands were selected, on the basis of apparent homogeneity, to represent the range of topographic and edaphic variation in the canyon. Sampling was done in the fall of 1974. Woody vegetation was divided into two categories, one including plants >1 m in height, the other including plants <1 m, and each category was sampled using the point-centered quarter method of Cottam and Curtis (1956). The distance to the center of the nearest plant in each quarter and canopy diameter and height of the plant were measured. The number of points sampled in each stand was determined by the abundance of woody cover in the stand and by the size of the stand. The number of points was usually 30-35 for shrubs <1 m and 20-25 for plants >1 m. Herbaceous vegetation was sampled by tallying occurrences of species in 1-dm intervals of a line intercept (Kennedy, 1972) which varied in total length from 500 dm to 2,000 dm depending on the size of the stand. Initially, a 1-cm diameter rope marked off in 50 1-dm intervals was arranged at regular intervals of 10 m or more throughout a stand. In stands 12-29, however, a 15-dm folding ruler was used for increased efficiency and convenience. This smaller line intercept could be "read" at a glance, one species at a time instead of 1-dm at a time. For both methods, species and other categories (rock, bare ground, and litter) occurring within a 1-cm strip along one side of each 1-dm interval were identified and recorded. Resulting data were compiled as both frequency (in 1x10 cm quadrats) and relative frequency. The latter was assumed, because of the small quadrat size, to be a reasonable estimate of relative cover.

Soil samples for physical and chemical analysis were collected at 0-15 cm at 3 points in each stand and composited. Gravel was removed from the samples and discarded at the time of collection. Soil was air dried, and visible organic material was removed. The remaining gravel was removed with a 2-mm sieve and discarded. Physical and chemical determinations were done with air-dry soil and results were converted to an oven dry basis.

The pH was determined by the glass electrode procedure described by Rice (1964) and a mechanical analysis was made with a modified Bouyoucos hydrometer method (Bouyoucos, 1936; Piper, 1942; Rice, 1964). After the pH and texture were determined, the samples were ground in a soil mill to pass a 0.5-mm sieve. Total carbon was determined by the Walkley and Black Method (Piper, 1942; Rice, 1964), and total base exchange capacity by the method of Noggle and Wynd (1941; Rice, 1964). Average annual potential insolation was determined for each stand using aspect, slope, and latitude with a table given by Frank and Lee (1966). Aspect and percent slope were measured with a Brunton compass. Elevation was determined from a 7.5 minute topographic map with a contour interval of 20 feet.

A principal component analysis of 12 environmental variables (percent sand, silt, and clay; mean particle size; frequency of surface rock in the line intercept; pH, base exchange capacity, organic carbon, elevation, % slope, aspect, and potential annual insolation) was performed using the method of Dixon (1971). A weighted-mean axis position (cf. Bray and Curtis, 1957) for each important species on each principal component was derived by the formula,

$$MAP_j = \sum_{i=1}^{29}(C_{ij} \times AP_i) \;/\; \sum_{i=1}^{29} C_{ij}$$

where C_{ij} is the cover value of the jth species in the ith stand, and AP_i is the axis position of the ith stand on the principal component. The variance of the mean axis position was used for selected species as a measure of niche width (McNaughton and Wolf, 1970).

A two-dimensional polar ordination (Bray and Curtis, 1957) was constructed using percent woody cover data and a computer program by Gauch (1971).

Step-wise multiple linear regression was conducted using species as dependent variables and nine environmental variables as independent variables (slope and aspect were combined in insolation).

CHAPTER IV

RESULTS AND DISCUSSION

Approximately 200 plant taxa were encountered in the 29 stands of vegetation, including 27 shrubs sampled by the quarter method and 170 herbs sampled by the line intercept method. The shrubs and the 35 most important herbs, chiefly perennial short- and mid-grasses, are listed in Tables 1 and 2, respectively, and 96 minor herbs are listed in Table 3 (nomenclature follows Correll and Johnston, 1970). (For simplicity, the term "shrub" is used here to mean woody species, except when there is a clear distinction to be made between tree-sized and shrub-sized vegetation.)

Most of the woody cover in the canyon is contributed by nine taxa (Table 1): *Prosopis glandulosa* (mesquite), *Juniperus pinchotii* (red-berry juniper), *J. monosperma* (one-seed juniper), *Rhus aromatica* (aromatic sumac), *R. microphylla* (little-leaf sumac), *Populus deltoides* (cottonwood), *Opuntia polyacantha* (prickly pear), *Yucca angustifolia*, and a hybrid juniper, *J. pinchotii* X *monosperma* (*J.p. X J.m.*).

Table 1. Trees and shrubs sampled, percent presence in stands, and maximum and mean percent cover in stands of occurrence.

	Percent Presence	Percent Cover	
		Max	Mean
Atriplex canescens (Atco)	34	4	6.0
Berberis trifoliolata (Betr)	3	1	1.2
Brickellia californica (Brca)	17	0.5	0.2
Celtis reticulata (Cere)	24	5	1.0
Cercocarpus montanus (Cemo)	14	2	1.0
Dalea formosa (Dafo)	76	3	0.8
Ephedra torreyana (Epto)	48	3	0.9
Forestiera pubescens (Fopu)	34	19	3.4
Forsellesia planitierum (Fopl)	7	7	3.6
Juniperus pinchotii (Jupi)	93	24	7.0
J. monosperma (Jumo)	72	71	8.2
J.p. X *J.m.* (JpJm)	76	24	4.1
J. scopulorum (Juse)	10	7	4.9
Lycium berlandieri (Lybe)	21	0.5	0.3
Mimosa borealis (Mibo)	69	7	1.2
Opuntia polyacantha (Oppo)	83	18	3.4
O. leptocaulis (Ople)	76	2	0.5
O. tunicata (Optu)	3	0.1	0.1
Populus deltoides (Pode)	3	111	111.0
Prosopis glandulosa (Prgl)	83	40	8.7

Table 1 (Concluded)

	Percent Presence	Percent Cover Max	Percent Cover Mean
Ptelea trifoliata (Pttr)	21	3	1.1
Quercus havardii (Quha)	10	7	6.0
Rhus aromatica (Rhar)	69	44	5.7
R. microphylla (Rhmi)	72	14	4.0
Sapindus saponaria var. saponaria (Sasa)	3	4	4.3
Xanthocephalum sarothrae (Xasa)	52	2	0.5
Yucca angustifolia (Yuan)	76	13	2.0
Ziziphus obtusifolia (Ziob)	45	4	1.0

Table 2. Important grasses and forbs sampled, percent presence, and maximum and mean percent relative cover in stands of occurrence. Taxa are included which had at least 10% presence and 1% maximum relative cover.

	Percent Presence	Percent Cover Max	Percent Cover Mean
Ambrosia psilostachya (Amps)	10	1	0.4
Artemisia ludoviciana (Arlu)	52	4	0.9
Aristida glauca (Argl)	52	12	2.3
A. adscensionis (Arad)	41	2	0.5
A. fenleriana (Arfe)	14	1	0.7
Bothriochloa saccharoides (Bosa)	21	1	0.6
Bouteloua curtipendula (Bocu)	90	23	8.9
B. eriopoda (Boer)	55	29	9.5
B. gracilis (Bogr)	90	46	10.1
B. hirsuta (Bohi)	66	13	3.6
Buchloe dactyloides (Buda)	52	23	5.6
Chamaesaracha sordida (Chso)	41	2	0.6
Erigeron modestus (Ermo)	31	2	0.5
Erioneuron pilosum (Erpi)	52	1	0.3
Hilaria mutica (Himu)	10	42	14.9
Kallstroemia hirsutissima (Kahi)	28	6	1.3
Krameria lanceolata (Krla)	21	1	0.3

Table 2 (Concluded)

	Percent Presence	Percent Cover	
		Max	Mean
Lecidea rubiformis Wahl. (Leru)	80	28	5.5
Leucelene ericoides (Leer)	24	1	0.2
Leptochloa dubia (Ledu)	62	15	3.0
Leptoloma cognatum (Leco)	62	3	0.9
Melampodium leucanthum (Mele)	52	1	0.2
Muhlenbergia porteri (Mupo)	24	2	0.5
Panicum obtusum (Paob)	52	20	3.4
P. hallii (Paha)	76	9	0.9
Portulaca retusa (Pore)	21	2	0.7
Salsola kali (Saka)	31	4	0.4
Schizachyrium scoparium (Scsc)	28	2	0.7
Setaria leucopila (Sele)	41	11	3.2
Solanum elaeagnifolium (Soel)	52	2	0.5
Sorghastrum avenaceum (Soav)	10	3	1.0
Sporobolus airoides (Spai)	31	1	0.6
S. cryptandrus (Spcr)	100	17	3.5
Stipa neomexicana (Stne)	17	9	2.0
Tridens muticus (Trmu)	59	8	1.6

Table 3. Minor herbs sampled, percent presence, maximum and mean percent relative cover in stands of occurrence. + = <0.1% relative cover.

	Percent Presence	Percent Cover	
		Max	Mean
Abutilon incanum	7	.1	+
A. parvulum	3	+	+
Acalypha ostryaefolia	3	+	+
Allionia incarnata	7	.1	+
Allium sp.	41	.8	.3
Ambrosia trifida var. *texana*	3	+	+
Andropogon gerardi	14	.5	.3
Aristida longiseta	10	.2	.1
A. purpurea	7	.4	+
Artemisia filifolia	3	.1	.1
Aster ericoides	3	+	+
A. fendleri	3	+	+
Astragalus missouriensis	21	.2	.1
Berlandiera lyrata	3	+	+
Caesalpinia jamesii	3	+	+
Calylophus hartwegii subsp. *fendleri*	10	.2	+
C. H. subsp. *pubescens*	17	.4	+
C. affin. serrulatus	3	+	+
Chloris cucullata	3	2	2
C. verticillata	7	.1	+

Table 3 (Cont'd)

	Percent Presence	Percent Cover	
		Max	Mean
Chrysothamnus nauseosus subsp. *graveolens*	3	+	+
C. pulchellus	3	+	+
Commelina erecta	3	+	+
Convolvulus equitans	3	+	+
Croton texensis	3	+	+
Cyperus sp.	10	.4	+
Dalea enneandra	3	+	+
Desmanthus cooleyi	3	+	+
Echinacea angustifolia var. *angustifolia*	3	.1	.1
Echinocerus viridiflorus	21	.1	+
Elymus canadensis	3	.2	.2
Enneapogon desvauxii	7	.2	.1
Eragrostis cilianensis	3	.1	.1
E. pectinacea	3	.1	.1
E. trichodes	7	1.2	.6
Eriogonum jamesii	3	.1	.1
E. longifolium	3	+	+
Euphorbia dentata	31	.3	+
E. fendleri	3	+	+
E. geyeri	3	+	+
E. glyptosperma	3	.1	.1
E. lata	34	.1	.1

Table 3 (Cont'd)

	Percent Presence	Percent Cover	
		Max	Mean
E. villifera	3	.1	.1
E. subg. Chamaesyce sp.	59	0.4	0.1
Evolvulus nuttallianus	7	.1	+
Gaura suffulta	3	+	+
Gaura sp.	3	+	+
Haploesthes greggii var. texana	3	.2	.2
Hedyotis nigricans var. rigidiuscula	3	+	+
Helianthus ciliaris	3	+	+
Hybanthus verticillatus var. verticillatus	3	.2	.2
Hymenoxys acaulis var. acaulis	3	.1	.1
H. scaposa	10	.3	.1
Kuhnia eupatorioides	3	+	+
Liatris punctata	17	+	+
Lesquerella ovalifolia	21	.1	+
Lithospermum incisum	10	+	+
Lygodesmia texana	7	+	+
Machaeranthera pinnatifida	17	.3	.2
Mentzelia decapetala	7	+	+
M. oligosperma	10	+	+
Mirabilis linearis	14	.2	+
Muhlenbergia arenicola	3	.2	.2

Table 3 (Cont'd)

	Percent Presence	Percent Cover	
		Max	Mean
M. racemosa	3	2.0	2.0
Oryzopsis micrantha	3	2.2	2.2
Panicum reverchonii	7	.8	.5
P. virgatum	3	4.2	4.2
Paronychia jamesii	3	.1	.1
Parthenosissus vitacea	3	+	+
Pellaea atropurpurea	10	.6	.3
Penstemon albidus	10	.4	.2
P. fendleri	14	.1	+
Physalis lobata	3	+	+
P. viscosa	28	.7	.1
Polanisia dodecandra var. trachysperma	3	1.4	1.4
Polygala alba	3	.2	+
Portulaca mundula	3	+	+
Prionopsis ciliata	3	+	+
Psilostrophe villosa	3	+	+
Ratibida columnaris	3	+	+
Sarcostemma crispum	14	.1	+
S. cynanchoides var. hartwegii	3	.3	+
Senecio longilobus	14	.2	.1
Sophora nuttalliana	3	+	+
Sorghum halepense	3	3.2	3.2

Table 3 (Concluded)

	Percent Presence	Percent Cover	
		Max	Mean
Sphaeralcea angustifolia var. *angustifolia*	7	.3	.2
S. coccinea	21	.6	.2
Sporobolus contractus	21	.5	.2
Talinum parviflorum	14	.2	+
Thelesperma megapotamicum	31	.5	.2
Tragia ramosa	31	.3	.1
Tribulus terrestris	3	.1	.1
Zinnia grandiflora	21	.4	.2

The most important herbs are *Bouteloua gracilis* (blue grama), *B. curtipendula* (side-oats grama), *B. eriopoda* (black grama), *B. hirsuta* (hairy grama), *Lecidea rubiformis* Wahl. (a terricolous lichen), *Buchloë dactyloides* (buffalo grass), *Leptochloa dubia* (green sprangletop), *Panicum obtusum* (vine-mesquite), *Setaria leucopila* (plains bristlegrass), *Hilaria mutica* (tobosa grass), and *Aristida glauca* (three-awn grass) (Table 2).

Tables 4 and 5 list the major shrubs and herbs, respectively, and the number of stands in which each occurred as leading or important subordinant species (relative cover at least 15%). *Prosopis glandulosa* was an important subordinant in seven stands and was the leading shrub in six stands; it comprised at least 50% of the woody cover in three stands (Table 4). The junipers led in 13 stands, sumacs (*Rhus* spp.) in five stands, and *Populus deltoides*, *Yucca angustifolia*, and *Quercus havardii* (shin oak) in one stand each. *Opuntia polyacantha*, which normally occurred as a secondary shrub in *P. glandulosa* stands, exceeded the latter by slight margins in two stands (Table 4).

With respect to grasses, 21 of the 29 stands sampled had a species of *Bouteloua* as the leading species.

Table 4. Number of stands in which important woody species were leading or subordinant in terms of relative cover.

Species	Leading		Subordinant	Total
	<50%	≥50%	≥15%	
Atriplex canescens	0	0	1	1
Juniperus pinchotii	6	2	7	15
J. monosperma	2	1	1	4
J.p. X *J.m.*	2	0	2	4
Mimosa borealis	0	0	1	1
Opuntia polyacantha	2	0	3	5
Populus deltoides	0	1	0	1
Prosopis glandulosa	3	3	7	13
Quercus havardii	1	0	0	1
Rhus aromatica	2	1	2	5
R. microphylla	2	0	2	4
Yucca angustifolia	1	0	2	3

Table 5. Number of stands in which important herbaceous species were leading or subordinant in terms of relative cover.

	Leading		Subordinant	
Species	<50%	≥50%	≥15%	Total
Aristida glauca	0	0	2	2
Bouteloua curtipendula	10	2	0	12
B. eriopoda	3	1	2	6
B. gracilis	1	4	3	8
B. hirsuta	0	0	2	2
Buchloe dactyloides	0	0	3	3
Hilaria mutica	0	1	0	1
Lecidea rubiformis Wahl.	1	1	1	3
Leptochloa dubia	0	0	2	2
Panicum obtusum	0	1	1	2
Setaria leucopila	1	0	1	2
Sporobolus cryptandrus	3	0	2	5

Bouteloua gracilis was the primary herb in five stands, *B. curtipendula* in 12 stands and *B. eriopoda* in four stands (Table 5).

The average composition of the stands, grouped by leading shrub, is shown in terms of average relative cover by associated species in Tables 6 and 7 and is discussed below.

Total shrub cover and total relative herb cover are listed in Table 8 and symbolized in Figs. 3 and 4. Total shrub cover varied considerably among the stands, ranging from 1% on the rim of the canyon to nearly 200% (as a result of cover repetition) on a protected north slope (Table 8 and Fig. 3). Total relative cover by herbs is generally greatest in the level stands located on the canyon's rim and floor (Fig. 4).

In Figs. 3 and 4 and subsequent figures, the symbols indicating stand cover are ordinated between two intuitively important topographic gradients: total annual potential insolation and elevation. The insolation gradient is, in effect, an exposure gradient, although it does not take into account the important factor of exposure to, or protection from, the nearly continuous wind that is characteristic of the region. The second gradient, elev-

Figure 3. Topographic ordination showing relativized total cover by trees and shrubs. The small number near each circle is a stand number. The two largest circles represent 195% and 165% cover, respectively. The remaining symbols in order of decreasing size denote the following cover ranges: 99.9-60.0, 59.9-40.0, 39.9-30.0, 29.9-20.0 and ≤19.9%.

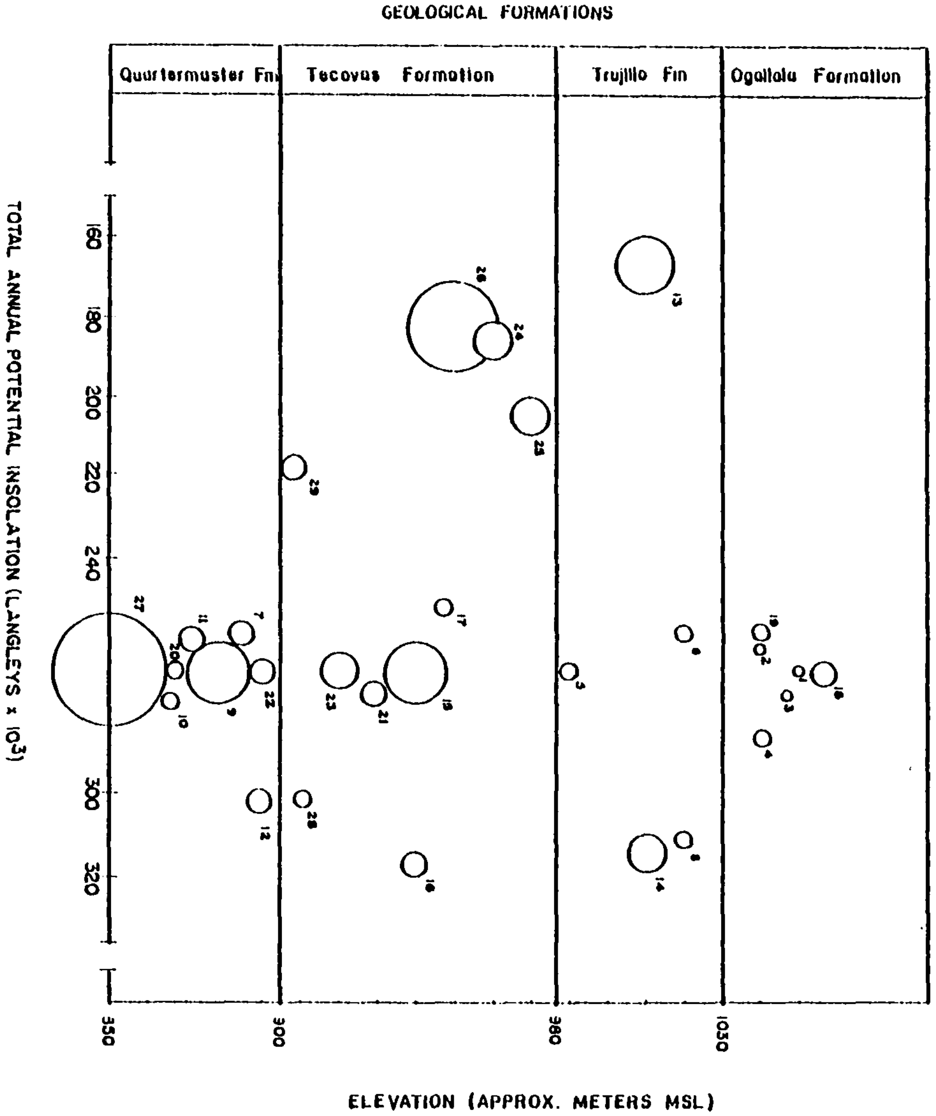

GEOLOGICAL FORMATIONS
Quartermaster Fm
Tecovas Formation
Trujillo Fm
Ogallala Formation
TOTAL ANNUAL POTENTIAL INSOLATION (LANGLEYS x 10³)
160
180
200
220
240
300
320
ELEVATION (APPROX. METERS MSL)
350
300
980
1030
27
11
7
20
22
9
10
12
29
26
24
25
17
23
21
15
28
16
13
5
6
8
14
19
2
1
3
18
4

Figure 4. Total herbaceous cover on topographic ordination. Symbols in order of decreasing size denote the following classes: ≥60%, 59-50%, 49-40%, ≤39% total relative cover by herbs.

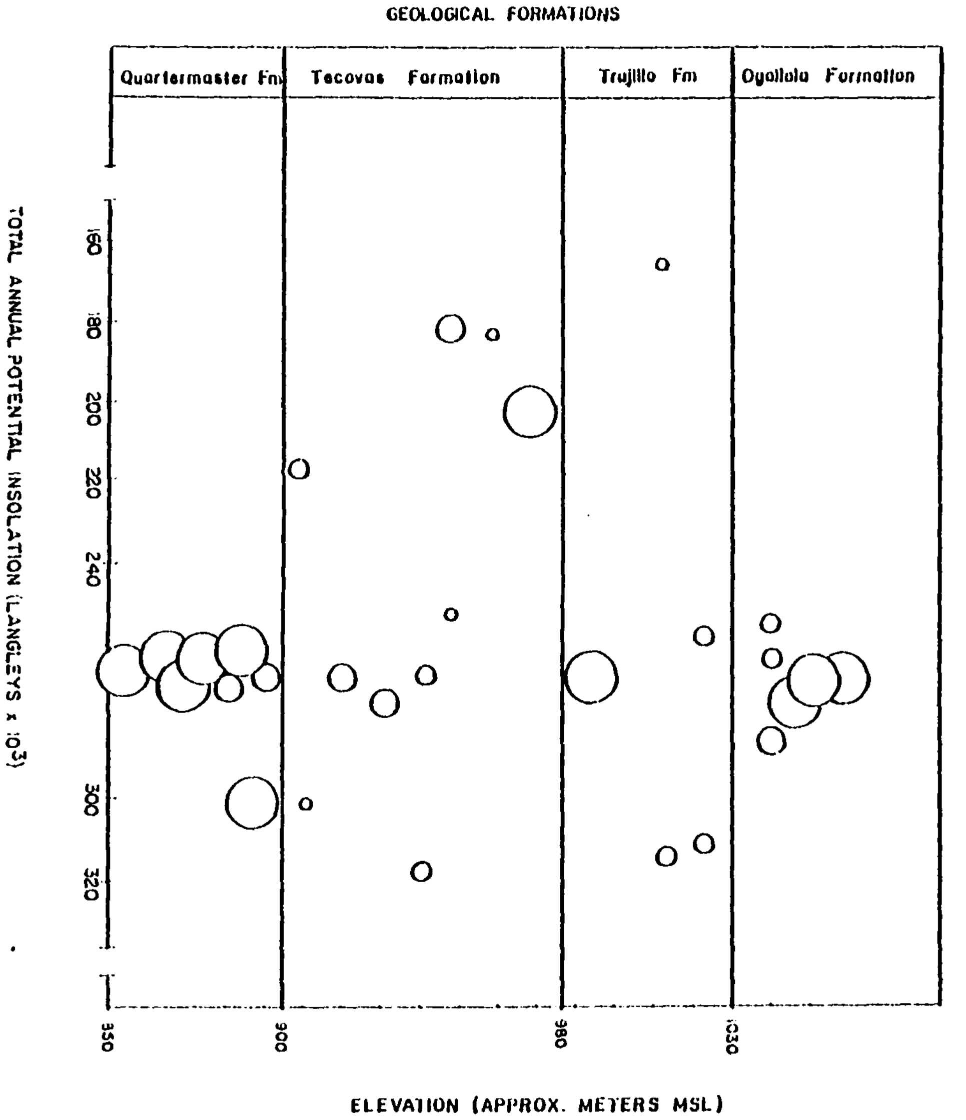

GEOLOGICAL FORMATIONS
Quartermaster Fm
Tecovas Formation
Trujillo Fm
Ogallala Formation
TOTAL ANNUAL POTENTIAL INSOLATION (LANGLEYS x 10³)
160
180
200
220
240
300
320
850
900
980
1030
ELEVATION (APPROX. METERS MSL)

Table 6. Leading woody species, number of stands, and average relative cover of associated woody species. + = <1% relative cover.

Leading Species	Number of Stands	Average Relative Cover of Associated Woody Species[1]											Total
		Prgl	Oppo	Jupi	Jumo	JpJm	Rhar	Rhmi	Yuan	Quha	Pode	Other	
Prosopis glandulosa	6	54	11	9	1	2	1	5	7	-	-	10	100
Opuntia polyacantha	2	35	38	8	4	1	2	-	6	-	-	6	100
Juniperus pinchotii	8	11	7	38	3	5	4	7	11	-	-	14	100
J. monosperma	3	5	2	13	46	3	12	2	1	-	-	16	100
J.p. X *J.m.*	2	10	5	16	8	33	8	13	+	-	-	7	100
Rhus aromatica	3	5	+	12	13	7	36	3	-	4	-	20	100
R. microphylla	2	15	-	12	2	11	7	41	-	-	-	12	100
Yucca angustifolia	1	-	-	11	-	-	-	33	45	-	-	11	100
Quercus havardii	1	6	-	20	1	13	-	2	2	39	-	17	100
Populus deltoides	1	7	-	6	10	1	2	3	+	-	58	13	100

[1] Species abbreviations are composed of the first two letters of the genus and species listed at the left of the table; see also Table 1.

Table 7. Average percent frequency of important herbs in stands grouped by leading woody species.

Leading Species	Number of Stands	Average Percent Frequency of Associated Herbs[1]											
		Bogr	Bocu	Boer	Bohi	Spcr	Buda	Ledu	Paob	Sele	Himu	Argl	Leru
Prosopis glandulosa	6	36	2	5	-	15	17	-	7	4	-	-	2
Opuntia polyacantha	2	45	-	-	-	15	17	-	15	-	-	-	6
Juniperus pinchotii	8	7	19	23	11	6	-	-	-	-	9	4	23
J. monosperma	3	9	26	-	2	-	-	11	-	-	-	-	6
J.p. X *J.m.*	2	26	17	10	-	-	-	-	6	-	-	-	6
Rhus aromatica	3	-	39	-	-	-	-	13	-	-	-	-	-
R. microphylla	2	9	-	36	-	-	-	10	-	-	-	-	-
Yucca angustifolia	1	-	39	-	-	-	-	-	-	-	-	36	-
Quercus havardii	1	6	31	-	16	-	-	-	-	-	-	-	-
Populus deltoides	1	-	23	-	-	12	-	-	-	24	-	-	-

[1] See Table 2 for definitions of abbreviations.

Table 8. Total stand cover and density of woody species and total relative cover of herbs.[1]

Stand	Leading Woody Species	Woody Cover (%)			Woody Density (stems/ha)		Leading Herb Species	Total Herb Relative Cover
		Total	≥1m	<1m	≥1m	<1m		
1	Prgl	10	6	4	79	2,062	Bogr	67
9	"	67	46	21	610	2,134	Paob	58
11	"	34	18	16	303	1,915	Spcr	66
18	"	39	35	4	312	134	Bogr	69
21	"	34	22	12	369	2,472	Spcr	53
28	"	28	14	14	447	2,833	Boer	38
5	Oppo	25	11	14	172	3,507	Bogr	62
7	"	32	16	16	289	1,387	Spcr	60
2	Jupi	12	7	5	165	2,721	Bocu	47
3	"	1	1	<1	29	87	"	61
10	"	23	7	16	102	4,130	Boer	66
12	"	36	30	6	552	717	Himu	74
20	"	24	13	11	202	2,503	Leru	69
22	"	38	22	16	411	3,082	"	58
25	"	44	24	20	444	4,954	Bocu	63
29	"	37	20	17	639	3,512	"	43
23	Jumo	45	29	16	523	2,383	Bogr	53
24	"	54	41	13	527	2,992	Bocu	39
26	"	165	114	51	1,415	3,371	"	56
14	JpJm	53	36	17	711	2,357	"	45
15	"	89	65	24	784	2,900	Bogr	47
6	Rhar	21	9	12	228	1,798	Bocu	43
13	"	70	<1	70	<1	15,154	"	39
17	"	25	16	9	423	1,866	"	22
8	Rhmi	24	8	16	312	2,432	Boer	44
16	"	38	17	21	375	2,001	"	44
4	Yuan	29	3	26	76	10,879	Bocu	53
19	Quha	27	8	19	222	4,709	"	42
27	Pode	196	171	25	1,060	1,382	Sele	61

---

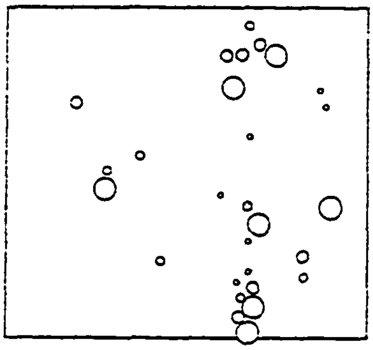
[1] Species abbreviations are defined in Tables 1-2.

ation, is important in the plant environment because both geology and soils, as well as protection from drying wind, change with elevation in the canyon. In Fig. 3, the 10 extreme stands -- five at the cool end (low sun) and five at the warm end (high sun) of the insolation gradient -- are situated on 40-65% slopes. The remaining 19 stands, located mainly in the middle of the insolation gradient, have 5-10% slopes, with the exception of Stands 6 and 17, which have 65-75% slopes. The six stands highest in elevation are located on nearly level terrain above the rim of the canyon (Fig. 3); stands 1, 2, and 18 are on mostly smooth, unbroken terrain a few hundred meters back from the canyon rim, while stands 2, 4, and 19 are on rocky, slightly sloping land very near the rim. The seven stands lowest in elevation are located on level terrain on the floor of the canyon. Stands 15, 21, and 23 are located on narrow, slightly rolling, colluvial plateaus about 75 m from the canyon floor. Stand 5 is on a level mesa.

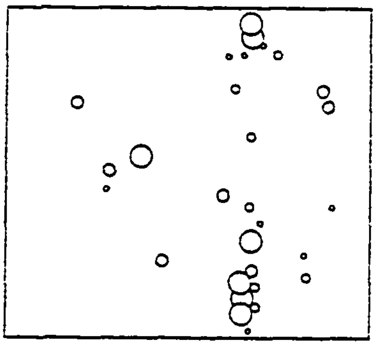
The stands are further characterized environmentally in Table 9, which lists the measured values of 10 edaphic and topographic variables, and Fig. 5, which symbolizes the variables on the topographic ordination. Some of the edaphic variables appear to be partially cor-

Figure 5. Soil variables, surface rock, and percent slope of the sampled stands on the topographic ordination. Circles in order of decreasing size indicate the quartiles of the data, beginning with the upper quartile. In the soil texture and % slope figures, circles in order of decreasing size denote loamy sand, sandy loam, and sandy clay loam; and slopes of 75-60, 55-40, and 10% or less, respectively.

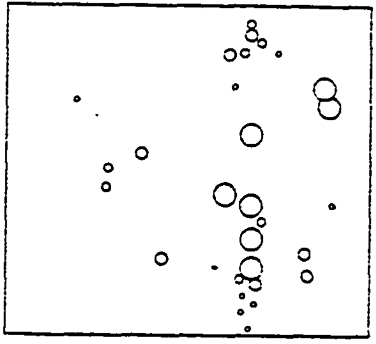
% Sand



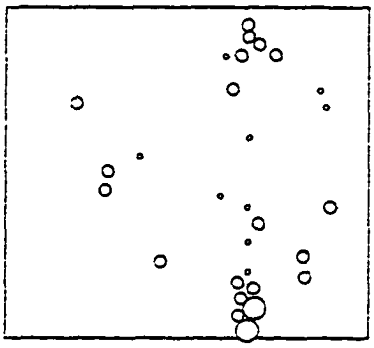
% Silt



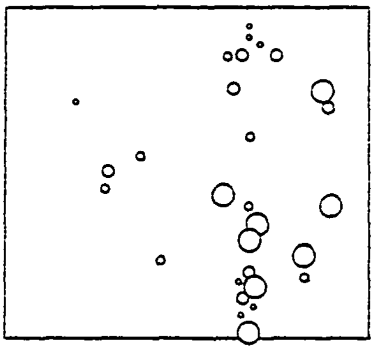
% Clay



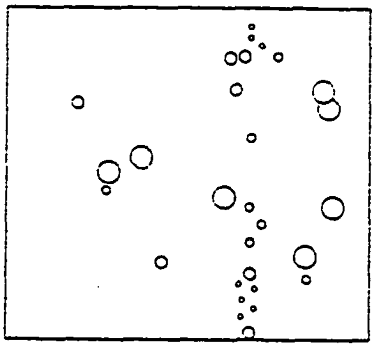
Soil Texture



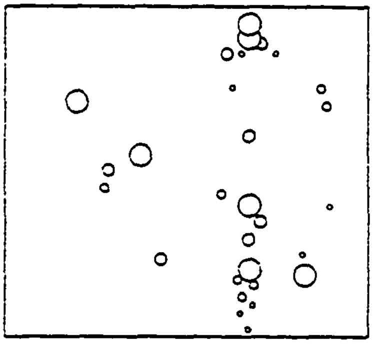
pH



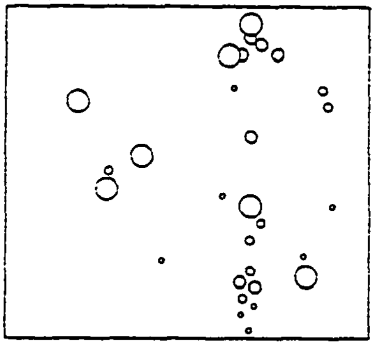
Surface Rock



Base Exchange Capacity



Organic Carbon



% Slope

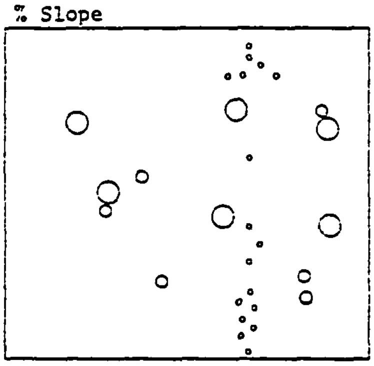


Table 9. Measured values of environmental variables in sampled stands. (Stand arrangement corresponds to Table 8).

Stand	Sand (%)	Silt (%)	Clay (%)	Rock (% Freq)	pH	Base Exchange Capacity	Organic Matter (%)	Elevation (m)	Slope (%)	Aspect
1	65.0	15.8	19.2	0	8.0	18.4	2.27	1049	-	-
9	71.8	9.0	19.2	0	8.7	13.3	1.98	887	-	-
11	69.0	14.4	16.6	0.1	8.5	13.8	1.51	880	5	SE
18	68.0	13.8	18.2	0	7.7	17.9	2.70	1045	-	-
21	74.4	8.3	17.3	7.3	8.8	15.0	1.28	930	10	WSW
28	71.8	9.0	19.2	73.2	9.1	11.7	0.80	914	55	SW
5	64.6	9.6	25.8	2.2	8.4	14.4	2.12	991	5	S
7	62.2	19.6	18.2	0	8.0	13.9	2.02	890	-	-
2	73.4	8.2	18.4	38.7	8.5	11.7	2.03	1039	10	WNW
3	73.4	8.0	18.6	1.8	8.2	16.2	2.30	1049	5	SSW
10	82.8	9.6	7.6	0.5	8.0	4.9	0.49	885	-	-
12	70.8	10.4	18.8	11.1	8.3	17.2	2.57	899	40	SE
20	72.0	19.8	8.2	0.3	8.0	6.3	0.58	867	-	-
22	63.0	11.8	25.2	36.7	8.5	24.0	1.89	893	5	N
25	67.0	12.8	20.2	66.5	8.4	17.4	3.04	991	50	NW
29	69.4	12.0	18.6	58.9	8.4	15.9	0.93	884	40	NE
23	56.8	14.0	29.2	32.9	8.8	16.4	1.61	927	5	E
24	70.7	11.8	17.5	67.3	8.5	14.3	1.69	963	60	NE
26	73.8	9.4	16.8	19.6	8.4	13.7	2.64	951	50	NNE
14	65.0	11.6	23.4	66.3	8.5	13.2	1.18	1006	60	SSW
15	67.7	10.0	22.3	20.7	8.5	16.7	2.68	948	5	SSW
6	74.8	9.6	15.6	60.6	8.5	8.5	1.12	1021	65	W
13	71.4	12.2	16.4	34.0	8.1	16.7	4.16	1003	65	NNW
17	59.0	11.0	30.0	87.0	8.7	13.9	0.93	963	75	E
8	62.6	12.6	24.8	65.4	8.6	12.3	1.71	1021	45	S
16	80.0	6.8	13.2	62.3	9.4	9.6	0.50	944	60	S
4	74.2	10.6	15.2	28.6	8.5	10.6	2.32	1039	10	SSE
19	71.8	7.6	20.6	34.2	8.9	16.2	2.54	1038	10	NE
27	84.8	4.6	10.6	50.2	8.8	8.2	0.50	856	-	-

related with one another and with the topographic gradients (Fig. 5). For example, the frequency of surface rock is greatest on steep slopes, where runoff and erosion are greatest, and least on level terrain, where rocks tend to be buried by transported soil. Soil texture varies fairly consistently with elevation. The loamy sands are found at the lowest elevation. The sandy clay loams are found at moderate elevations. Other correlations with topographic gradients are less apparent.

Several of the common species in the canyon show peak cover concentrations in one or another fairly well-defined areas. This is illustrated in Figs. 6-8, which are identical to the topographic ordination in terms of the relative positions of stands, but different in terms of symbol definition. In Fig. 6, *Juniperus pinchotii* and *J. monosperma* have peak coverage on the cool end of the insolation gradient. Interestingly, the hybrid juniper, *J.p. X J.m.*, has peak coverage on the warm end. *Prosopis glandulosa* is most important in the middle of the insolation gradient, i.e., on level terrain at all elevations. The two *Rhus* species peak at opposite ends of the insolation gradient (Fig. 6). Similar distributional differences are evident among the smaller shrubs (Fig. 7), part-

Figure 6. Percent cover of nine important woody species on the topographic ordination. Symbols in order of decreasing size denote the following cover classes: 10, 9.9-7.5, 7.4-5.0, 4.9-2.5, ≤2.4%. Absence is denoted by a dash. Circles with a center dot indicate stands in which a species leads in terms of relative cover.

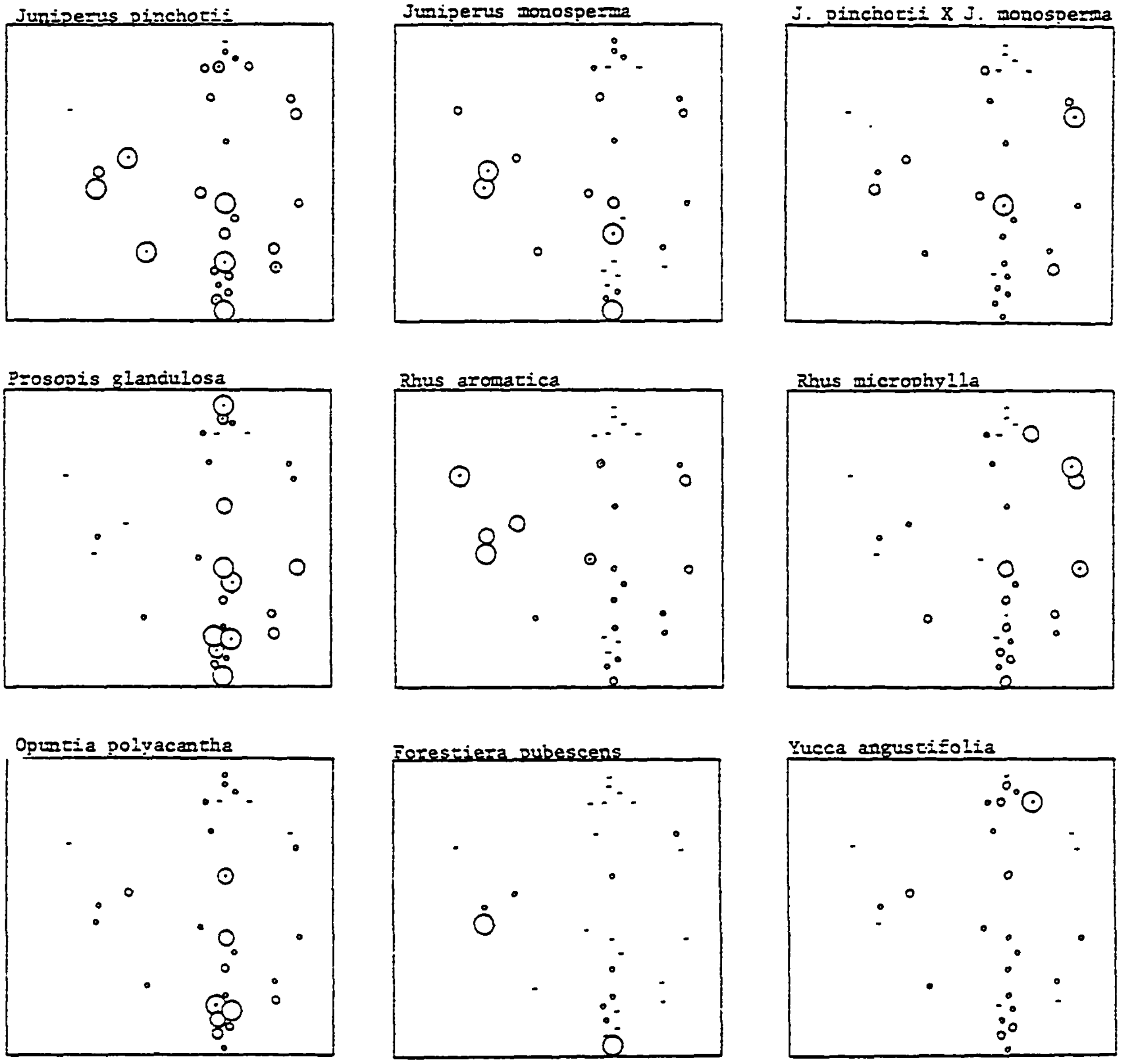
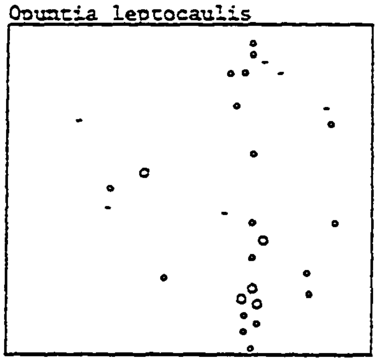
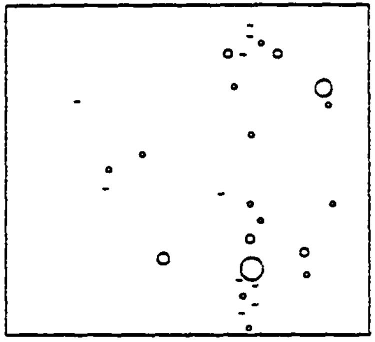

Juniperus pinchotii
Juniperus monosperma
J. pinchotii X J. monosperma
Prosopis glandulosa
Rhus aromatica
Rhus microphylla
Opuntia polyacantha
Forestiera pubescens
Yucca angustifolia

Figure 7. Percent cover of 12 woody species on the topographic ordination. Circles in order of decreasing size denote the following cover classes: ≥4.0, 3.9-3.0, 2.9-2.0, 1.9-1.0, ≤0.9%. Absence is indicated by a dash.

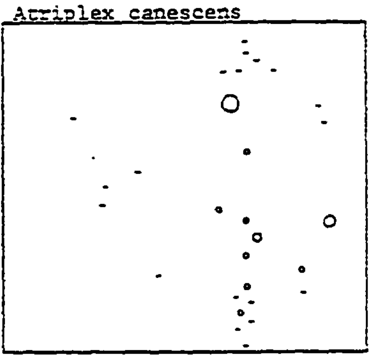
Opuntia leptocaulis



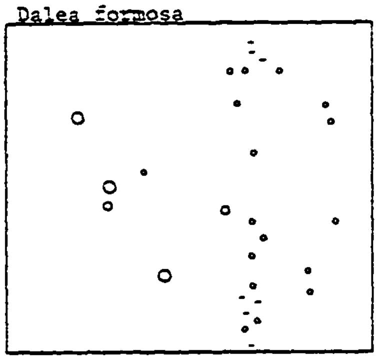
Mimosa borealis



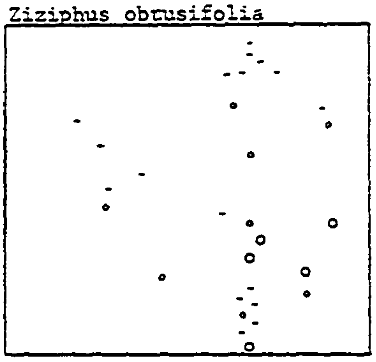
Atriplex canescens



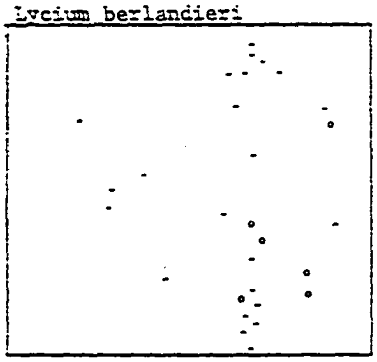
Dalea formosa



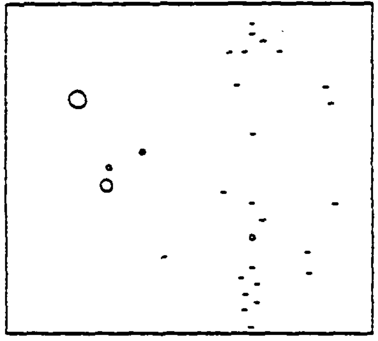
Ziziphus obtusifolia



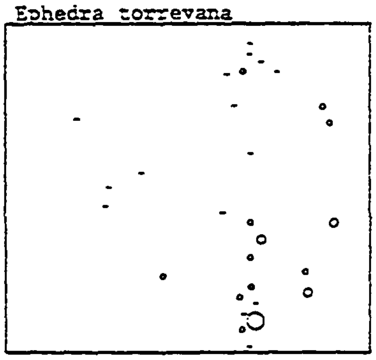
Lycium berlandieri



Ptelea trifoliata



Ephedra torreyana



Cercocarpus montanus

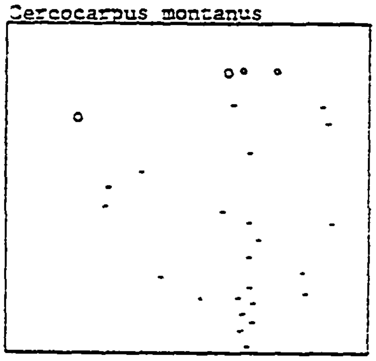
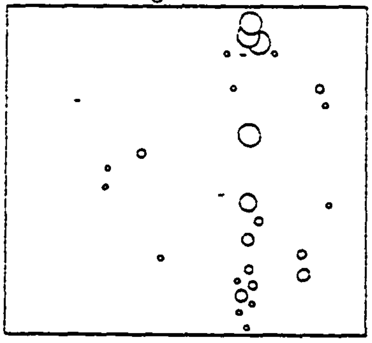
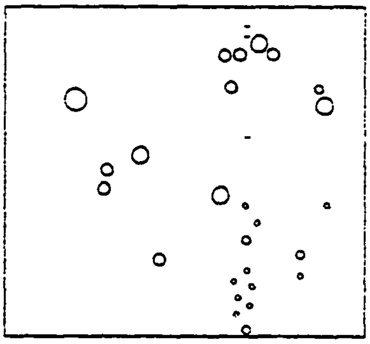


Figure 8. Percent relative cover of 12 grasses on the topographic ordination. Symbols in order of decreasing size denote 20.0, 19.9-15.0, 14.9-10.0, 9.9-5.0, and ≤4.9% relative cover. Dash denotes absence.

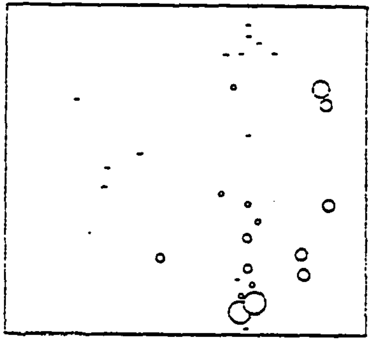
Bouteloua gracilis



Bouteloua curtipendula

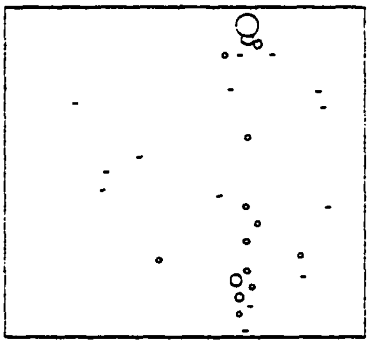


Bouteloua eriopoda

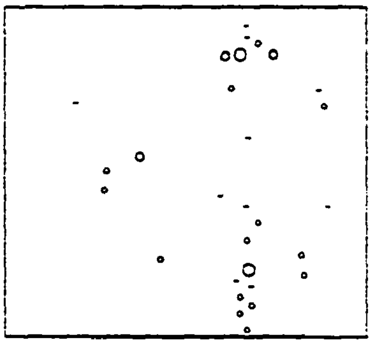


Sporobolus cryptandrus

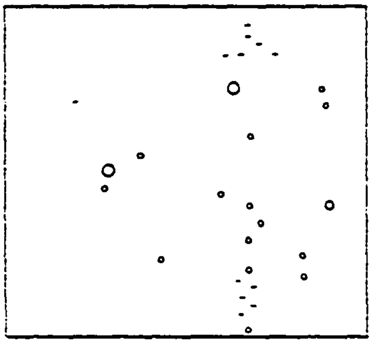
Buchloe dactyloides



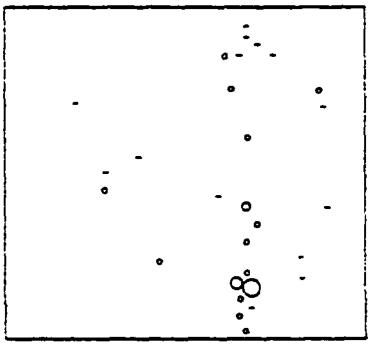
Bouteloua hirsuta



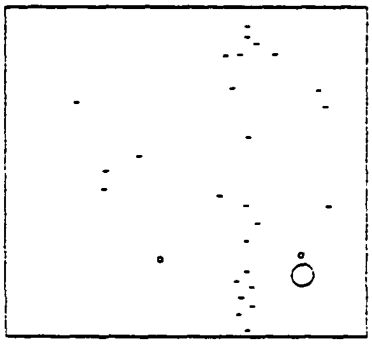
Leptochloa dubia



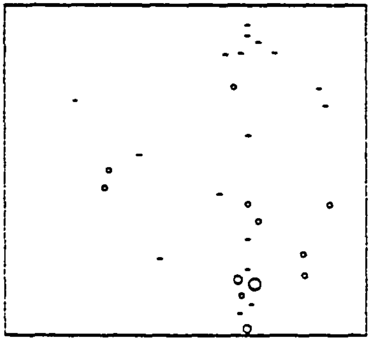
Panicum obtusum



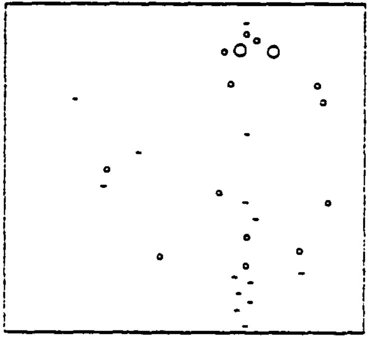
Hilaria mutica



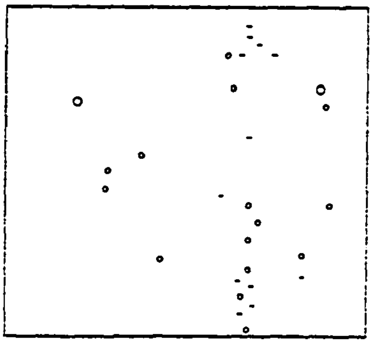
Setaria leucopila



Aristida glauca



Tridens muticus



icularly *Dalea formosa* (feather dalea), *Ptelea trifoliata* (water ash), *Ephedra torreyana* (torrey joint-fir), and *Cercocarpus montanus* (mountain mohogany). The last is one of the few species whose distribution is clearly related to elevation or, probably more accurately, geological formation. This species appears to be limited to the slight talus slopes in the immediate vicinity of the caliche caprock of the Ogallala Formation.

Patterns of cover distribution that appear to be related to exposure are also evident among herbaceous species in the canyon (Fig. 8). For example, the three species of *Bouteloua* have approximately complimentary distributions, with *B. gracilis* most important on level terrain in the middle of the insolation gradient, *B. curtipendula* most important at the cool end of the gradient, and *B. eriopoda* most important at the warm end (Fig. 8).

Figure 8 indicates that *B. eriopoda* is one of the most important grasses on exposed slopes, a phenomenon probably related to Knipe and Herbel's (1960) findings that this species has a relatively high germination percentage under conditions of high osmotic concentrations. The latter would suggest that *B. eriopoda* caryopses germinate under conditions of very limited moisture. In the rocky outcrops of the canyon slopes, where crevices would quickly catch and retain runoff from a light rain, this ability to exploit limited moisture supplies would be beneficial. That *B. eriopoda* is successful in areas of limited moisture is emphasized by Stoddart and Smith's (1943) observation that it is the most important single species in the desert grassland.

A comparison of juniper distributions (Fig. 6) with grass species (Fig. 8) indicates that all or nearly all grasses have peak coverage in stands where junipers are not important. This phenomenon is probably related to shading and a number of other factors, including allelopathy. For example, Johnsen (unpublished; cited in Lavin, Jameson, and Gomm, 1968) found that both soil adjacent to juniper roots and ground-up roots mixed with potting soil inhibited leaf growth of *Bouteloua gracilis* and *B. curtipendula*.

Geological Relationships

The vegetation of the canyon appears to exhibit some relationships with elevation (e.g., Fig. 3). However, none of the relationships are with elevation per se, but with edaphic and exposure conditions which change with parent material, the steepness of slopes, and protection from wind. Thus, the same species and associations that occur on the canyon floor also occur on the plain and gentle slopes above the rim of the canyon. The canyon walls are more unique, however, and have no environmental counterparts on the plain or on the floor of the canyon. Although the same species are present throughout the area (with one or two exceptions, such as Cercocarpus montanus), the extreme range of exposure found on the canyon walls provides the opportunity for first one species and then another to gain dominance. For example, Juniperus pinchotii, Prosopis glandulosa, Rhus aromatica, and R. microphylla all occur on the floor of the canyon, where their relative contributions to stand structure are fairly consistent from one stand to another, with the first two usually dominant. On the canyon walls, however, all four species predominate, but in different intervals of the exposure gradient (Fig. 6). Some additional generalizations relating vegetation and geology are discussed in the following paragraphs, which deal with each of the four geological formations.

Ogallala Formation. Six stands were sampled above the rim of the canyon on the Ogallala Formation and

Pleistocene eolian deposits of the surrounding plains (Figs. 4-6). The stands generally had sandy loam soils and slopes of less than 10%.

The three stands farthest from the rim occurred on deeper soils, had slopes of 5% or less, low frequency of surface rock, relatively low pH (7.7-8.2), high to moderate base exchange capacity (16.2-18.4 meq), high organic matter (2.27- 2.70%), and high clay content (18.2-19.2%) (Fig. 5 and Table 9). *Prosopis glaundulosa* was the leading shrub in all three stands. *Bouteloua gracilis* and *Buchloë dactyloides* were the leading grasses, and *Opuntia polyacantha*, *Juniperus monosperma*, and *Sporobolus cryptandrus* (sand dropseed) were important secondary species (Figs. 6-8).

The three stands closest to the rim occurred in the thin, rocky soils of the upper caprock zone within a few meters of the canyon rim. All three stands had a high frequency of surface rock, moderate pH (8.4-8.5), low to moderate base exchange capacity (10.6-16.2 meq), high organic matter (2.03-2.54%) and high sand content (72-74%) (Fig. 5 and Table 10). The stands each had a different leading shrub (*Juniperus pinchotii*, *Quercus harvardii*, and *Yucca angustifolia*) (Fig. 6), but generally had the same secondary shrubs (*Dalea formosa*, *Cercocarpus montanus*, *Y.*

angustifolia, *J. pinchotii*), the same primary grass (*Bouteloua curtipendula*), and several of the same secondary grasses (*Sporobolus cryptandrus*, *B. hirsuta*, and *Aristida glauca*) (Figs. 6-8).

Quartermaster Formation. The vegetation of the Quartermaster Formation tends to occur on level to rolling terrain, with relatively little surface rock and a texture of sandy loam or loamy sand. Steeper slopes occur in the upper part of the Quartermaster but tend to be bare or very sparsely vegetated because of rapid erosion. However, in some areas boulders and other landslide debris are perched on the upper slopes of the Quartermaster, where they serve to retard erosion and enhance soil accumulation. In these areas, which are usually vegetated, soils consist mainly of colluvial materials which originated from higher up on the canyon walls or from above the canyon rim. Stand 12 was a bowl-shaped area near the top of the Quartermaster that was apparently created by a large landslide. It was not typical of other stands sampled in the Quartermaster in that it supported a pure dense stand of *Hilaria mutica*, which typically occurs in dense, pure stands on concave sites (H. Wright, 1974). The area was isolated from most directions by steep cliffs and its atypical vegetation may be a result of its having escaped burns and consequent heavy grazing; according to H. Wright (1974) *H. mutica* is unpalatable to cattle unless grazed within a few weeks after new growth begins on a burn.

Probably because of the mostly level terrain in the Quartermaster, *P. glandulosa* and *Opuntia polyacantha* are among the most important species there. Of the eight stands sampled in the Quartermaster (Fig. 3), three were dominated by *P. glandulosa* and/or *O. polyacantha*, two by *J. pinchotii*, two by a mixture of *J. pinchotii* and *P. glandulosa*, and one by *Populus deltoides*. The four stands in which *J. pinchotii* was most important had *B. eriopoda* and *Lecidea rubiformis* as primary herbs. The primary herbs in the *Prosopis* stands were *Panicum obtusum*, *Buchloë dactyloides*, and *Bouteloua gracilis*. *Sporobolus cryptandrus* was fairly important in seven of the eight stands sampled in the Quartermaster.

Trujillo and Tecovas Formations. In contrast to the usually level and fairly homogeneous topography of the Ogallala and Quartermaster Formations, the topography of the Trujillo and Tecovas Formations is quite diverse. Most of the variation in exposure in the canyon occurs in these formations. This is illustrated in Fig. 3, which shows that the stands in the Quartermaster and Ogallala Formations occur in the insolation interval from about 260 to 290 kilolangleys/year, while those in the Trujillo and Tecovas Formations occupy a much larger interval, from about 160 to 320 kilolangleys/year. Slopes of the Trujillo and Tecovas range from 10% to 75%, while those of the Quartermaster and Ogallala are nearly always less than 10% (Fig. 5). The vegetation of the Trujillo and Tecovas is correspondingly diverse, showing wide variation in total cover of shrubs (Fig. 3), herbs (Fig. 4), and individual species (Fig. 6-8). The leading shrubs in the 15 stands sampled on these two formations are *Prosopis glandulosa* (2 stands), *Juniperus monosperma* (3), *J. pinchotii* (2), *J.p. x J.m.* (2), *Rhus aromatica* (3), *R. microphylla* (2), and *Opuntia polyacantha* (1). All three of the juniper taxa and the two *Rhus* spp. have peak cover here, and only one of these, *J. pinchotii*, is a leading shrub in any other formation (Fig. 6). Secondary shrubs which reach peak cover in this zone are *Atriplex canescens* (fourwing saltbush), *Dalea formosa*, *Ziziphus obtusifolia* (jujube), and *Ptelea trifoliata* (Fig. 7). In addition, a few grasses have peak cover here, including *Bouteloua curtipendula*, *Leptochloa dubia*, and *Tridens muticus* (slim tridens) (Fig. 8).

Classification by Primary Woody Species

The grouping of stands by major shrubs is convenient, and the similarity among such groups can usually be related to the insolation gradient. In the following paragraphs, which are summarized in Tables 6 and 7, the composition of stands grouped by leading shrub species is discussed. The major weakness of this approach is that all of the stands generally contain the same important species, with different species attaining primary importance in different stands. In some cases, stands with equivalent environments have different leading species, but generally the stand composition can be related to obvious environmental differences, at least qualitatively.

Prosopis-*Opuntia* Stands

The six stands in which *Prosopis glandulosa* is the leading shrub and the two stands in which *Opuntia polyacantha* is the leading shrub are very similar and should logically be treated together. Both groups of stands have the same secondary woody species (Table 6) and the same important grasses (Table 7). In the two stands where *O. polyacantha* comprises slightly more areal cover than *P. glandulosa*, the latter still appears to be more important in the community in terms of biomass, space occupied and vertical diversity and the consequent influence of these factors on the environment of the community. *Prosopis*-*Opuntia* stands generally occur on level terrain at all elevations in the canyon (Table 9). Both species are always present in stands on level terrain, usually with relative cover values of at least 20%. Conversely, on slopes they usually do not attain absolute cover values greater than 5% (Fig. 6).

Prosopis-*Opuntia* stands have relative cover values of 29-90% *P. glandulosa*, 7-44% *O. polyacantha*, 5-28% *Juniperus pinchotii*, 11-25% *Yucca angustifolia*, and 9-14% *Rhus microphylla*. These stands tend to be heavily dominated by the two primary shrubs at the expense of secondary shrubs. The relatively low average cover of secondary shrubs is probably because these species do not compete well on level terrain, where they must compete not only with *P. glandulosa* and *O. polyacantha* but also with a usually dense cover of short grasses. With the exception of *Y. angustifolia*, the secondary shrubs are more competitive on rocky slopes where grass cover is relatively sparse and *P. glandulosa* and *O. polyacantha* are generally absent.

Historical factors may be partly responsible for the predominance of Prosopis glandulosa on level sites. Although Wright, Bunting, and Neuenschwander (1976) feel that the range of mesquite has not increased significantly since the mid-1800's, there is evidence that it was much less important in the canyon before the introduction of cattle in 1876. Marcy (1853) reported mesquite along the Red River below the mouth of the canyon but made no mention of the now-extensive coverage by mesquite on the redbed flats in the canyon floor. There are also later reports which indicate that the mesquite flats in the canyon were more open at one time; Clothier (1904), for example, recommended that the large open areas in the canyon floor be planted in Prosopis for wood production.

Total absolute woody cover in Prosopis-Opuntia stands ranges from 10% to 67% but is usually 25-39%. The relative cover of P. glandulosa is greatest on the deeper loamy soils above the rim of the canyon, where it comprises as much as 90% of the woody cover. However, in terms of absolute cover, it is slightly more important in the more protected stands on the canyon floor, where its peak absolute cover (40%) is attained, as is that of Opuntia polyacantha (18%).

The most important grasses in *Prosopis-Opuntia* stands are *Bouteloua gracilis*, *Sporobolus cryptandrus*, and *Buchloë dactyloides*; the last is usually a secondary species, while the first two are usually dominant. Two other grasses also attain their peak importance in these stands: *Setaria leucopila* and *Panicum obtusum*. Of the five, only *B. gracilis* is of much importance in other stands.

Juniperus Stands

Junipers were the leading shrubs in 45% of the sampled stands and were important subordinants in another 20% (Table 4). Collectively, junipers generally predominated on slopes and in some level stands on the floor of the canyon. The most widespread of the junipers was *Juniperus pinchotii*, which was the primary shrub in eight stands scattered from canyon rim to floor (Fig. 6). It peaked in the moderate to cool exposure zones, along with *J. monosperma*, which predominated in three stands in this zone. The hybrid juniper, *J. pinchotii* X *monosperma*, peaked at the dry end of the exposure gradient and led in only two stands (Table 4, Fig. 6). *Juniperus scopulorum* occurred, as a minor component only, in the floodplain and on a steep NNE slope.

The hybrid and both of its parental species all had greater absolute cover at the extremes of the exposure gradient than in some intermediate stands (Fig. 6). The explanation for this appears to be that most of the intermediate stands occur on relatively deep, level soils where the deeper taproot of *Prosopis glandulosa* give it a competitive advantage over the junipers (e.g., Cannon, 1911; Simpson, 1977). This is supported by observations by Cannon (1911), who reported *Prosopis* to have an 8-m taproot, and Johnsen (1962) who found *Juniperus monosperma* to have a taproot over 4-m in length.

Animals may be a factor in the continuing dominance of the slopes by junipers. Juniper berries, consumed by raccoons and other animals, are frequently deposited on boulders and other promontories on the slopes of the canyon. Seeds deposited on boulders on rocky slopes have a good chance of lodging in a moist crevice with good conditions of fertility and organic matter. Johnsen (1962) found that the germination rate of *Juniperus monosperma* seeds is increased by digestion, but seeds do not germinate unless continuously moist for more than a week. Johnsen noted that, in general, juniper seedlings occurred in protected areas, for example, under tree canopies or near rocks. Rocks not only provide a protective haven for juniper seedlings, but also tend to enhance soil moisture conditions by retarding runoff and increasing infiltration. Johnsen (1962) indicated that water infiltrating into rocky soils is concentrated and thus available in the early summer longer in rock outcrops than in the adjacent grasslands. He concluded that *J. monosperma* was dominant on rock outcrops because of a combination of improved competitiveness over grasses and better moisture conditions for seed germination.

In the present study it was seldom easy to distinguish between the hybrid juniper and its two parental species; in many cases they were identified only after considerable arbitration. The difficulty is illustrated by the finding that, toward the end of the study in late October, when the distinct colors of mature fruits made the parental species readily distinguishable, a smaller proportion of individuals were identified as hybrids, and virtually all so-called hybrids were males. (Curiously, the fruits did not ripen all at the same time, but in a sequence related to exposure; on November 8 it was observed that fruits of *Juniperus pinchotii* were generally ripening in the order: canyon floor, canyon rim, SE facing slopes, and west facing slopes. This sequence suggests that the fruits ripen more slowly on more exposed sites, possibly as a result of greater moisture stress.)

The distribution of the junipers in the canyon, as determined by the present study, does not show that the hybrid juniper is intermediate in behavior between its parental species. The hybrid peaks on dry, exposed slopes, while the parents both peak on cool, protected slopes (Fig. 6). Whether this is an example of hybrid vigor or purely a case of difficult taxonomy is unclear. The determination of a given juniper as a hybrid was based on a judgemental decision that it was intermediate in the morphological characters described by Hall and Carr (1968). Since none of the characters were quantified, evidence of the intermediate morphology of the hybrid is not available. The only quantitative evidence that the hybrid was intermediate between the parental species is that its average height was intermediate between that of _Juniperus pinchotii_ and the usually taller _J. monosperma_. In stands where both members of a pair occurred, _J. pinchotii_ averaged 13% (n=19, s=2.68) shorter than the hybrid and 37% (n=19, s=3.98) shorter than _J. monosperma_, a difference that is highly significant (P<.0005). The hybrid was taller than

J. pinchotii in 79% of the stands and shorter than *J. monosperma* in 88% of the stands. Although by no means conclusive, these data support the conclusion that the so-called hybrid is intermediate between the parental species.

Contrary to the findings of Hall and Carr (1968), the present study indicates that *Juniperus monosperma* is relatively more important than *J. pinchotii* in mesic areas. This is in accord with Clothier's (1904) observations in the canyon and also with Adams' (1972) observations in the Guadalupe Mountains, where *J. pinchotii* seemed to be generally restricted to the rocky slopes up to about 1800 m, while *J. monosperma* generally occurred in the more mesic areas above this elevation. Hall and Carr apparently arrived at the opposite conclusion in Palo Duro Canyon on the basis of an unrepresentative sample of the exposure gradient. Their primary evidence appeared to be the relative importance of *J. monosperma* on a steep, presumably dry slope having a large clay component. The aspect of the slope was not reported. In any case, convincing evidence was not presented that *J. monosperma* was relatively more common on xeric than on mesic sites in the canyon.

Observations in the canyon also seem to indicate that *Juniperus monosperma* is more important than *J.*

pinchotii in mesic areas and relatively less important in xeric areas. For example, on colluvial benches in one deep arroyo in the floor of the canyon, where moisture stress could be expected to be relatively low, of 71 junipers counted within a 300-m stretch of the arroyo, 59 were *J. monosperma,* 11 were *J. pinchotii* and one was *J. scopulorum*.

In stands on the upper caprock, *J. monosperma* tends to occupy the outer margin of the stand on the canyon edge, while *J. pinchotii* is found more frequently farther back from the rim. This pattern is distinct on the lower caprock, where *J. monosperma* occurs almost entirely on the periphery of the mesa, while *J. pinchotii* occupies the more central portion. Although soils are shallower on the periphery than toward the middle of the mesa, runoff water would presumably be more abundant on the periphery because of its lower elevation. The surface rocks and fissures which become more frequent there would also tend to retard and collect runoff. Weaver and Albertson (1956) and Johnsen (1962) indicate that rocky soils support more mesic plants than adjacent rock-free soils because rocks interspersed in the soil matrix tend to concentrate soil moisture supplies. Midgrasses, which require more moisture than short grasses but are not rooted deeper (Weaver and Albertson, 1956) become relatively more abundant toward the rim of the canyon (R. Wright, 1973). Further, the imperviousness of the caprock would tend to disperse any excess soil water from the middle of the mesa toward the periphery. This same argument applies to the canyon rim as well as to mesas.

Further evidence that J. monosperma grows in relatively mesic sites was observed in Stand 13. This stand was perhaps the most mesic stand sampled in the present study, not only because of its steep, generally NNW aspect, but also because its crescent shape provided still more protection from sun and wind. In this stand a dense, low growth of Rhus aromatica and Quercus havardii covered about 70% of the ground. The only trees were a few individuals of J. monosperma which generally occurred at the foot of a 10-15 m cliff at the top of the crescent.

The junipers predominated in 13 of the stands sampled in the present study. In the following paragraphs, these stands are grouped by leading juniper species and generally described in terms of structure and environment.

Juniperus pinchotii Stands. Juniperus pinchotii comprises a large part of the woody cover in all geological formations and all along the insolation gradient, but it peaks mainly in the moderate to cool end of the gradient in the Tecovas and Quartermaster Formations (Fig. 6). The eight stands led by *J. pinchotii* have *Prosopis glandulosa*, *Yucca angustifolia*, and *Rhus microphylla* as secondary woody species (Table 6). The hybrid juniper and *J. monosperma* are usually not important in *J. pinchotii* stands. Curiously, the reverse is not true; *J. pinchotii* is in fact usually important in stands led by either *J. monosperma* or the hybrid. Part of the explanation for this inconsistency is that *J. pinchotii* is more common and wide-spread than the other two taxa and has greater opportunity to occur without them.

Peak relative cover of *Juniperus pinchotii* (about 50%) occurred on the talus slopes of the upper caprock zone where the total cover by all woody species was only 12% or less. In the eight stands where *J. pinchotii* was the primary shrub, total shrub cover averaged 27% (range 1-44%), of which *J. pinchotii* comprised an average of 38% relative cover (Tables 6 and 8).

In terms of absolute cover, however, *Juniperus pinchotii* peaks (25%) not in the caprock zone, where it has little competition from other shrubs and grasses, but on a steep, NNE slope in the Tecovas (Stand 26), where it is subordinate to both *J. monosperma* and *Rhus aromatica* (Fig. 6). In three of the six stands where *J. pinchotii* has highest absolute cover (Fig. 6) it is subordinate to one or two other species, including *J. monosperma*, *R. aromatica*, *Populus deltoides*, *Prosopis glandulosa* and the hybrid juniper. These three stands (Stands 15, 26 and 27) have total woody cover values (89%, 165%, and 196%, respectively) higher than any other sampled stands. This illustrates a major weakness of using leading dominants classification in areas where stands have a wide structural variation.

The mesic stand (26) is also where *Juniperus monosperma* peaked in terms of absolute cover (70%). And, although all three major junipers reached their greatest average height in the floodplain (Stand 27), they all had secondary peak average heights in Stand 26. (The average heights of the species on the mesic slope and in the floodplain (Stands 26 and 27 respectively) were: *J. pinchotii*, 2.86 m and 3.20 m; *J. monosperma*, 4.54 m and 5.26 m; *J. pinchotii* X *monosperma*, 4.33 m and 6.00 m.)

The *Juniperus pinchotii* stands are divided about half and half among steep and shallow slopes. Soil texture varies from loamy sand to sandy loam to sandy clay loam (cf. Fig. 5 and 6). Base exchange capacity and organic matter are variable, while pH is fairly consistent (8.0-8.5). The frequency of surface rock is high on steep slopes but low on shallow slopes (Table 9).

Of the species which are of secondary importance in *Juniperus pinchotii* stands, only *Yucca angustifolia* usually has its highest importance in these stands. The primary ground cover species are *Bouteloua curtipendula*, *Lecidea rubiformis*, *B. eriopoda*, and *Hilaria mutica*. Although *B. curtipendula* leads in half of the stands, *B. eriopoda* and *L. rubiformis* have the highest average frequency and both have their peak importance in *J. pinchotii* stands (Table 7).

Juniperus monosperma Stands. *Juniperus monosperma* is the primary species in three stands (Table 6). *J. monosperma* stands have high frequency of surface rock (20-59%), and shallow to steep slopes (5-60%) having easterly to northerly aspects (Table 5). In contrast to the relatively low total shrub cover found in *J. pinchotii* stands, cover in *J. monosperma* stands ranged from 45% to 165%, a reflection of the relatively mesic habitat conditions under which this species prevails. Also unlike *J.*

pinchotii, its peak absolute and relative cover occurred in the same stands, whereas *J. pinchotii* had its greatest cover in stands dominated by other species (Fig. 6). This suggests that *J. pinchotii* has a broader niche than *J. monosperma*; the latter may have put more of its adaptive effort into thriving in mesic habitats, whereas the former is able to thrive in relatively xeric sites at the expense of being less competitive where growing conditions are less severe (e.g., Grime, 1979).

The most important secondary shrubs in *Juniperus monosperma* stands (Table 6) are *J. pinchotii* (10-15% relative cover) and *Rhus aromatica* (1-17%). The hybrid juniper, *J.p. X J.m.*, which peaks at the opposite end of the insolation gradient, has a low relative cover (1-5%) in *J. monosperma* stands. The most frequent ground cover species are *Bouteloua curtipendula*, *Leptochloa dubia*, and *B. gracilis*, all of which are more important in stands with other leading shrubs.

Juniperus pinchotii X monosperma Stands. The hybrid juniper, *Juniperus pinchotii X monosperma*, is the major shrub species (28-37% relative cover) in only two stands, both occurring in the drier half of the exposure gradient (Fig. 6), but both having relatively high total shrub cover (57-89%) and both having *J. pinchotii* as a major species (15-16% relative cover). The major grasses are *Panicum obtusum*, *Bouteloua gracilis*, *B. curtipendula* and *B. eriopoda*. The seven stands having the highest relative cover of *J.p. X J.m.* occur in the moderate to dry interval of the exposure gradient.

Rhus Stands

Rhus aromatica stands. In terms of absolute cover, *Rhus aromatica* clearly peaks in the cool end of the exposure gradient, with small secondary peaks in the dry end (Fig. 6). Its tendency to be less important on level ground and intermediate exposures than at either end of the exposure gradient is clear, more so than with any of the three juniper taxa (Fig. 6). *Rhus aromatica*'s peak relative and absolute cover values coincide in one stand at the extreme cool end of the exposure gradient (stand 13); however, in the other two stands in which it is the leading species, its absolute cover is less than that attained in three or four other stands (Fig. 6).

Three secondary species attain peak coverage in *Rhus aromatica* stands: *Bouteloua curtipendula*, *Leptochloa dubia*, and *Atriplex canescens*. *B. curtipendula* is the primary ground cover species in all three stands, and *Leptochloa dubia* is the second species in two of these. *Atriplex canescens* is important in only one other stand, one dominated by *R. microphylla* at the extreme dry end of the exposure gradient (Fig. 6). Both *Juniperus pinchotii* and *J. monosperma* are important shrubs in *R. aromatica* stands (Table 6). In the seven stands where *R. aromatica* attains a relative cover of about 15% or more, *J. monosperma* and *J. pinchotii* both have about the same or greater relative cover than it does.

Rhus microphylla stands. The two stands having *Rhus microphylla* as the primary shrub both occur on steep south slopes (Fig. 6). The peak relative and absolute cover values of this species coincide in both stands. This is an indication that this species is particularly well adapted to xeric environments, although it occurs almost throughout the canyon. It is more widespread among the four geological strata than is *R. aromatica*, which is mainly concentrated on steep, cool slopes in the Tecovas and Trujillo Formations (Fig. 6).

The primary grass in both *Rhus microphylla* stands is *Bouteloua eriopoda* (Table 7). The secondary shrubs are *Juniperus pinchotii*, *Prosopis glandulosa*, and the hybrid juniper. In stands where *R. microphylla* is important, *J. pinchotii* is also usually important, while other species, including *P. glandulosa* and *J.p. X J.m.*, are not consistently important.

Miscellaneous Stands

Yucca angustifolia, *Quercus havardii*, and *Populus deltoides* are the primary species in one stand each (Table 6). *Yucca angustifolia* has greatest absolute cover in level stands having relatively little shrub cover (cf. Figs. 3 and 6). Its peak relative and absolute cover coincide in Stand 4 in the upper caprock zone. In the eight stands where *Y. angustifolia* has a relative cover of about 10% or greater, no other woody species is consistently important, although *Juniperus pinchotii* attains at least 10% relative cover in most of the stands and *Prosopis glandulosa*, *Opuntia polyacantha*, and *Rhus microphylla* are occasionally important. *Yucca angustifolia* comprises 25% or more of the woody cover in three stands, and in each stand the codominant species is different (*R. microphylla*, *J. pinchotii*, or *P. glandulosa*). The major grass in stands where *Y. angustifolia* is important is also variable, but *B.*

curtipendula is the usual one. *Aristida glauca* has its peak relative cover in the one stand where *Y. angustifolia* is the leading shrub.

Quercus havardii occurred in three stands, all located on the upper caprock zone or upper Trujillo Formation toward the cooler end of the exposure gradient. Two of the stands had *Rhus aromatica* as the leading species, while the third had *Quercus havardii* as the leading species. The distribution of *Q. havardii* in the canyon is extremely patchy but generally limited to the canyon floor and rim. Tree-sized specimens were observed in small, widely separated stands on sandy soil in the canyon floor.

Populus deltoides predominates in the floodplain in the floor of the canyon. The sampled stand 27 had 165% canopy cover because of cover repetition and was composed (in terms of relative cover) of *P. deltoides* (58%), *Juniperus monosperma* (10%), *Prosopis glandulosa* (9%), *J. pinchotii* (6%) and others (Table 5). *Juniperus scopulorum* occurred only in this and one other of the stands sampled, although it is not uncommon in the canyon. The stand was heterogeneous in structure, in that *P. deltoides* occurred mainly on the stream margin while the other woody species were more important farther from the stream, although there was no distinct terrace within the stand.

Polar Ordination

It is clear that most of the vegetational variation in the canyon is correlated with differences in exposure as expressed by total annual insolation. A polar ordination of the stands based on total woody cover was constructed as a means of summarizing the compositional variation of the stands and searching for additional influential environmental factors which might be acting on the vegetation. Fig. 9(a) shows shrub cover on the polar ordination. In Fig. 9(b-d), the peak distributions of the important shrubs are shown by delineating the stands in which the shrubs attained at least 15% relative cover. In Fig. 9(e-i), peak distributions of grass species are shown. These figures are useful in showing the peak distribution of particular species relative to other species.

Not surprisingly, the polar ordination (Fig. 9) resembles the topographic ordination (Figs. 6-8) with respect to the relative locations of species concentrations along the exposure gradient. Thus, Juniperus pinchotii, J. monosperma, Rhus aromatica, Quercus havardii, Bouteloua

Figure 9 (a-d). Polar ordination of stands based on total woody cover. (a) Total woody cover, as in Fig. 3. (b-d) Lines enclose the stands in which the indicated species attained ≥15% relative cover.

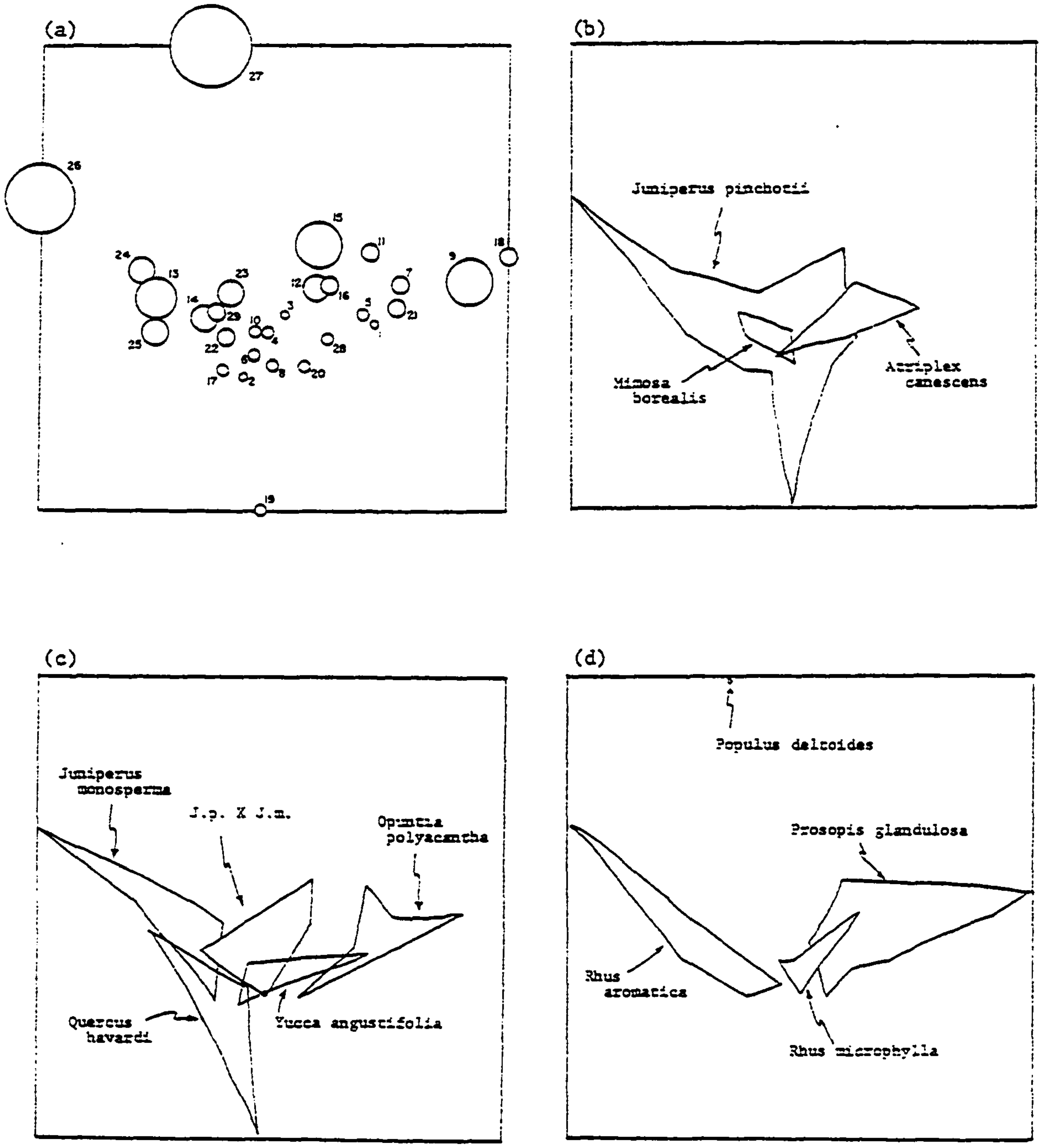
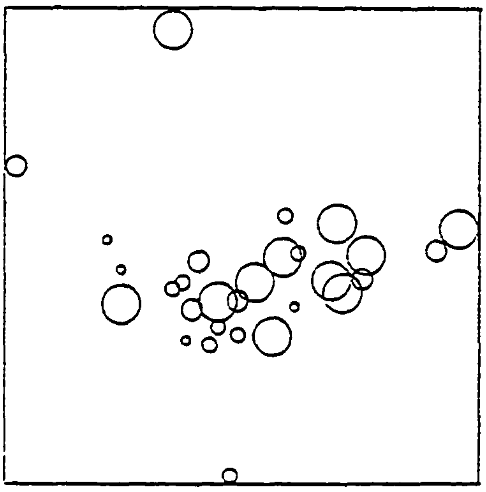
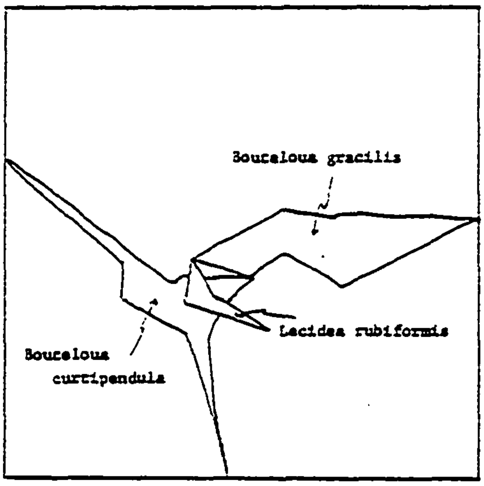

(a)
27
26
24
13
25
14
29
23
22
10
4
3
6
17
2
8
20
12
15
16
28
11
5
7
21
9
18
19
(b)
Juniperus pinchotii
Mimosa borealis
Atriplex canescens
(c)
Juniperus monosperma
J.p. X J.m.
Opuntia polyacantha
Quercus havardi
Yucca angustifolia
(d)
Populus deltoides
Prosopis glandulosa
Rhus aromatica
Rhus microphylla

Figure 9 (e-i). Herbaceous species plotted on woody cover polar ordination. For each species, lines delineate the four stands of greatest cover or all of the stands in which the species attained ≥10% relative cover, whichever involves the most stands.

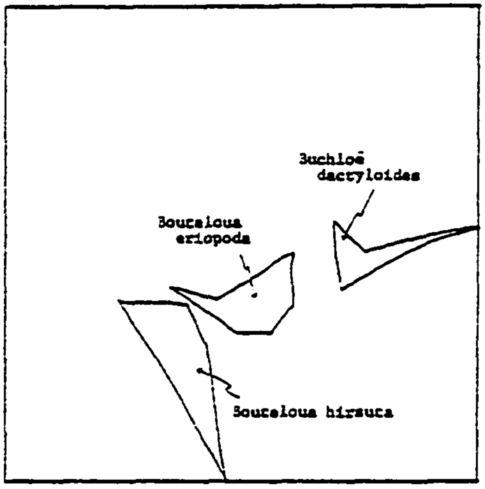
(e)



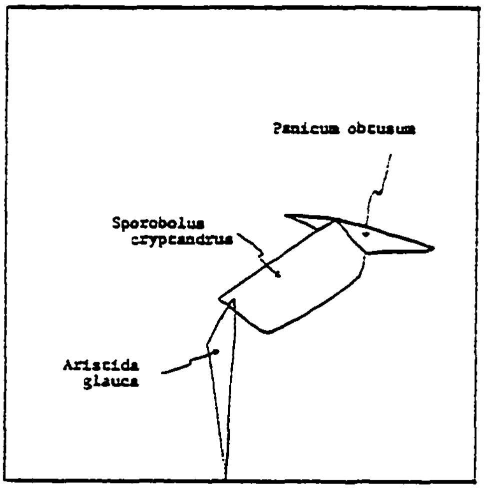
(f)


Bouteloua gracilis
Lecidea rubiformis
Bouteloua
curtipendula

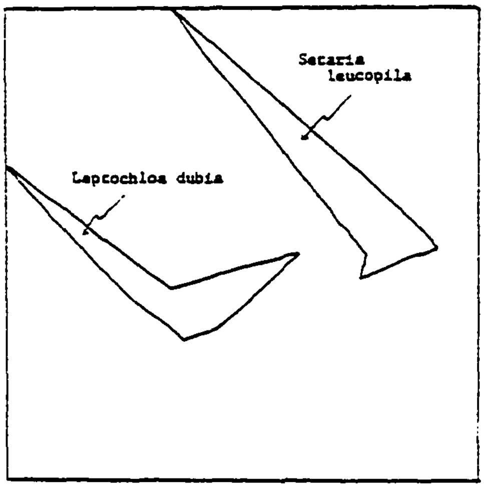
(g)


Buchloë
dactyloides
Bouteloua
eriopoda
Bouteloua hirsuta

(h)


Panicum obtusum
Sporobolus
cryptandrus
Aristida
glauca

(i)

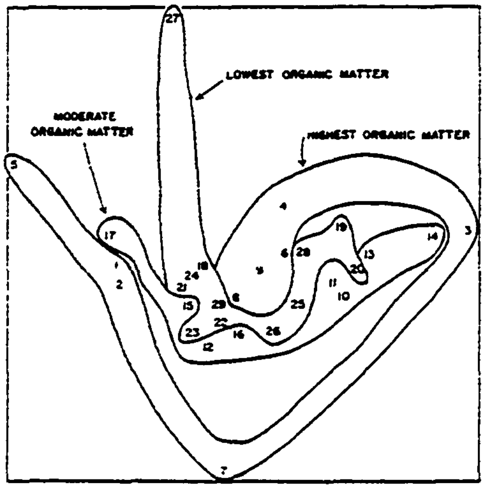

Setaria
leucopila
Leptochloa dubia

curtipendula, and Leptochloa dubia are concentrated on the left side of the polar ordination; R. microphylla and J.p.X J.m. are concentrated near the center; and Prosopis glandulosa, Opuntia polyacantha, Setaria leucopila, Buchloë gracilis, and B. dactyloides are concentrated on the right side of the ordination. Species which tend to peak in both moderate and warm parts of the topographic ordination are found near the center or a little right of center in the polar ordination (Atriplex canescens, Yucca angustifolia, Mimosa borealis and Bouteloua eripoda).

An attempt to correlate these general patterns with similar patterns in environmental variables met with little success, primarily because of the spiraled arrangement of the stands (Fig. 10). The patterns of sun, elevation, organic matter, and surface rock shown in Fig. 10 appear related to species concentrations in the polar ordination (Fig. 10). None of the other eight environmental variables, including sand, silt, mean particle size, clay, base exchange, pH, slope, and aspect, displayed more than fragmentary relationships to the vegetational polar ordination. The relationships of elevation and sun to vegetational variation have been previously illustrated in Figs. 6-8, and the importance of surface rock has been

Figure 10. Woody cover polar ordination showing patterns of four environmental variables. (a) Potential annual solar insolation. (b) Elevation. (c) Soil organic matter. (d) Frequency of surface rock.

(a)


LOWEST ORGANIC MATTER
MODERATE ORGANIC MATTER
HIGHEST ORGANIC MATTER
27
5
17
1
2
24
18
21
15
29
8
9
4
6
28
19
13
14
3
20
11
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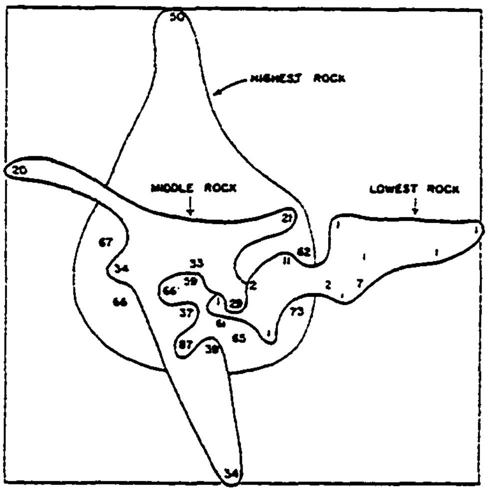
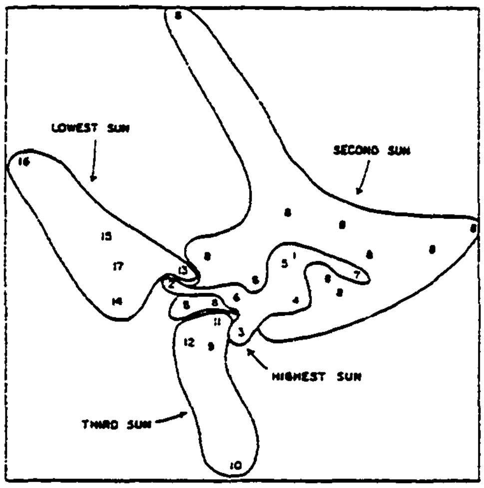
23
16
26
12
7

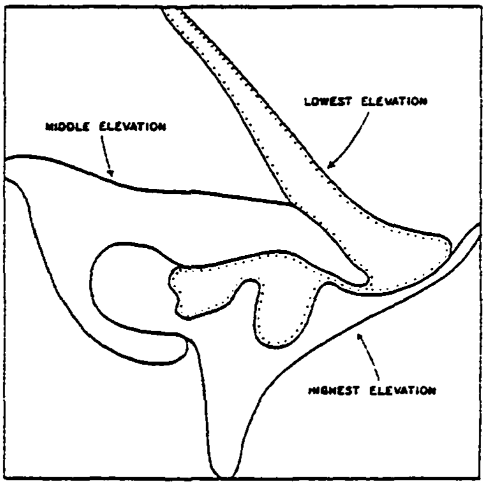
(b)


HIGHEST ROCK
MIDDLE ROCK
LOWEST ROCK
50
20
21
67
34
33
59
66
66
37
87
38
61
65
1
29
2
11
62
1
1
1
1
2
7
1
73
1
34

(c)


LOWEST SUN
SECOND SUN
HIGHEST SUN
THIRD SUN
8
16
15
17
14
13
2
8
8
8
8
8
8
8
5
1
7
6
6
4
8
8
8
11
3
12
9
10

(d)


LOWEST ELEVATION
MIDDLE ELEVATION
HIGHEST ELEVATION

briefly addressed. The presence of surface rock or sloping terrain can significantly influence the amount of infiltration and the retardation of erosion. It is obvious in the canyon that boulders create favorable microhabitats for seed germination and that they function as dams in retarding erosion. On canyon slopes unprotected by surface rocks, erosion is rapid and plants are unable to become established. Wells (1965) has pointed out the importance of surface rock in permitting the deep infiltration of water and retarding runoff, allowing deep penetration of the roots of woody species, and in retarding the spread of grass fires.

Multiple Regression

In an attempt to isolate other pertinent environmental variables, multiple linear regression equations were derived for the important species using cover (shrubs) or relative cover (grasses). The results are presented in abbreviated form in Tables 10-12, in which only the sign and rank of each variable (the order in which it was selected for the multiple regression equation) are presented. Since independent (environmental) variables are selected in order of decreasing importance in

Table 10. Cover and density of woody species. Rank and sign of environmental variables in significant multiple regression equations.

Dependent Variable		R	R^2	F	Independent Variables								
					Sand	Silt	Clay	H^+	BE	OM	Sun	Elev.	Rock
Prosopis glandulosa	C	.47*	.22	3.73							2+		1-
	D	.74**	.55	5.58		5-		4+		3+	1+		2-
Juniperus pinchotii	C	.60*	.36	3.37				3-	4+		2-	1-	
	D	.70**	.49	5.76					4+		3-	2-	1+
J. monosperma	C	.56**	.32	6.05				2-			1-		
	D	.56**	.32	6.08				2-			1-		
J.p. x J.m.	C	.28	.08	2.26			1+						
	D	.61*	.37	2.67			1+			4+	2+	5-	3+
Rhus aromatica	C	.81**	.65	11.08					3-	2+	1-		4+
	D	.76**	.58	8.22					4-	2+	1-		3+
R. microphylla	C	.64**	.42	4.26			4-	2-			1+		3+
	D	.78**	.61	7.07			3-	5-		4+	1+		2+
Mimosa borealis	C	.62**	.38	5.08					1+	2-			3+
	D	.57	.32	3.98					3+		2+		1+
Dalea formosa	C	.83**	.69	28.70							1-		2+
	D	.55	.30	5.49							2-		1+
Ephedra torreyana	C	.59**	.35	4.56	1+						2+	3-	
	D	.61**	.37	3.56				2+	1-		4+	3-	
Forestiera pubescens	C	.52**	.27	3.13		3-					1-	2-	
	D	.48	.23	2.53		2-					1-	3-	
Opuntia leptocaulis	C	.72**	.52	4.99		3+			2+	4+	5+	1-	
	D	.80**	.64	10.86	4+				2+		3+	1-	
Ziziphus obtusifolia	C	.59*	.35	3.25		2-		1-			4+	3-	
	D	.71**	.50	6.08	2+						1+	4-	3+
Xanthocephalum sarothrae	C	.53*	.29	5.18					2-				1-
	D	.49	.24	2.62					3-	2+	1-		
Yucca angustifolia	C	.62**	.38	3.66			4-	3-				1+	2-

*$p \leq 0.05$
**$p \leq 0.01$

Table 11. Relative cover of herbs. Rank and sign of environmental variables in significant multiple regression equations.

Dependent Variable	R	R^2	F	Independent Variables								
				Sand	Silt	Clay	H^+	BE	OM	Sun	Elev.	Rock
Bouteloua gracilis	.76**	.57	8.08	4+		2+	1+					3-
B. curtipendula	.84**	.71	14.69		4-					2-	3+	1+
B. eriopoda	.64**	.41	4.12	4-		3-			1-	2+		
B. hirsuta	.40	.16	2.46				2-	1+				
Sporobolus cryptandrus	.79**	.63	10.18		4+			3-			1-	2-
Buchloë dactyloides	.83**	.69	18.98				1+	2+		3+		
Leptochloa dubia	.55**	.31	5.71			2-						1+
Lecidea rubiformis	.60*	.36	4.66		1+				2-			3-

$^*p \leq 0.05$

$^{**}p \leq 0.01$

Table 12. Total woody cover and density and total herb relative cover. Rank and sign of environmental variables in significant multiple regression equations.

Dependent Variables	R	R^2	F	Independent Variables								
				Sand	Silt	Clay	H+	BE	OM	Sun	Elev.	Rock
Woody Cover												
<1 m	.80**	.64	6.47				2-	4-	3+	1-	5-	6+
≥1 m	.58**	.33	4.15		2-					3-	1-	
Total	.66**	.43	4.51		2-				4+	3-	1-	
Woody Density												
<1 m	.68**	.46	5.17					2-	1+		4-	3+
≥1 m	.60**	.36	3.35		2-				3+		1-	4+
Total	.71**	.51	6.14					2-	1+		4-	3+
Herb Cover	.73**	.53	6.81			2-	4+			3-		1-

$^{**}p \leq 0.01$

explaining the variation in the dependent (vegetation) variable, this method of presenting the data seems defensible. The number of variables in each equation was allowed to increase as long as the mean square ratio continued to increase. In Table 10, only rock and sun were useful in explaining the distribution of _Prosopis glandulosa_ cover; rock correlated negatively and sun positively. With respect to density, however, three additional variables were significant: percent organic matter, hydrogen ion concentration (instead of pH), and silt. The improved correlation with density was surprising; data analysis was oriented primarily toward the use of the cover variable because of an _a priori_ assumption that cover would be the more useful variable. However, as shown in Table 10, half of the woody species have better fit with density than with cover and total woody density fits slightly better than total woody cover (Table 12).

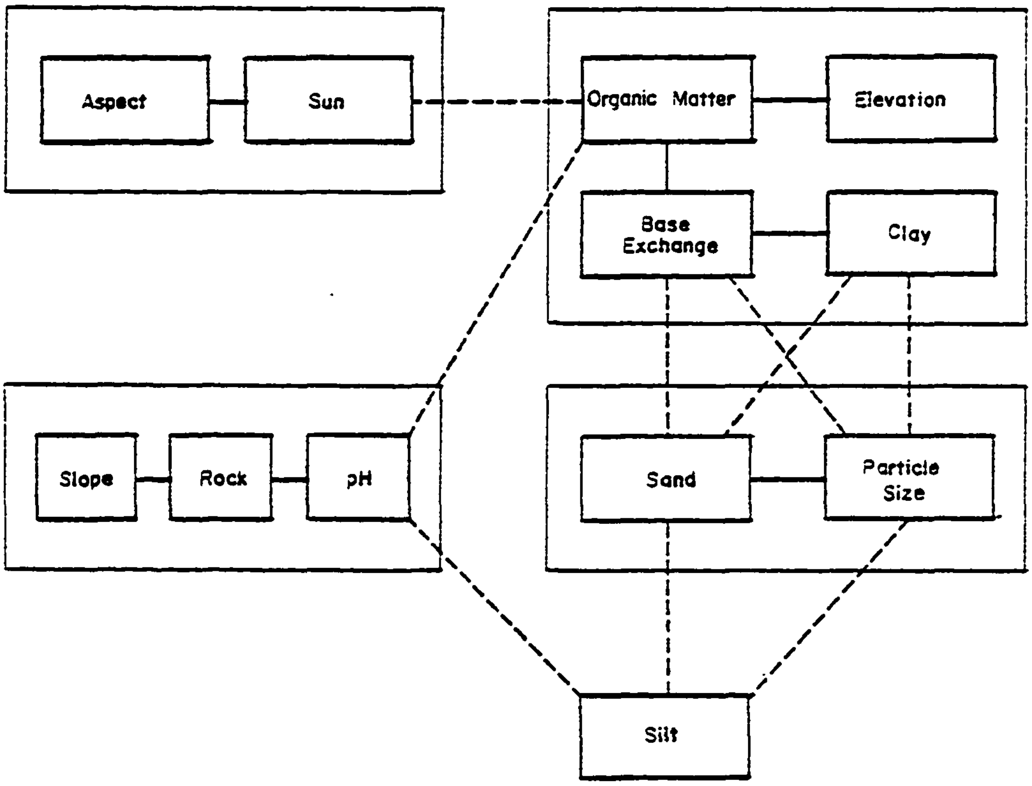
Table 10 demonstrates again the predominant influence of exposure on vegetational variation. Exposure (sun) is the primary independent variable for half of the species, including all of those shown earlier (in Figs. 6-8) to be concentrated at one extreme or another on the exposure gradient. Exposure appears to be less important for the grasses (Table 11). Only *Bouteloua curtipendula*, which peaks on cool slopes, and *B. eriopoda*, which peaks on warm slopes, are strongly correlated with exposure. The frequency of surface rock is correlated with several species. However, since rock and slope are highly positively correlated, as will be discussed below, the actual correlation is more complex than it appears.

The point that is most clearly demonstrated by Tables 10-12 is that, while one or two variables, such as insolation, may have a generally pervasive influence on the distribution of vegetation, the species appear to respond individually to different environmental variables or complexes. Complicating the identification of causative environmental variables is the highly significant correlation of most of the measured variables (Fig. 11). Elevation, for example, is shown to be part of a complex of edaphic variables that are impossible to isolate from one another or from several topographic factors.

Principal Component Analysis

Principal components analysis provides a means of extracting uncorrelated (orthogonal) environmental complexes or components. Thus, it permits the isolation of

Figure 11. Highly significant correlations ($P<0.01$) between environmental variables. Dashed lines indicate negative correlations, solid lines indicate positive correlations, and large boxes delineate groups of positively correlated variables.


Aspect
Sun
Organic Matter
Elevation
Base Exchange
Clay
Slope
Rock
pH
Sand
Particle Size
Silt

uncorrelated complexes from one another, rather than the isolation of individual variables. Johnson and Risser (1972) have used this approach to relate vegetational and environmental variation. This method was applied to the environmental data in the present study; it resulted in the extraction and retention of four principal components which together accounted for 81% of the variability in the data. Principal Component 1 (PC-1) was a contrast between particle size and fertility; PC-2 was mostly rock, pH and clay; PC-3 was mostly insolation; and PC-4 was mostly elevation (Table 13).

By way of relating the PC analysis and the topographic ordinations, note that PC-3 and PC-4 are composed mainly of the same two variables (insolation and elevation) against which the stands are ordinated in Figs. 3-8. It is reasonable to assume that an ordination based on PC-3 and PC-4 would resemble the topographic ordination. This is the case. Fig. 12a is the topographic ordination again, with stands having similar insolation values delineated and identified by Roman numerals. Fig. 12b is the ordination on the PC-3 and PC-4 (PC-3/4) axes. The similarity between the two is apparent if Fig. 12b is rotated 180 degrees.

Table 13. Composition of Four Principal Components

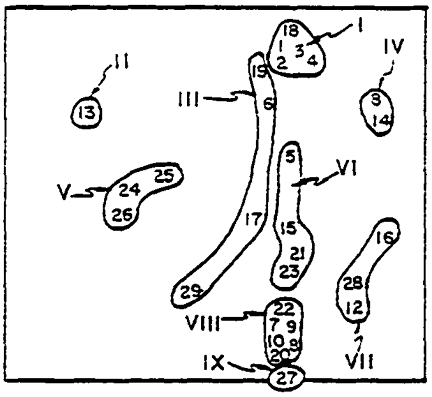
Principal Components	Variables	Eigenvectors	Cumulative Variability Accounted For
1	sand	-1.00	30%
	mean particle size	- .99	
	base exchange	.91	
	organic matter	.77	
	clay	.77	
2	rock	1.00	55%
	pH	.97	
	clay	.91	
	slope	.74	
3	insolation	-1.00	70%
4	elevation	-1.00	81%
	aspect	- .72	

When ordinations were made using various other combinations of the PC components, no additional vegetation-environment relations become obvious -- at least none that were generally useful. However, almost all of the ordinations had one or two species which exhibited tight distributional clusters which were intelligible with reference to the principal components. Thus, a PC-1/2 ordination shows Bouteloua gracilis to be tightly clustered in an area of high fertility (high base exchange and organic matter) and low rock, pH, and slope. This and most of the other relationships that were shown, however, had already been revealed by the topographic ordinations (Figs. 5-8) and/or by multiple regression analysis (Tables 10-12).

Perhaps the most useful information that resulted from the PC analysis was the confirmation that annual insolation and percent surface rock are the major variables showing correlations with vegetation. This was shown by a comparison of the topographic ordination (Fig. 12a) and an ordination on axes PC-2 (rock) and PC-3 (sun) (Fig. 12c). The Roman-numeraled groups on the topographic ordination and its counterpart, the PC-3/4 ordination (Fig. 12b) generally are intact in a PC-2/3 or-

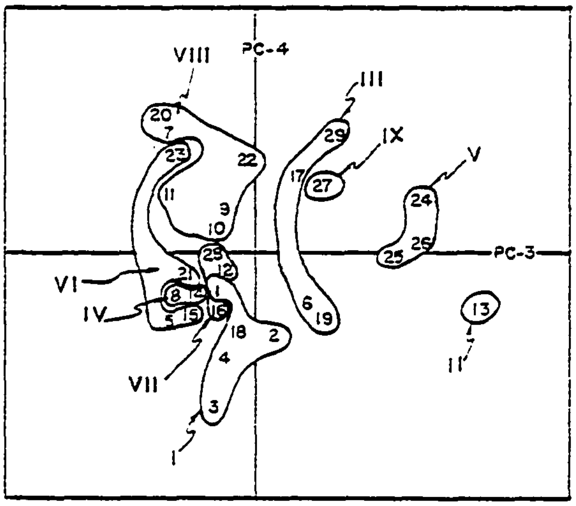
Figure 12. Comparison of stand arrangement in the topographic ordination with two principal component ordinations. (a) topographic ordination. (b) PC-3/4 ordination. (c) PC-2/3 ordination.

(a)



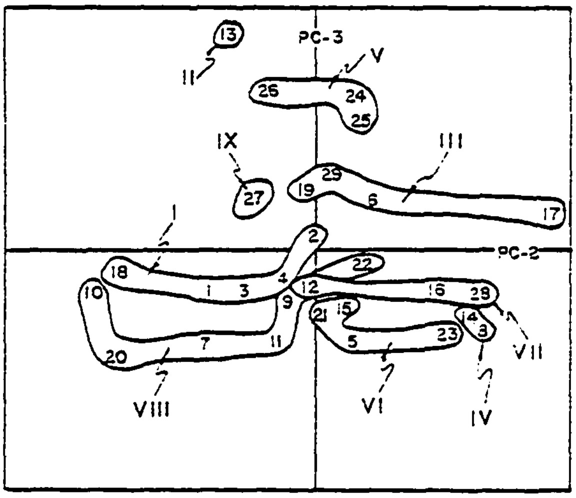
I
18
1
2
3
4
II
13
III
19
6
17
29
IV
8
14
V
24
25
26
VI
5
15
21
23
VII
16
28
12
VIII
22
7
9
10
8
20
IX
27

(b)



PC-4
PC-3
VIII
20
7
23
22
11
9
10
III
29
17
6
19
IX
27
V
24
26
25
VI
21
28
12
IV
8
14
1
5
15
16
VII
18
2
4
3
I
II
13

(c)

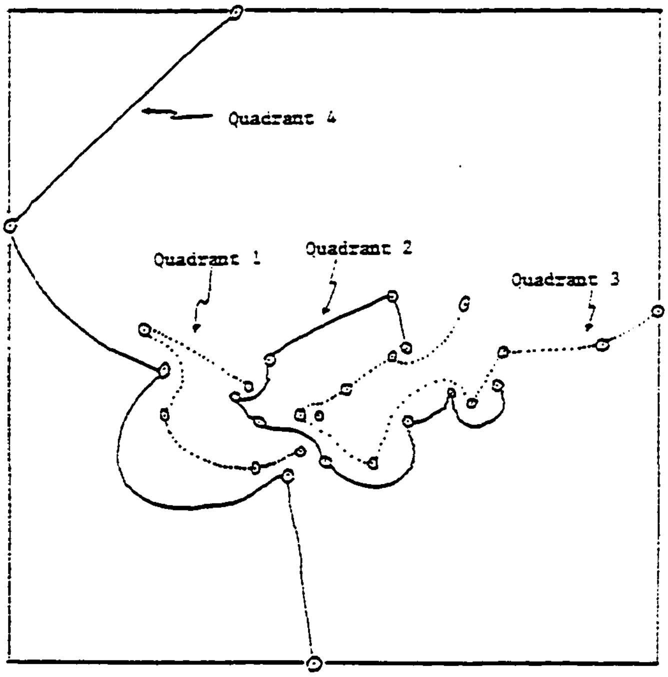


PC-3
PC-2
II
13
V
26
24
25
IX
27
III
29
19
6
17
I
2
18
1
3
4
22
12
16
28
10
9
21
15
14
3
VII
7
11
5
23
20
VIII
VI
IV

dination (Fig. 12c), and even the relative position of the groups to one another is generally maintained, although rotated somewhat from the original. Since PC-2/3 is an ordination between insolation (PC-3) and a rock-pH-clay-slope complex (PC-2), the similarity between Figs. 12a and 12c suggests that it is the rock complex which is responsible for the elevational relationships of the vegetation. However, since the rock and elevation variables are concentrated in two separate orthogonal components (PC-2 and PC-4, respectively), this suggestion is not supported. Nevertheless, most of the variation within the groups is parallel with the rock axis (Fig. 12c), suggesting that it is the rock complex which is the second major variable complex in the environment, after annual insolation.

Still more evidence suggests that the PC-2/3 ordination is particularly useful in explaining the vegetational cover in the canyon. In an attempt to relate the PC-2/3 ordination with the polar ordination discussed above and shown in Fig. 9, it was discovered that the four quadrants of the PC-2/3 ordination are intact in the polar ordination. This is shown in Fig. 13. The importance of the relationship between the two ordinations is that the PC ordination is based on environmental variables, while the

Figure 13. Polar ordination showing stands grouped according to their occurrence in quadrants 1-4 of PC-2/3 ordination.


Quadrant 4
Quadrant 1
Quadrant 2
Quadrant 3
G

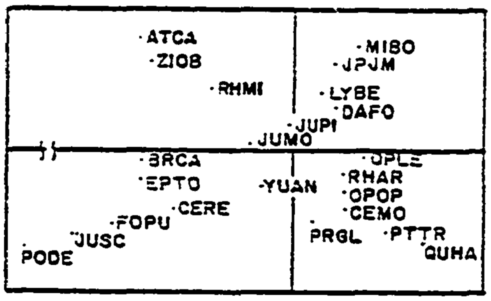
polar ordination is based solely on vegetational variables. The correspondence of the two ordinations that is suggested by Fig. 13 is an indication that the vegetation represented in the polar ordination is responding, to an observable degree, to the particular environmental variables which comprise the principal components of the PC-2/3 ordination. In effect, the correspondence provides additional evidence that both insolation and the rock-pH-clay-slope complex are important determinants of vegetational variation in the canyon.

Mean Axis Positions

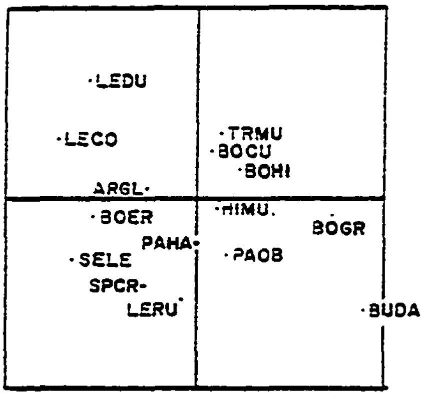
As mentioned above, most of the PC ordinations were less useful than the topographic ordination in explaining the distribution of the vegetation. The PC ordinations usually showed only one or two species to be fairly tightly grouped, while other species were so scattered as to appear only weakly related to the components. On the assumption that a more general approach to relating the vegetation to the ordinations might prove useful, a mean axis position was calculated for the major shrubs and herbs on each of the principal components. The results for PC-1 through -3 are shown in Fig. 14a-f. The

Figure 14. Mean axis positions of (a) shrubs and (b) herbs on the PC-1/2 ordination; (c) shrubs and (d) herbs on the PC-1/3 ordination; (e) shrubs and (f) herbs on the PC-2/3 ordination.

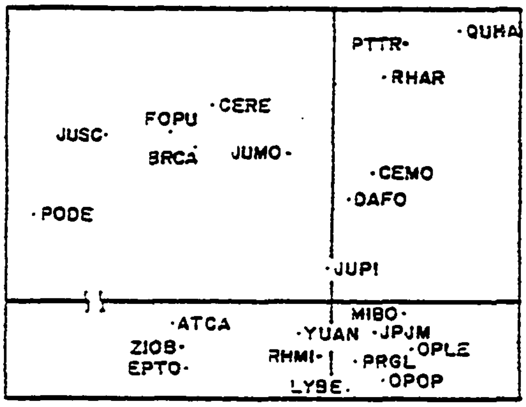
(a) PC - 1/2



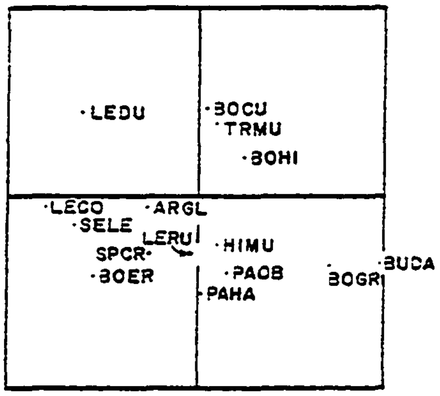
(b) PC - 1/2



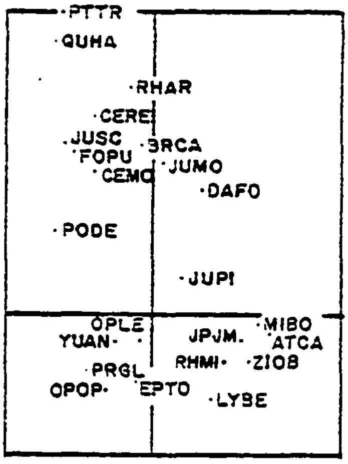
(C) PC - 1/3



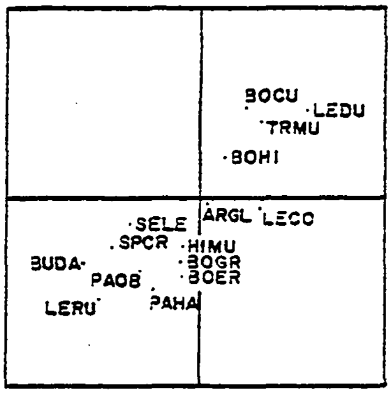
(D) PC - 1/3



(E) PC - 2/3



(F) PC - 2/3



mean axis positions usually have variances (Tables 14 and 15) so large that they can not be usefully displayed on the same figures with the means. However, in spite of the large variances, the means do appear to show the relative responses of the various species to the environmental complexes represented by the principal components; species whose habitats are known to be similar occur closer together on an axis, while those known to have dissimilar habitats occur farther apart. The species most accurately represented by the mean axis positions are those which have more limited areas of concentration, such as *Populus deltoides*, *Rhus microphylla*, and *Quercus havardii*, and *Buchloë dactyloides*. On the other hand, species with more general distributions are shown to be located near the center of the ordinations (e.g., *Juniperus pinchotii*), and species with general distributions with respect to one component tend to be located near the midpoint of the components (e.g., *J. pinchotii* and *Panicum hallii* on PC-1, Fig. 14c, d).

The mean axis positions generally are distributed widely throughout the ordination. However, this is not the case with Fig. 14f, which shows that the major grasses (and one lichen) are concentrated in a diagonal

Table 14. Variance of percent cover of selected woody species on four principal components.

	Principal Components			
Species	PC1 Sand vs. Base Exchange	PC2 Rock	PC3 Sun	PC4 Elevation
Atriplex canescens	16.9	3.6	1.8	1.8
Brickellia californica	1.0	0.3	1.7	0.1
Celtis reticulata	6.1	2.8	25.4	0.6
Cercocarpus montanus	1.2	0.6	4.7	1.2
Dalea formosa	2.2	2.8	8.9	2.5
Ephedra torreyana	10.9	12.8	0.7	0.8
Forestiera pubescens	115.2	11.3	72.8	7.5
Juniperus monosperma	69.9	34.9	243.4	14.3
J. scopulorum	70.6	5.3	26.9	4.5
J. pinchotii	8.2	23.4	13.1	7.0
J.p. X *J.m.*	36.9	17.1	34.9	11.8

Table 14 (Concluded)

Species	Principal Components			
	PC1 Sand vs. Base Exchange	PC2 Rock	PC3 Sun	PC4 Elevation
Lycium berlandieri	0.4	0.5	0.3	0.2
Mimosa borealis	11.0	5.0	1.9	7.0
Opuntia leptocaulis	2.9	1.4	1.5	1.5
O. polyacantha	19.8	14.1	10.1	13.0
Prosopis glandulosa	114.0	85.5	8.3	20.9
Ptelea trifoliata	5.7	4.0	28.3	1.2
Quercus havardii	29.7	17.8	117.8	6.6
Rhus microphylla	12.0	14.0	9.0	8.4
R. aromatica	12.9	31.5	32.3	28.1
Xanthocephalum sarothrae	5.3	6.4	1.6	1.1
Yucca angustifolia	11.3	8.2	5.1	13.6
Ziziphus obtusifolia	13.5	5.9	1.6	1.6

Table 15. Variance of relative cover of selected grasses on four principal components.

Species	Principal Components			
	PC1 Sand vs. Base Exchange	PC2 Rock	PC3 Sun	PC4 Elevation
Aristida glauca	5.9	2.4	1.9	19.8
Bouteloua curtipendula	29.0	36.6	47.3	22.9
B. eriopoda	94.6	139.7	13.7	22.3
B. hirsuta	18.6	5.4	6.7	15.8
B. gracilis	125.1	80.5	19.2	31.5
Buchloë dactyloides	74.8	65.5	5.6	19.3
Hilaria mutica	3.9	2.1	9.6	3.6
Leptochloa dubia	42.4	11.5	22.6	7.4
Leptoloma cognatum	15.9	3.4	1.0	2.3
Panicum hallii	4.9	3.9	8.5	5.8
P. obtusum	21.6	10.4	9.5	12.7
Setaria leucopila	66.5	6.8	7.2	8.6
Sporobolus cryptandrus	31.0	28.0	14.3	13.7
Tridens muticus	13.6	21.2	34.3	3.1

band between low sun/high rock-pH-clay and high sun/low rock-pH-clay. Another ordination, Fig. 14e, shows that roughly the reverse relationship exists for shrubs, which show a tendency to trend between high sun/high rock-pH-clay and low sun/low rock-pH-clay. The pattern shown by the grasses in Fig. 14f suggests that grasses were less important on exposed slopes (high sun/high rock-pH-clay) where moisture stress is greatest, and on protected slopes (low sun/low rock-pH-clay) where woody cover and shade are greatest. Figure 14e shows a tendency toward the opposite response for woody species, an indication that woody species would be better able than grasses to exploit deep ground water resources and thus survive on exposed slopes as well as protected slopes.

Because the importance of the variables represented by PC-2 (rock), -3 (sun), and -4 (elevation) is generally understood, the mean axis positions of particular interest are those which show the relative responses of species to the particle size-fertility gradient (PC-1). Figure 14a-d shows that the species have widely varying requirements with respect to the particle size-fertility gradient. For example, _Populus deltoides_ and _Prosopis glandulosa_ occur in sandy and clayey soils, respectively, and the two species are widely spaced on the gradient.

Species Niche Widths

The variances calculated for each mean axis position provide an estimate of the niche widths (ecological amplitudes) of the species concerned (Tables 14 and 15). A similar calculation was proposed by McNaughton and Wolf (1970) as an estimate of niche width. The assumption is that a species which has a fairly narrow tolerance with respect to a particular environmental variable will occur within a fairly small interval on a gradient of that variable. Consequently, the species mean position on the gradient will have a correspondingly small variance. On the other hand, species with broader tolerances with respect to the same variable will have larger variances. Moreover, the variance of a single species on different gradients will be large or small, depending on the species' tolerances to the various variables.

These assumptions are borne out at least partially by the variances shown in Tables 14 and 15. For example, the first species in Table 14, _Prosopis glandulosa_ has a large variance on PC-1, the particle size-fertility gradient, and a small variance on PC-3, the insolation gradient. This suggests a narrow niche with respect to insolation, but a broad niche with respect to particle size and fertility. (Pairs of variances in Tables 14 and 15 are significantly different ($P \leq 0.05$) if one exceeds the other by a factor of 1.91 (cf. statistical F-tables and 28 degrees of freedom for both numerator and denominator.) *Prosopis glandulosa* has a significantly smaller variance on the insolation component than on the other three components. This is a reflection of this species' preference for level terrain and its infrequent occurrence on steep slopes. *Prosopis glandulosa*'s variance on the elevation component is significantly narrower than on either the particle size-fertility component (PC-1) or the surface rock component (PC-2) (Table 14). *Juniperus monosperma* has a wide variance on the sun component, a reflection of its importance in both moderate and cool portions of the insolation gradient. On the other hand, it has a relatively small variance on the rock component, which is an indication that this species is correlated with surface rock; in this case the correlation is positive.

Besides the variables themselves, there are two additional sources of variation in Tables 14 and 15. One is that the ranges of the components decrease consistently from PC-1 to -4, thereby reducing the maximum possible variance in the same direction. This means that variances on PC-4, for example, are artificially smaller than those on PC-1. In an attempt to compensate for this, variances were divided by the range of the corresponding principal component. Although this procedure changed the relative sizes of the variances, the changes were not statistically significant ($P \geq 0.1$).

The second source of variation is the relative importance of the species. Two species could occupy the same tolerance interval (niche) on a component, but if one species is considerably more important than the other, it will have a larger variance. An example of this is given by the variances of *J. pinchotii* and *J. monosperma* on PC-3 (Table 14). Evidence has been presented for the wider distribution of *J. pinchotii* with respect to the insolation gradient. However, the table indicates that *J. monosperma* has a wider variance. This is mainly a function of the relatively large cover values for the latter species compared with the former. A partial solution to this second source of variation may be to standardize the variances by dividing by the average cover value of the respective species. However, this procedure does not result in a significant improvement with respect to the variances of *J. pinchotii* and *J. monosperma* in Table 14.

Because of these additional sources of variance, the best use of the values in Tables 14 and 15 is in comparing species of similar importance in one column at a time. For example, *Rhus aromatica* and *R. microphylla* are of about equal importance in the canyon (Table 1). They have equal variances on the particle size-fertility component (PC-1), but *R. microphylla* has significantly smaller variances on the other three components than does *R. aromatica* (Table 14). Examination of the distributional patterns of these two species (Fig. 6) indicates that *R. aromatica* is at least moderately important all along the insolation gradient, while *R. microphylla* is of relatively little importance at the cool end of the gradient, and the latter thus has a narrower variance on the insolation component (Table 14). With respect to the variances of these two species on the rock and elevation components, Fig. 6 and Table 14 are contradictory. While Table 14 shows that *R. microphylla* has a significantly narrower variance than *R. aromatica* on the elevation component, the distribution patterns shown in Fig. 6 suggest that the reverse should be true.

Using variances on principal components as estimates of niche widths is intuitively appealing, but it is not clear from the present study that the method is accurate enough to be generally useful. However, Tables 14 and 15 suggest that the method may be useful under some circumstances.

CHAPTER V

SUMMARY

The woody and herbaceous vegetation of Palo Duro Canyon was sampled in 29 stands using techniques of gradient analysis. The purpose of the study was to characterize the vegetation and demonstrate its variability along certain environmental gradients, particularly that of exposure. Environmental variables measured in the stands were soil texture, pH, organic matter, base-exchange capacity, surface rock, slope, aspect, elevation, and potential annual insolation.

The woody cover in the canyon is dominated by nine taxa, most of which occur throughout the canyon but have maximum cover in one segment or another of the insolation gradient. Stands in the middle of the insolation gradient, occupying level to gently sloping, deep soils above the rim and in the floor of the canyon, are usually dominated by *Prosopis glandulosa* and *Opuntia polyacantha*. Total woody cover is usually 25-40%. Important grasses are *Bouteloua gracilis*, *Buchloë dactyloides*, *Panicum obtusum*, and *Sporobolus cryptandrus*.

Other mid-exposure stands occur on the rim of the canyon on rocky, shallow soils. Total woody cover is less than 30% and the characteristic species are *Juniperus pinchotii*, *Yucca angustifolia*, *Cercocarpus montanus*, and *Dalea formosa*. The primary grasses are *Bouteloua curtipendula*, *Sporobolus cryptandus*, *B. hirsuta* and *Aristida glauca*.

Stands at the mesic end of the insolation gradient occur on steep, northerly slopes. Woody cover ranges from 40% to 165% and the characteristic species are *J. monosperma*, *J. pinchotii*, and *Rhus aromatica*. The most important grasses are *Bouteloua curtipeudula* and *Leptochloa dubia*.

Stands at the xeric end of the gradient occur on steep southerly slopes and have 25-55% woody cover. Major shrubs are a hybrid juniper (*J. pinchotii* x *monosperma*), *Rhus microphylla*, and *J. pinchotii*, and the major grass is *Bouteloua eriopoda*.

In the floor of the canyon occur riparian woodlands dominated by Populus deltoides. The major woody species in the canyon all attain maximum development in this habitat, where total woody cover approaches 200%.

The most useful method of data analysis involved the construction of graphs which related cover by species to insolation and elevation. Further analysis involving polar ordination, step-wise multiple regression, and principal components analysis confirmed the importance of insolation as a causal factor and also implicated frequency of surface rock as a possibly important factor. In general, exposure appears to be of overriding importance in determining vegetational variation in the canyon.

Weighted mean axis positions were calculated for species on the first four principal components as a means of demonstrating the relative behavior of each species with respect to the major environmental variables. Also, the variance of the mean axis position of a species was calculated as an estimate of ecological amplitude. The usefulness of this method in comparing niche widths is tentatively demonstrated.

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