CLIMATIC AND PHYSIOGRAPHIC

INFLUENCES ON SAND HILL

VEGETATION

By

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# CLIMATIC AND PHYSIOGRAPHIC

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# PREFACE

Distribution patterns of vegetation on the sand hills of north-central and northwestern Oklahoma are investigated in this study. Two relatively distinct physiognomic groups are encountered along the environmental gradient, deciduous forest to the east, and grass/shrub to the west. The boundary between these two groups corresponds with a change from sandy soils having higher organic matter content in the east to very sandy soil with little organic matter to the west. The objectives of this study are to describe the pattern of vegetational change, identify distinct communities if they exist, and relate community boundaries to the environmental gradient.

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### FOUR LETTER CODES FOR SPECIES NAMES

AMHY – <u>Amaranthus hybridus</u> L. – annual

AMPS – <u>Ambrosia psilostachya</u> DC. – perennial

ANHA – <u>Andropogon hallii</u> Hack. – perennial

APSK – <u>Aphanostephus skirrhobasis</u> (DC.) Trel. – annual

ARFI – <u>Artemisia filifolia</u> Torr. – perennial

ARPU – <u>Aristida purpurea</u> Nutt. – perennial

BIBI – <u>Bidens bipinnata</u> L. – annual

BLVS – <u>Scleranthus annuus</u>? was not collected flowering – annual

BULA – <u>Bumelia lanuginosa</u> (Michx.) Pers. – perennial

CATO – <u>Carya tomentosa</u> (Poir.) Nutt. – perennial

CAGI – <u>Calamovilfa gigantea</u> (Nutt.) Scribn. and Merr. – perennial

CECA – <u>Cercis canadensis</u> L. – perennial

CHAL – <u>Chenopodium album</u> L. – annual

CHHY – <u>Chenopodium hybridum</u> L. – annual

CHLE – <u>Chenopodium leptophyllum</u> Nutt. – annual

CHVI – <u>Chrysopis villosa</u> (Pursh) Nutt. – perennial

CLTS – <u>Celtis laevigata</u> Willd, <u>C. occidentalis</u> Pursh, and <u>C. reticulata</u> Torr. – perennial

CODR – <u>Cornus drummondii</u> Meyer – perennial

COMM – <u>Commelina erecta</u> L. – perennial

CRGL – <u>Croton glandulosus</u> L. – annual

CRTX - *Croton texensis* (Klotzsch) Muell. Arg. - annual

ELVI - *Elymus virginicus* L. - perennial

ERAN - *Eriogonum annum* Nutt. - annual

ERBE - *Erigeron bellidiastrum* Nutt. - annual

ERTR - *Eragrostis trichodes* (Nutt.) Nash - perennial

EUMI - *Euphorbia missurica* Raf. - annual

FEOC - *Festuca octoflora* Walt. - annual

GAAP - *Galium aparine* L. - annual

GILO - *Gilia longiflora* (Torr.) Don - annual

GYDI - *Gymnocladus dioica* (L.) K. Koch - perennial

HEPE - *Helianthus petiolaris* Nutt. - annual

JUNI - *Juglans nigra* L. - perennial

JUVI - *Juniperus virginiana* L. - perennial

LAAM - *Lamium amplexicaule* L. - annual

LEDE - *Lepidium densiflorum* Schrad. - annual

MEST - *Mentzelia stricta* (Osterhout) Stevens ex Jeffs &
*Little* - perennial

MORU - *Morus rubra* L. - perennial

MOPU - *Monarda punctata* L. - perennial

MSDG - *Cyperus schweinitzii* Torr. - perennial

OPMA - *Opuntia macrorhiza* Engelm. - perennial

PAPE - *Parietaria pensylvanica* Muhl. - annual

PAQU - *Parthenocissus quinquefolia* (L.) Planch. - perennial

PASP - *Paspalum setacium* Michx. - perennial

PHYS - *Physalis virginiana* Miller, and others

PLPU - *Plantago purshii* R. & S. - annual

QUMA - *Quercus macrocarpa* Michx. - perennial

QUMR - *Quercus marilandica* Muenchh. - perennial

QUMU - _Quercus muehlenbergii_ Englem. - perennial

QUST - _Quercus stellata_ Wang. - perennial

QUVE - _Quercus velutina_ Lam. - perennial

RHAR - _Rhus aromatica_ Ait. - perennial

SADR - _Sapindus drummondii_ H. and A. - perennial

SAKA - _Salsola kali_ L. - annual

SCSC - _Schizachyrium scoparium_ (Michx.) Nash =
       _Andropogon scoparius_ Michx. of nomenclature
       used by Waterfall (1972) - perennial

SEDG - _Cyperus_ spp., possibly 4 species

SMBO - _Smilax bona-nox_ L. - perennial

SMTA - _Smilax tamnoides_ L. - perennial

SPCR - _Sporobolus cryptandrus_ (Torr.) Gray - perennial

STSY - _Stillingia sylvatica_ L. - perennial

SYOB - _Symphoricarpos orbiculatus_ Moench - perennial

TOTL - total frequency

TLVS - three leaved seedling, was not collected flowering

TRPU - _Triplasis purpurea_ (Walt.) Chapm. - annual

ULAM - _Ulmus americana_ L. - perennial

ULRU - _Ulmus rubra_ Muhl. - perennial

VIRA - _Viola rafinesquii_ Greene - annual


Nomenclature from Waterfall (1972).

CHAPTER I

INTRODUCTION

The classification of vegetational communities and the understanding of the processes of their development has been the subject of considerable discussion and research (Clements, 1916; Gleason, 1917; Whittaker, 1956). The complexity of the environments, and the varied responses of different species to environmental conditions and competition, has complicated the elucidation of the mechanisms involved and identification of the stages of vegetational succession, and the resulting stable climax communities.

Across north-central and northwestern Oklahoma there exists a series of sand dunes associated with the Cimarron and North Canadian rivers. These dunes occur along an environmental gradient of steadily changing climatic and physiographic factors. Along this gradient from east to west, there is a steady decline in annual precipitation, a similar trend in length of growing season, and a gradual increase in elevation.

These sandy soils support two readily identifiable physiognomic communities, deciduous forest and grass/shrub lands. The adjacent non-sandy soils (loams and clay loams) support, from east to west respectively, deciduous forest,

tall grass, mixed grass and short grass prairie (Bruner, 1931). In the eastern part of the area included in this study, sandy soils typically are inhabited by more xeric species, while in the west they support the comparatively more mesic species. This is due primarily to the low water holding capacities, but high infiltration rates and low evaporative losses of sandy soils compared to finer textured soils (Alizai and Hulbert, 1970; Taylor, 1960).

The presence of similar soils and the elimination of pre-existing vegetation by the deposition of the sand, present an opportunity to study the effects of other factors on the development of vegetational communities. The objectives of this study were to describe the pattern of vegetational change across the environmental gradient, to identify distinct communities if they exist, and to relate community boundaries to the changing environment, if possible.

CHAPTER II

LITERATURE REVIEW

Two main theories have been postulated explaining the nature and development of distributional patterns of vegetation. Clements' (1916) view was to consider a stable assemblage of plants as an organism. This organism was thought to develop through a series of distinct stages, the sere, and resulted in a final condition, the climax. Climax vegetation was postulated as being determined by the regional climate, and being capable of sustaining itself indefinitely. In contrast, Gleason's (1917) individualistic theory proposed that the vegetation of an area was determined by the selective action of the environment for adapted species, and the dispersal of seeds from surrounding populations and accidental introductions. Succession in the individualistic theory, was the response of the vegetation to changing environmental conditions and/or the introduction of new, adapted species.

Tansley (1935) modified the organismal theory of Clements, rejecting the concept of the plant community as an organism, but retaining the idea of distinct identities to the stages of vegetational development and climax. Morrison and Yarranton (1974) investigated the succession

of vegetation on the sand dunes associated with Lake Huron. They concluded that the stages they observed supported the organismal concept presented by Tansley (1935). Chadwick and Dalke (1965) described five successional stages on sand deposits left behind active dunes in Idaho.

Curtis and McIntosh (1951) investigated the upland forests of Wisconsin. They did not identify distinct species groups, but rather described a continuum of vegetation, changing in response to the environmental gradients. Whittaker (1956) observed the same type of vegetational change in the Great Smoky Mountains. Curtis (1955) studied the prairies of southern Wisconsin on wet to xeric sites and found no groups of species with similar patterns of occurrence. Adams and Anderson (1980, p. 384) found "... a continuous and gradual change in species composition along the delineated gradient" in forests of Illinois. Rice and Penfound (1959) investigated the upland forests of Oklahoma. They found no groups of species which achieved their optimum development in the same stands, and thus no distinct communities were identified on the basis of combinations of leading dominants.

One of the first studies done specifically on sand dune vegetation in the United States was by Cowles (1899). He recognized the opportunity presented by the dunes in simplifying the problems of pre-existing vegetation and edaphic conditions for the study of vegetational

development. Several subsequent studies have been made of the vegetation on dunes across North America; Great Lakes (Van Denack, 1961; Morrison and Yarranton, 1974; Yarranton and Morrison, 1974), coastal (Kumler, 1969), and inland (Chadwick and Dalke, 1965; Daley, 1972; Pool, 1914; Sherwood, 1980).

Bruner (1931) recognized the effect of edaphic conditions on the distribution of vegetation in Oklahoma. He described a postclimax prairie of Andropogon associes progressing east to west across central Oklahoma. These were located on sand deposits found adjacent to the rivers. The Andropogon associes crossed the tall grass prairie in the east, the mixed grasses of west central Oklahoma, and continued into the short grass prairie of the panhandle.

Recently Sherwood (1980) investigated the vegetation of sand dunes in Woods County of northwestern Oklahoma. He compiled a species list for dunes in the area, attempted to identify separate communities in relation to dune topography, and investigated mineral relationships of some of the species. He concluded that the vegetation could not be divided into distinct communities based on the topographical positions of dune crest, mid-dune slope and slack.

CHAPTER III

STUDY SITES

Nine geographic locations were selected for this study. They were located along an east-west transect across north-central and northwestern Oklahoma (Figure 1). Each of the sites was within a few miles of the Cimarron or North Canadian rivers. Table I lists the general location, soil, and elevation of each site. The specific location of each site is presented in Table II.

The soil at all sites was sandy. The western sites were located on Tivoli fine sand, which was deposited during the Pleistocene Epoch of the Quaternary Period (Soil Survey, Beaver Co., 1959). The Tivoli Series are deep, loose, structureless sandy soils of the sand hills (Soil Survey, Beaver Co., 1959). Site 3 was located on Eufaula fine sand (Soil Survey, Kingfisher Co., 1959). The Eufaula series, like the Tivoli, are deep sandy soils, but unlike the Tivoli, they have a thick A2 horizon. Site 2 was on Derby loamy fine sand which contains more organic matter in the surface layer than Tivoli or Eufaula and was thus more fertile and less droughty (Soil Survey, Logan Co., 1960). Site 1 was on Pulaski fine sandy loam. Unlike the other sites, the Pulaski soils have not been subject to extensive

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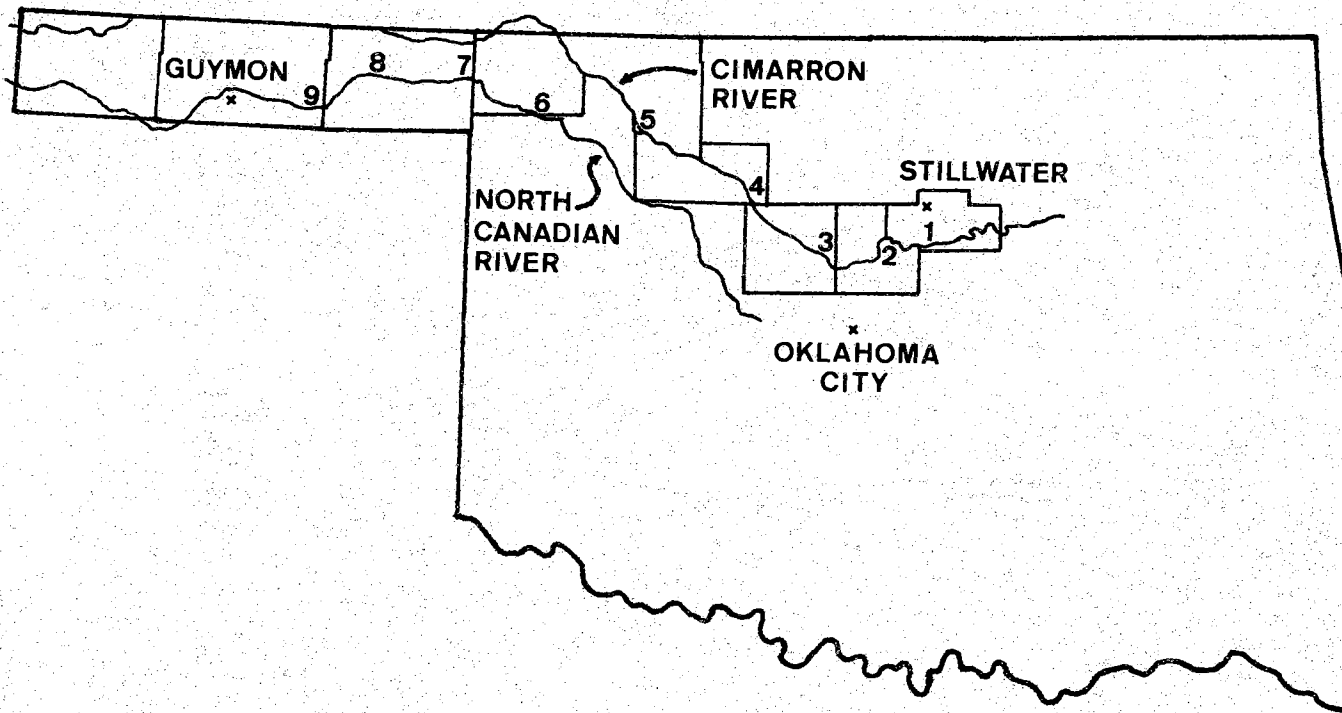
Figure 1.   Map of Study Site Locations

TABLE I

PHYSIOGRAPHY OF STUDY SITES

| SITE NUMBER | NEAREST TOWN | RIVER DRAINAGE | SOIL TYPE | ELEVATION (FEET) |
|---|---|---|---|---|
| 1 | Perkins | Cimarron | Pulaski fine sandy loam | 900 |
| 2 | Guthrie | Cimarron | Derby loamy fine sand | 1015 |
| 3 | Crescent | Cimarron | Eufaula fine sand | 1170 |
| 4 | Ames | Cimarron | Tivoli fine sand | 1213 |
| 5 | Waynoka | Cimarron | Tivoli fine sand | 1500 |
| 6 | Ft. Supply | North Canadian | Tivoli fine sand | 2075 |
| 7 | Gate | North Canadian | Tivoli fine sand | 2220 |
| 8 | Beaver | North Canadian | Tivoli fine sand | 2475 |
| 9 | Adams | North Canadian | Tivoli fine sand | 2710 |

TABLE II

LOCATION OF STUDY SITES

| SITE | COUNTY | RANGE | TOWNSHIP | SECTION | DIRECTIONS |
|------|--------|-------|----------|---------|------------|
| 1A | Payne | R2E | T17N | 10 | 1 mi. S of Hwy 177-Hwy 33 intersection; 1/2 mi. W to end of dirt road; 1/2 mi. W along fencerow; site S of fence. |
| 1B | Payne | R3E | T17N | 1 | 6 mi. E of Hwy 177-Hwy 33 intersection; 3/4 mi. S; walk 1/4 mi. E along sandy ridge. |
| 2A&B | Logan | R2W | T17N | 16 | 6 mi. W of Langston Univ. exiting off Hwy 33 after 3/4 mi. when Hwy 33 turns southward; 1.5 mi. N.; 1mi. W; 1/2 mi. S to small bridge; sites immediately to E. |
| 3A&B | Kingfisher | R5W | T16N | 12 | 2 mi. N of Hwy 33-Hwy 74 intersection; 4.5 mi. W; 1.5 mi. S; site A about 500 yds. W of road; site B 50 yds. W of road. |
| 4A&B | Major | R10W | T20N | 10 | 4.5 mi. W of Ames leaving paved road as it turns S.; 1.5 mi. S along dirt road to dead end at Cimarron River; site A large dune about 1/4 mi. ENE; site B adjacent dune to the E. |
| 5A&B | Woods | R16W | T24N | 26&27 | 1/2 mi. W of Hwy 281 along fence forming S boundary of Little Sahara State Park; site A first large dune to N; site B 200 yds. to the ENE. |

TABLE II (Continued)

| SITE | COUNTY | RANGE | TOWNSHIP | SECTION | DIRECTIONS |
|------|--------|-------|----------|---------|------------|
| 6A&B | Harper | R22W | T25N | 30 | small turn-out about 1/2 mi. N of W entrance of U. S. Southern Great Plains Field Station along Hwy 183 N of Fort Supply; site A immediately E of hwy.; site B adjacent dune to the E. |
| 7A&B | Beaver | R28E | T4N | 20&21 | 4 mi. S of Hwy 64 along paved road S out of Gate; site A 1/4 mi W on first dirt road N of river bridge, site to the N; site B about 1/2 mi. E of paved road, site N of road after gas well. |
| 8A&B | Beaver | R23E | T4N | 6 | about 3 mi. S of Floris, past T Bar T Ranch buildings to last road N of river; about 3 mi. E staying parallel to river to dead end at gas well; site A, N past first low dunes; site B adjacent dune to E. |
| 9A&B | Texas | R19E | T3N | 35 | 2.5 mi. S of Ames; 5 mi. E on dirt road; about 3 mi. S to last E road; about 3/4 mi E to cattle-guard; site A immediately to N; site B about 200 yds. to the SW of site A. |

movement by wind action after deposition by water (Soil Survey, Logan Co., 1960). The sandy soils at sites 1 and 2 did not appear to be as deep as those of the other sites. Also, Site 1 appeared to be the closest, in elevation, to the river, and thus probably had the shallowest depth to the water table of any of the sites.

The climate changes considerably along the transect. The climatic data for the study area is summarized in Table III. The normal annual precipitation, and precipitation effectiveness index (Thornthwaite, 1931) decreases from east to west across the study area. Thornthwaite (1931) classified 32-64 as subhumid, and 16-32 as semiarid. Sites 1 through 6 are in the subhumid range and 7 through 9 are semiarid. The normal pan evaporation for May through September increases from east to west. The average length of the growing season, defined as the time between the last occurrence of 0 degrees C (32 degrees F) in the spring to the first freeze of the fall, increases from site 1 to site 4, and then generally decreases to the west.

Bruner (1931), Blair and Hubbell (1938), and Duck and Fletcher (1945) each described the vegetation of Oklahoma and divided the state into general vegetational areas. Table IV summarizes the vegetational types they identified and the corresponding study sites of this study.

## TABLE III

## CLIMATIC DATA

| SITE | PEI[a] | PAN[b] | NAP[c] | AP[d] | NGS[e] | GS[f] |
|------|--------|--------|--------|-------|--------|-------|
| 1 | 50.60* | 43.74* | 35.35 | 34.55 | 202.5* | 232* |
| 2 | 50.60 | | 31.40 | 27.94 | 205.4 | 214 |
| 3 | | | 29.36 | 27.97 | | 217 |
| 4 | 47.15+ | | 28.12 | 28.92 | 209.9+ | 221+ |
| 5 | 41.40 | | 24.81 | 34.00 | 198.7 | 205 |
| 6 | 33.35 | 54.49 | 21.97 | 25.27 | 194.9 | 214 |
| 7 | | | 20.53 | 28.99 | 196.4 | 166 |
| 8 | 28.75 | | 20.32 | 19.79 | 185.2 | 166 |
| 9 | 27.60^ | 60.91^ | 16.86 | 16.50 | 177.6^ | 167^ |

a - Precipitation Effectiveness Index
b - Normal Pan Evaporation (in.) (May-Sept., 10 yr. ave.)
c - Normal Annual Precipitation (in.)
d - 1981 Annual Precipitation (in.)
e - Normal Growing Season (1970 - 1980 average)
f - 1981 Growing Season (days between dates of 32 degrees)
* - data from Stillwater weather station
+ - data from Enid weather station
^ - data from Goodwell Research Station

Data from 1981 annual summaries of U.S. Dept. of Commerce
  Climatological Data, and Hourly Precipitation.

TABLE IV

SUMMARIZATION OF VEGETATIONAL TYPES

| SITE | BRUNER (1931) | BLAIR & HUBBELL (1938) | DUCK & FLETCHER (1945) |
|---|---|---|---|
| 1 | Oak-Hickory Association mixing with Oak-Hickory Saavannah | Osage Savannah | Post Oak-Blackjack Forest Type |
| 2 | | | |
| 3 | | | |
| 4 | Andropogon Associes | sand areas | Stabilized Dune Type |
| 5 | | | |
| 6 | | | Sand-Sage Grassland Type |
| 7 | | | |
| 8 | | | |
| 9 | | | |

CHAPTER IV

METHODS

Nine sites, each with two replicates, were selected
for this study. Each replicate, except for one at site 2,
was located on a generally south facing slope of an
arrested and nearly stabilized dune. The one exception was
a west facing slope, which was selected since there were no
other suitable southern exposures in the immediate vicin-
ity. A consistent slope exposure insured that differences
between sites were due to macro- and not microenvironmental
changes. Also, the south-facing slopes are characteristi-
cally more xeric (Barbour, et al., 1980), and thus changes
due to water relations should be more pronounced. The dune
faces sampled were approximately equal in area, but
differed somewhat in height and width. In general, the
three eastern most sites tended to be lower and broader
than the more conical western sites.

The sites were selected by visual inspection.
Initially, a large number of potential sites were
identified via review of county soil surveys. After
visiting the potential sites, nine pair were selected. The
sites selected appeared to be in equilibrium with the long
term environment. This was concluded after looking for

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signs of disturbance and early seral vegetation. An attempt was made to keep the topography of the selected dunes as similar as possible. Also the sites were spaced so that there was approximately a two inch (five cm) change in average annual precipitation between adjacent sites. The two inch interval was selected because of site availability and observed changes in vegetation.

Sampling was conducted using an approximately one square meter rectangular quadrat, 141 cm by 71 cm, and an approximately five square meter arm's length rectangle, 185 cm by 270 cm. The one square meter quadrat was used on all sites. The five square meter quadrat was used to sample trees only on sites 1 through 3. No assessment of appropriate quadrat size was made. The one square meter area was selected because it had been successfully utilized by Adams and Anderson (1980), Curtis (1955), Dix and Butler (1960), and Sherwood (1980). A single size quadrat was not equally effective on all sites or for all species (Hyder, et al., 1963). Frequency as a nonabsolute measure is in part a function of the size and shape of the quadrat (Mueller-Dombois and Ellenberg, 1974). Therefore, if frequency values are to be compared directly, they must have been determined using the same sized quadrat (Kershaw, 1973).

The five square meter quadrat was considerably smaller than those normally used for forest sampling. For the upland forests of Oklahoma, Rice and Penfound (1959)

utilized and arms length rectangle of 0.01 acre (approximately 40.5 square meters). Five square meters was selected primarily to keep sampling within the approximate boundaries used when sampling with the one square meter quadrat. It was added because samples obtained using the one square meter quadrat included very few mature trees.

Sampling was accomplished by pacing a series of horizontal transects across the south face of the dune at a relatively constant elevation. The transects were equally spaced along the slope from immediately below the crest down to where the dune began leveling off at the base. The number and length of the transects varied accordingly with the dimensions of each dune. Each one square meter quadrat was aligned with the longer side parallel to the slope. Exact placement was determined by placing the frame down with the midpoint of the longer side immediately ahead of the leading foot. The sample size at each location was 100 quadrats. The surface area of each dune face sampled was approximately 0.04 hectare (0.1 acre).

Sampling with the arm's length rectangle was accomplished in essentially the same manner. The long side of the rectangle was oriented parallel to the transects rather than perpendicular. Because the arm's length rectangles covered a larger area than the one square meter quadrats, a sample size of 100 was obtained by traversing the dune face twice. The transects were staggered to prevent identical replicates.

Only frequency was recorded in order to save time and permit the sampling of all sites within the shortest period possible. Curtis (1955, p. 562) suggested quadrat frequency as "... perhaps the best method of gaining information on quantitative relations of the prairie plants.". Frequency data have been used in describing sand-sage vegetation of Colorado (Daley, 1972), sagebrush-bunchgrass vegetation in Oregon (Hyder, et al., 1963), and herbs, shrubs and tree seedlings in Wisconsin forests (Curtis and McIntosh, 1951).

Frequency data were obtained by recording the species present in each quadrat. The numbers of individuals per quadrat were not recorded and thus no estimates of density were obtained. With the one square meter quadrat, a plant was recorded as present if at least half of its rooted shoot at ground level was within the inner edge of the frame. In the case of bunchgrasses, half of the crown had to be included for the plant to be recorded. Woody plants at least one meter tall were considered present in the arm's length rectangle if the main rooted shoot was touched by outstretched arms as the transect was paced.

In order to measure compositional changes though the growing season, data were collected during three sampling periods. These began on April 1, June 3, and August 2, 1981. In each case, sampling was initiated at the eastern-most site and progressed westward. This was done in an attempt to compensate for the spring lag in the

initiation of the growing season that occurs from east to west. Each site was visited approximately once every two weeks to note phenological differences.

Statistical analysis of the data was accomplished by first identifying the more important species. Initial inspection of the data indicated that a relative frequency of five percent generally provided a consistent break between the ten to fifteen highest frequency species and those remaining. An analysis of variance (ANOVA) was then run on the observed frequency values for each sampling period of those species which had a relative frequency of five percent or greater for any site or sampling period. Duncan's Multiple Range (DMR) was run on those species which were identified by the ANOVA to have significantly different (PR>F less than or equal to 0.10) frequency values at the various sites. This identified for each species, groups of sites which were significantly different from one another. Frequency distributions of individual species were also investigated by plotting mean frequencies versus sampling period and site.

Comparisons of species composition between sites was accomplished using Jaccard's Community Coefficient. It was calculated by the formula, [C/(A+B-C)]100, in which A was the number of species encountered at the first site, B was the number of species from the second site, and C was the number of species that the two sites had in common (Jaccard, 1902).

Several comparisons were made using community coefficients. Used in the traditional manner of including all species present at the selected sites, community coefficients were calculated for adjacent sites and also for all possible site pair combinations. Finally community coefficients were calculated using only species with a relative frequency of five percent or greater at any one site.

Continuing to treat each site as a unit, sites were compared on the basis of mean total frequencies, mean species richness, and mean frequency per species. Relating total frequency to environment, mean total frequencies were plotted against normal annual precipitation. Correlation coefficients were calculated on various subgroups of sites within this comparison to test for linear relationships.

CHAPTER V

RESULTS

Community Coefficients

It was obvious from even casual observation that the
vegetation present on the stabilized sand dunes of north-
central and northwestern Oklahoma changes across the
environmental gradient. One way to confirm this was to
quantify the extent of change in species composition from
site to site along the gradient. This can be done by
directly comparing sites species by species, or through the
use of a similarity index. Figure 2 was constructed by
plotting Jaccard's Community Coefficient versus consecutive
pairs of sites, e.g. 1-2, 2-3, etc.. Jaccard's Community
Coefficient (JCC) gives the fraction of the species encoun-
tered at any two sites which were shared in common.

The results given in Figure 2 indicate a sudden change
in species composition between sites 3 and 4. The community
coefficient for these two sites was much lower than for any
of the other consecutive site pairs. Another observation
from Figure 2 was that the values for site pairs 4-5
through 8-9 were rather constant.

To get a better idea of how each site differed from
the others, the same method of calculating similarity
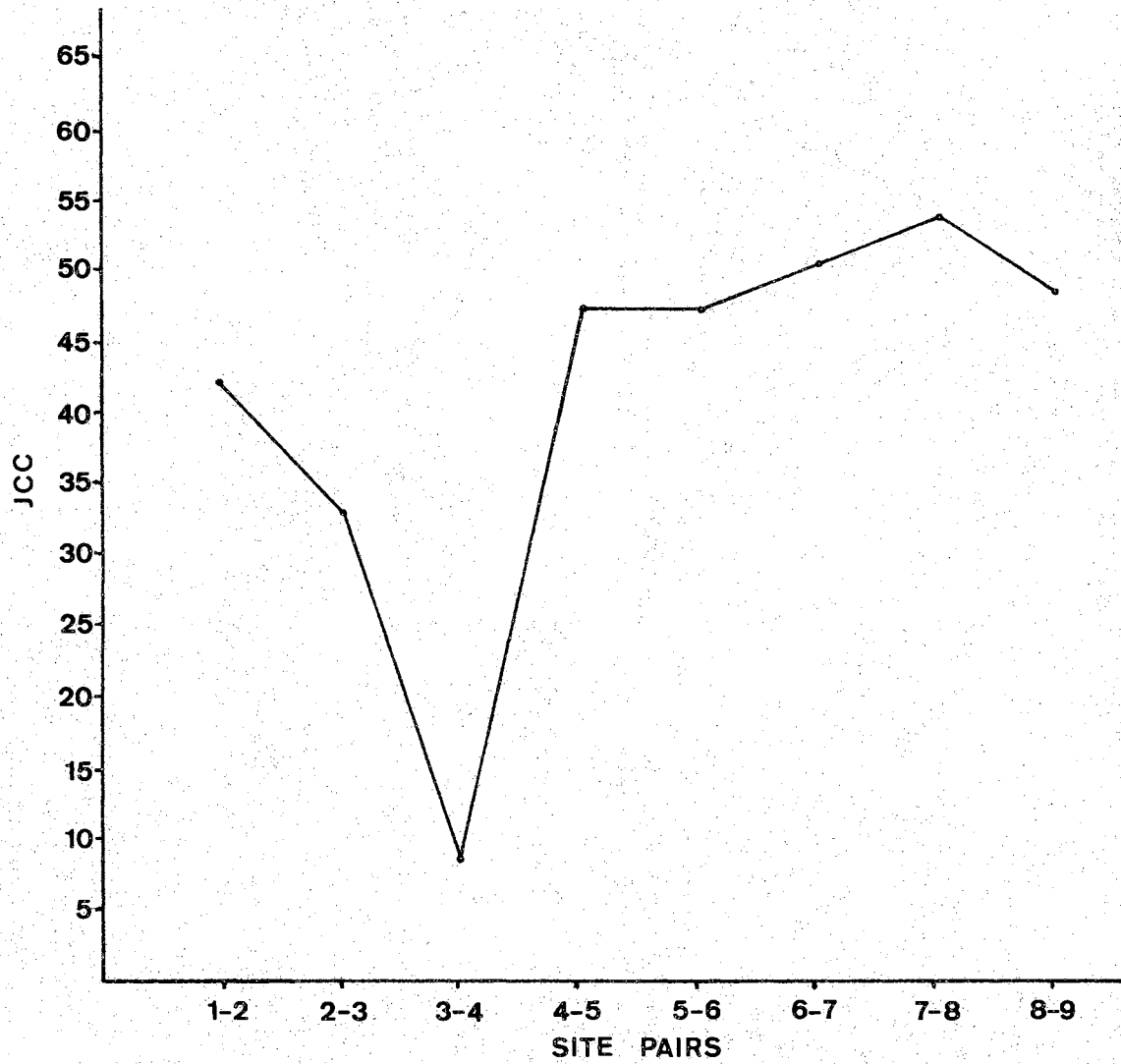
Figure 2. Jaccard's Community Coefficients for Consecutive
Site-Pairs Based on Combined Species Lists for
All Three Sampling Periods

indices was used to compare all possible site pairs. Each
site was compared directly to every other site. Table V
gives the resulting values for all the possible site-pair
combinations.

The results given in Table V substantiate the
potential community boundary suggested in Figure 2. Two
regions of higher community coefficient values were
evident. One was composed of all the possible combinations
of sites 1, 2 and 3, and the other, sites 4 through 9. None
of the values obtained in the comparison of sites between
these two groups approached the magnitude of the within
group comparisons. Although there were exceptions, there
was a trend of decreasing similarity with increasing
distance between site pairs within the group of sites 4
through 9.

One last comparison was made using the community
coefficient. The hypothesis investigated was that lower
frequency species were largely responsible for the site-
to-site differences observed between sites 4 through 9.
Community coefficients were again calculated, but only
those species which had a relative frequency of five
percent or greater at any site or sampling period were
included. The results are given in Figure 3. These results
did not correspond with the trends observed in Table V.
Except when Site 5 was compared to the others, there was no
consistent trend between similarity and distance between
sites.

TABLE V

JACCARD'S COMMUNITY COEFFICIENTS
FOR ALL SITE PAIR COMBINATIONS

| SITE | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|------|------|------|------|------|------|------|------|------|------|
| 1 | | 41.7 | 36.0 | 4.2 | 3.4 | 3.7 | 3.2 | 1.3 | 0.6 |
| 2 | 41.7 | | 33.0 | 7.1 | 6.3 | 5.9 | 5.2 | 4.0 | 3.0 |
| 3 | 36.0 | 33.0 | | 9.7 | 9.0 | 10.2 | 7.0 | 4.7 | 5.2 |
| 4 | 4.2 | 7.1 | 9.7 | | 47.0 | 39.8 | 39.5 | 31.5 | 34.2 |
| 5 | 3.4 | 6.3 | 9.0 | 47.0 | | 46.9 | 44.0 | 40.0 | 37.3 |
| 6 | 3.7 | 5.9 | 10.2 | 39.8 | 46.9 | | 50.0 | 50.5 | 44.2 |
| 7 | 3.2 | 5.2 | 7.0 | 39.5 | 44.0 | 50.0 | | 53.2 | 46.6 |
| 8 | 1.3 | 4.0 | 4.7 | 31.5 | 40.0 | 50.5 | 53.2 | | 48.1 |
| 9 | 0.6 | 3.0 | 5.2 | 34.2 | 37.3 | 44.2 | 46.6 | 48.1 | |

Values were calculated from the formula, $[C/(A+B-C)]100$,
where A = no. of species at site X, B = no. of species
at site Y, and C = no. of species shared by both sites.
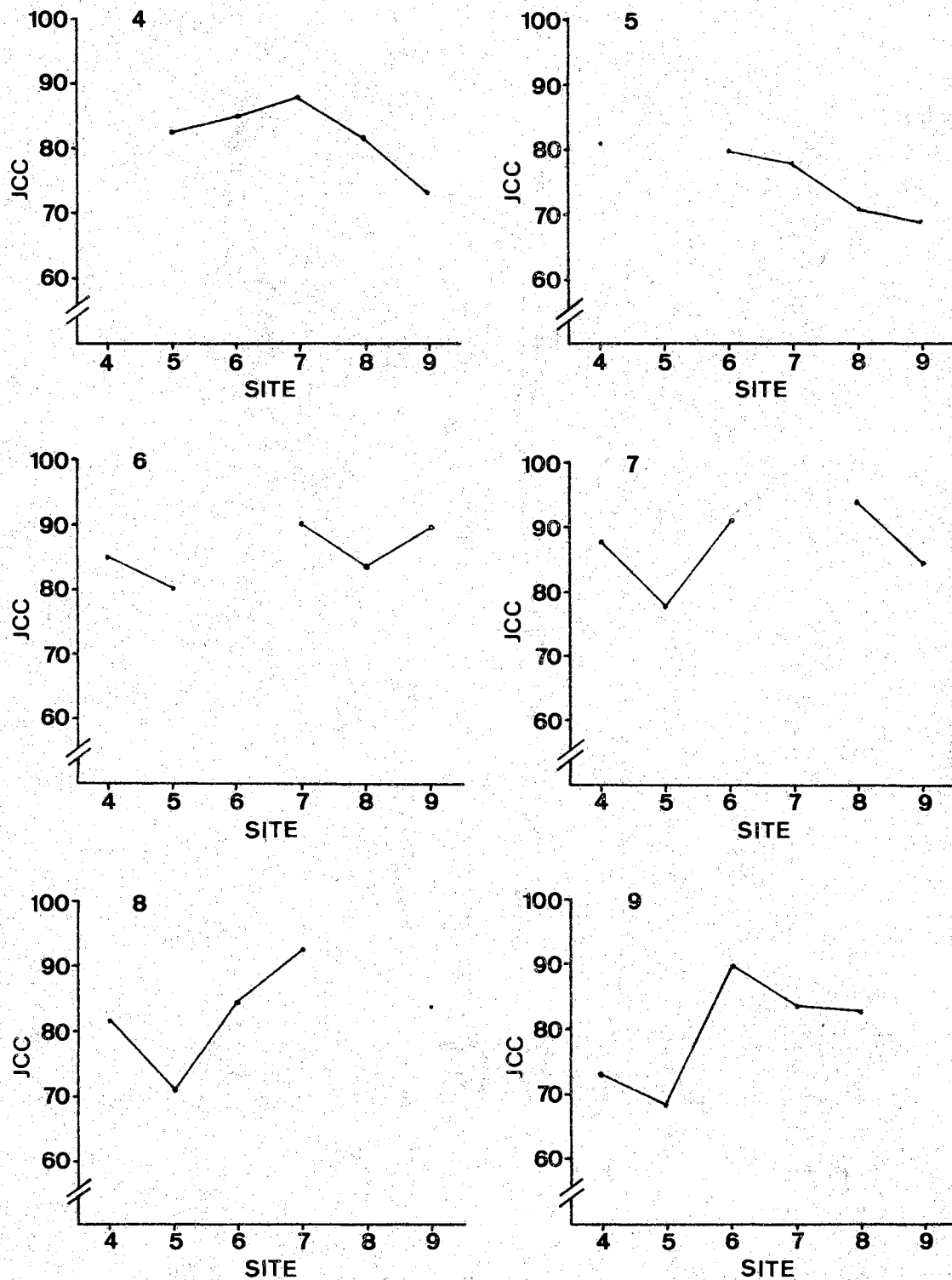
Figure 3.  Jaccard's Community Coefficients for Species with
           a Relative Frequency of Five Percent or Greater
           at Any One  Sampling Period or Any One of Sites
           4 through 9

## Species Distribution

Frequency was the only indicator of dominance available because density and biomass data were not collected. An arbitrary value of five percent relative frequency at any one site during any one sampling period was again selected to distinguish between more and less important species. Table VI lists the species, indicates at which sites they were found, and gives a relative frequency class, based on data obtained from the one square meter quadrats. The relative frequency classes given in Table VI were calculated from the summed frequencies for all three sampling periods.

What resulted was essentially two exclusive groups of species, those found at sites 1 through 3 and those of sites 4 through 9. Only nine of the 52 species listed were found on both sides of the boundary between between sites 3 and 4. Nine were at all three of sites 1 through 3, and none of the others. Sixteen were present at all six sites from 4 through 9, and not at sites 1 through 3. Five species which found only at sites 4 through 9, but not all six, were present at consecutive sites on the east or west end of the group. Five species were found at only one site.

Table VII lists the tree species that were present in the five square meter quadrats at sites 1 through 3. As in Table VI a relative frequency class is indicated, but

## TABLE VI

### DISTRIBUTION OF SPECIES WITH RELATIVE FREQUENCY GREATER THAN OR EQUAL TO FIVE PERCENT DURING AT LEAST ONE SAMPLING PERIOD

| SPECIES | 1 | 2 | 3 | SITE 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| GYDI | - | | | | | | | | |
| LAAM | O | | | | | | | | |
| CECA | O | X | | | | | | | |
| QUVE | O | X | | | | | | | |
| ELVI | * | O | O | | | | | | |
| SMBO | * | * | + | | | | | | |
| GAAP | X | O | - | | | | | | |
| BIBI | - | | - | | | | | | |
| TLVS | | X | | | | | | | |
| CHAL | - | O | X | | | | | | |
| SEDG | X | + | - | | | | | | |
| PAQU | X | X | + | | | | | | |
| SYOB | - | + | + | | | | | | |
| PAPE | - | X | * | | | | | | |
| SMTA | - | - | X | | | | | | |
| ULAM | - | - | - | O | | | | | |
| VIRA | - | O | - | O | | O | | | |
| CLTS | + | * | + | O | O | | | | |
| SADR | + | O | + | | O | | O | | |
| CRGL | O | O | - | + | + | + | | | |
| APSK | | | | O | X | | | | |
| BLVS | | | | | - | | | | |
| CHVI | | | | | - | | | | |
| RHAR | | | O | X | - | O | X | | |
| MOPU | | | | X | X | O | - | O | |
| ERTR | | | | X | X | X | + | O | |
| CHLE | | O | O | - | O | + | X | * | X |
| SCSC | | O | | X | * | - | X | O | - |
| AMPS | | | O | X | O | O | O | O | * |
| EUMI | | | | + | X | X | X | O | X |
| ANHA | | | | X | O | O | - | O | - |
| PLPU | | | | O | X | - | - | O | O |
| MEST | | | | - | O | * | O | + | - |
| SPCR | | | | - | X | * | * | * | * |
| PASP | | | | O | - | + | X | X | X |
| ARFI | | | | O | X | X | * | * | O |
| ERAN | | | | - | X | - | X | + | - |
| ERBE | | | | O | - | O | - | O | O |
| FEOC | | | | O | - | O | - | O | - |
| ARPU | | | | O | O | O | X | O | X |
| CAGI | | | | X | X | O | X | X | - |
| MSDG | | | | - | O | + | - | + | X |
| COMM | | | | X | - | X | X | - | X |
| TRPU | | | | X | - | X | - | O | X |

TABLE VI (Continued)

| SPECIES | | | | SITE | | | | | |
|---------|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| SAKA | | | | O | O | O | O | X | - |
| HEPE | | | | X | | O | O | + | * |
| PHYS | | | | O | | O | O | - | - |
| GILO | | | | O | - | O | O | | O |
| CRTX | | | | X | O | | - | O | |
| LEDE | | | | | - | - | O | X | - |
| STSY | | | | | - | O | | | X |
| AMHY | | | | | - | | O | X | O |

O - Species present but relative frequency less than 1%

- - Relative frequency greater than or equal to 1% but
  less than 3%
X - Relative frequency greater than or equal to 3% but
  less than 6%
+ - Relative frequency greater than or equal to 6% but
  less than 9%
* - Relative frequency greater than 9%

Based on frequencies obtained from one square meter
  quadrats. Relative frequencies calculated from summed
  frequencies of all three sampling periods. See List of
  Symbols for species codes.

## TABLE VII

## DISTRIBUTION OF TREE SPECIES

|         |      | SITE |     |
| ------- | :--: | :--: | :-: |
| SPECIES |  1   |  2   |  3  |
| CATO    |  O   |      |     |
| QUMU    |  O   |      |     |
| GYDI    |  X   |  O   |     |
| QUMA    |  O   |  O   |     |
| CODR    |  O   |  O   |     |
| MORU    |  O   |  O   |     |
| JUNI    |  O   |  O   |     |
| CECA    |  O   |  *   |     |
| QUVE    |  O   |  *   |     |
| ULRU    |      |  O   |     |
| QUST    |  X   |      |  X  |
| SADR    |  *   |  O   |  *  |
| CLTS    |  *   |  *   |  *  |
| JUVI    |  X   |  *   |  *  |
| ULAM    |  O   |  X   |  *  |
| BULA    |  O   |  O   |  *  |
| QUMR    |      |      |  X  |

O - Relative frequency was
    less than 5%
X - Relative frequency was
    greater than 5% but
    less than 10%
* - Relative frequency was
    greater than 10%

Based on frequencies obtained
    from five square meter
           quadrats.
    See List of Symbols
     for species codes.

because the trees were sampled only once with the five square meter quadrats, it is not based on summed frequencies. Five species were found at all three sites, and three species were present at only one site.

## Total Frequency and Species Richness

Another mode of comparing sites is to utilize total frequency, the sum of all the individual species' frequencies at a given site. Figure 4 is a histogram of the mean total frequencies for each of the three sampling periods at the nine sites. Again there was a sharp delineation between sites 3 and 4. There was a trend of decreasing total frequency, within the group of sites 4 through 8, as the distance west along the transect increased.

Figure 5 is a histogram of the mean species richness, the number of species present, for each site and sampling period. The general trend was similar to that seen for the total frequencies, but the magnitudes were reduced. One distinct difference between Figures 4 and 5 is that the differences in the number of species present at sites 1 through 3 versus 4 through 9 is not of the same magnitude as the observed differences in total frequencies. Also in two of the three sampling periods, June and August, the increase in total frequency at Site 9 compared to Site 8 was not reflected in a corresponding increase in number of species present.
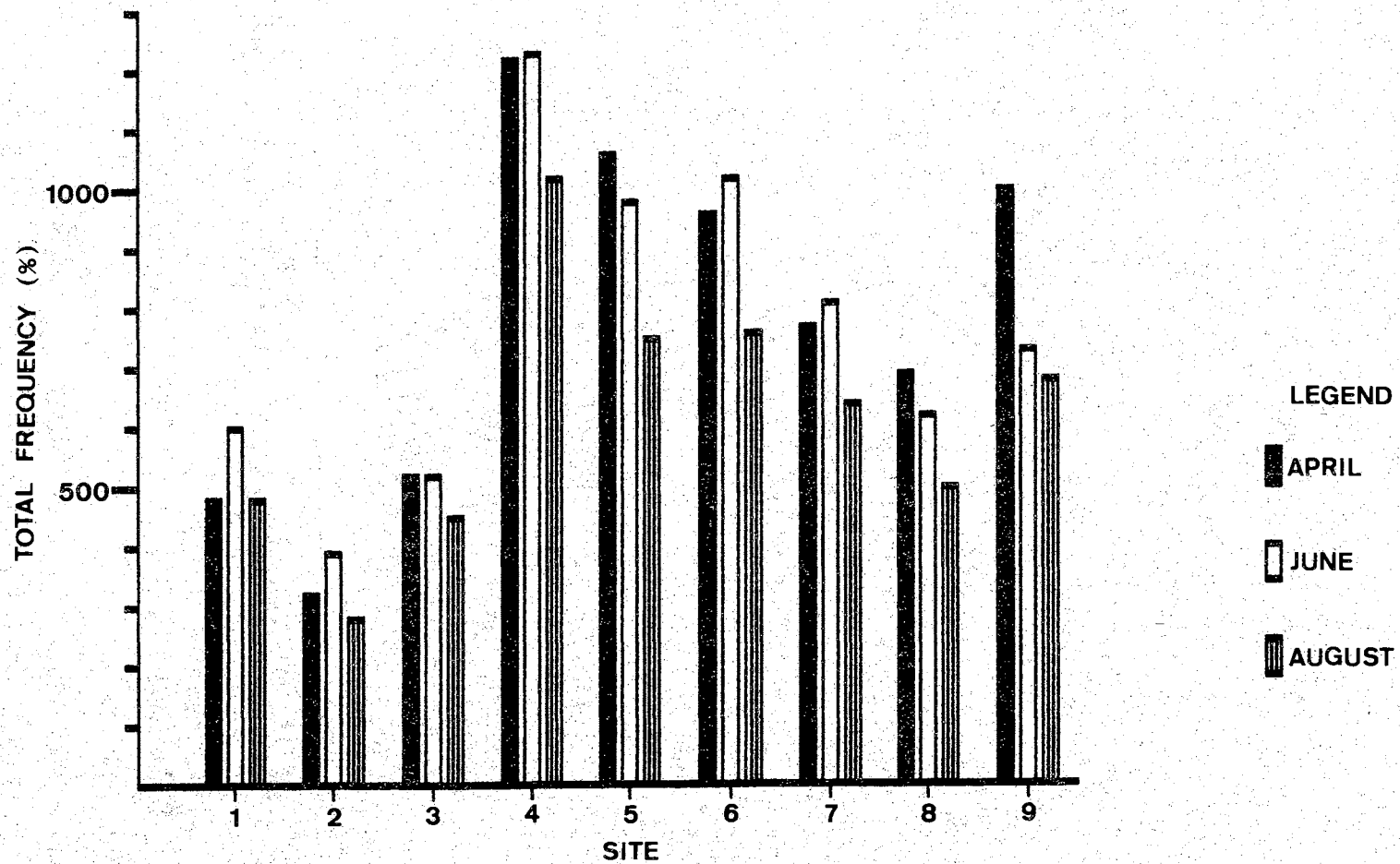
Figure 4. Mean Total Frequencies for Each Site and
Sampling Period

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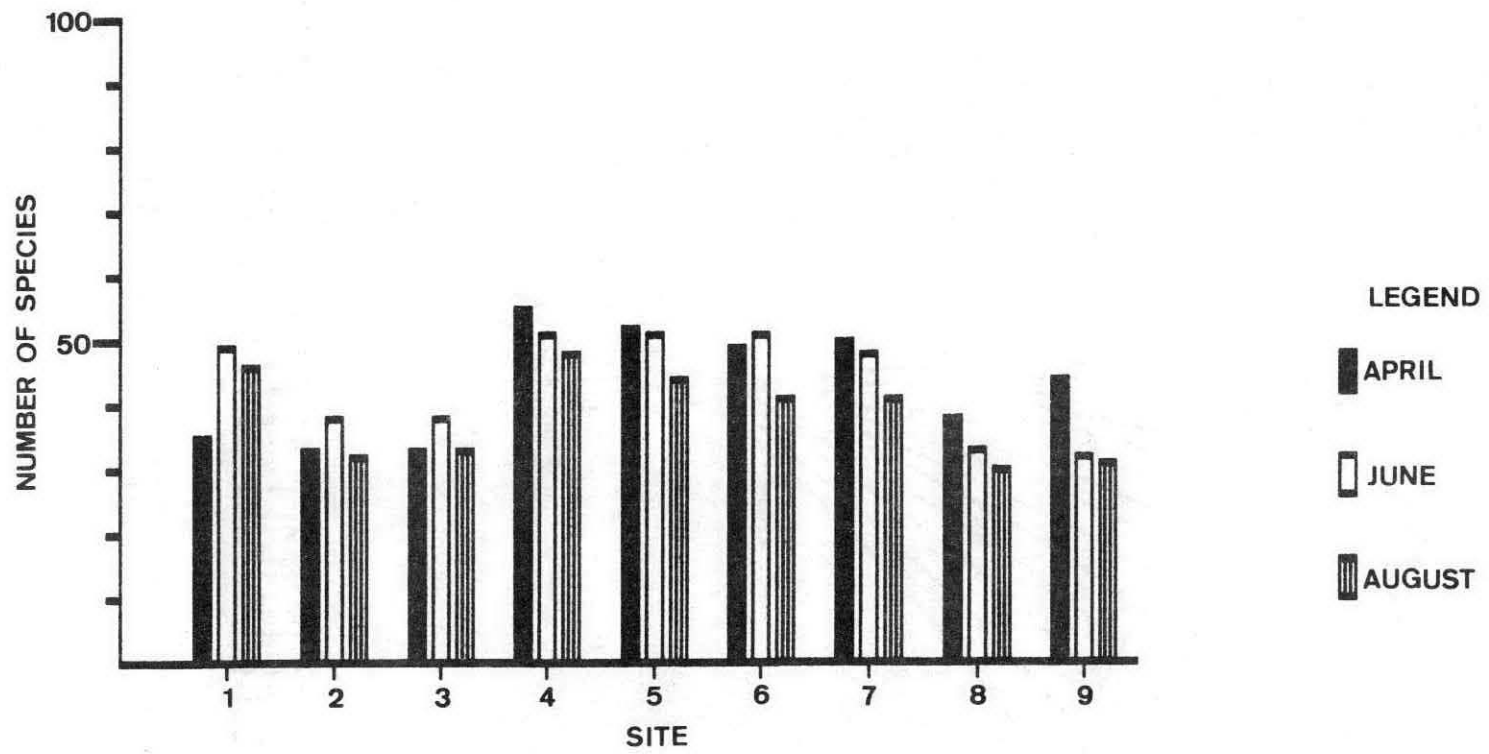
Figure 5.   Number of Species Included in Each Sampling
Period for Each Site

The mean frequency for all species, total frequency/ number of species, for each site is shown in Figure 6. As expected from comparing Figures 4 and 5, sites 1, 2 and 3 had the lowest mean frequencies, and Site 4 consistently had the greatest mean frequency. When variation between replicates was taken into account, the trend of decreasing total frequencies and species richness observed for sites 4 through 8 was not readily apparent for mean frequencies.

Figure 7 was obtained by plotting the mean total frequencies for the sampling periods, April and August, versus the average annual precipitation. Correlation coefficients were calculated for sites 1 through 9, 4 through 9, and 4 through 8. Sites 4 through 8 were found to have linear relationships with confidence levels of 90 percent or greater for all three sampling periods. Sites 4 through 9 were found to have a linear relationship with a confidence level of 95 percent for the June sampling period. The remaining comparisons were not found to be linear. The dashed lines were hand fitted and only serve to emphasize the linear relationship of sites 4 through 8.

## Analysis of Individual Species

The mean frequencies for each sampling period for those species with relative frequencies of five percent or greater at any site and during any sampling period were plotted. Histograms for those species which had the five highest frequencies at each site are given in Appendix A.
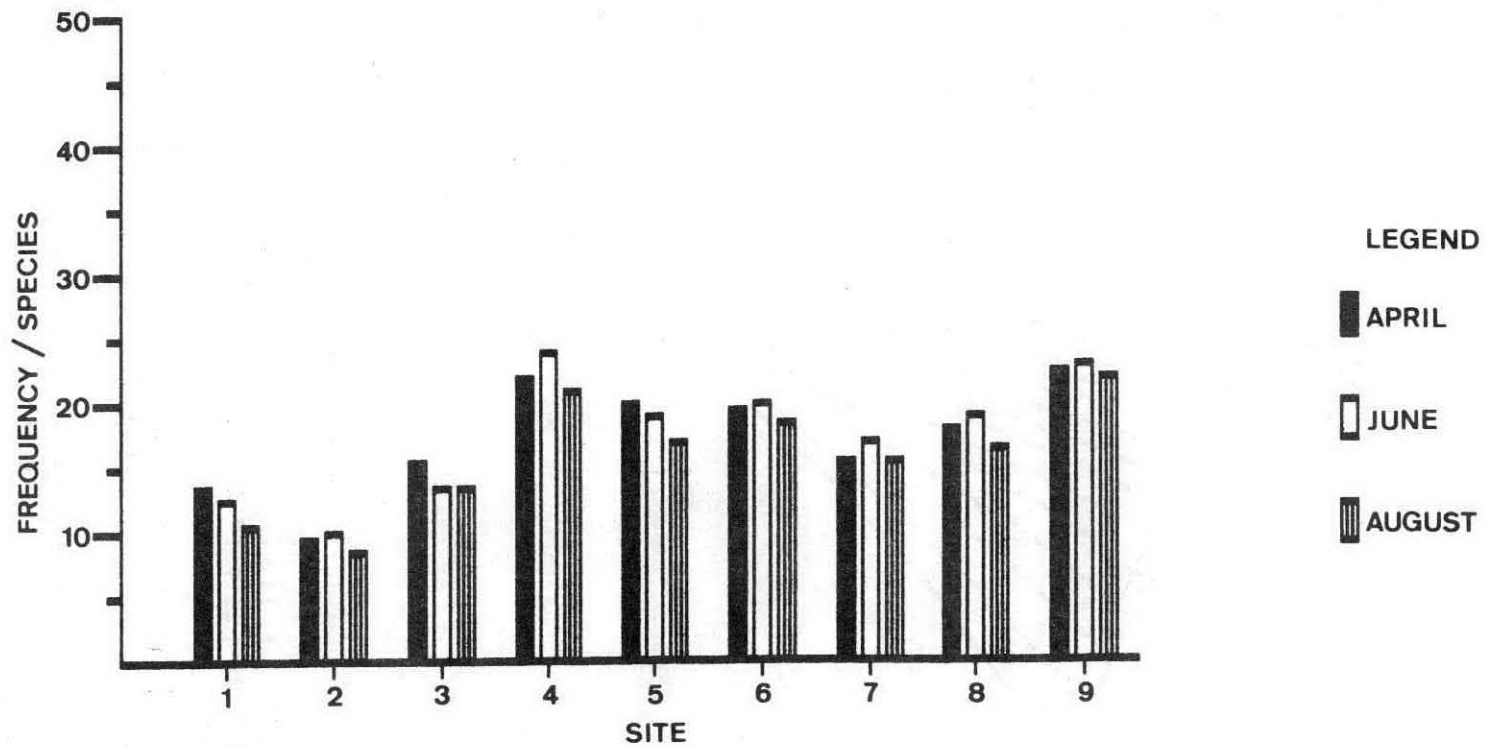
Figure 6.   Total Frequency Divided by the Number of Species
Present for Each Site and Sampling Period
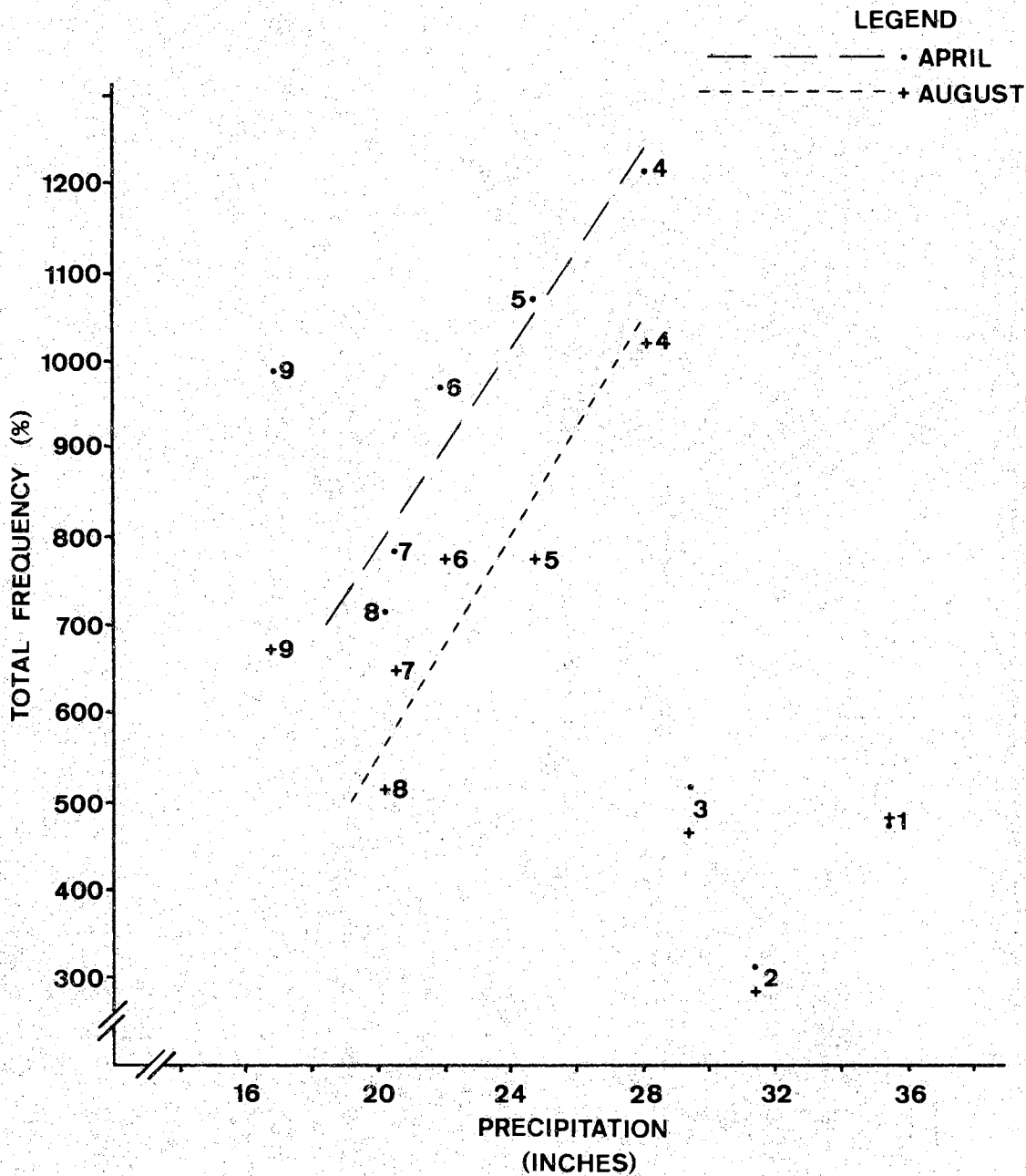
Figure 7.  Total Frequency Versus Normal Annual
Precipitation at Each Site for the
April and August

An analysis of variance (ANOVA) was then run on the species identified as having a relative frequency of five percent or greater. In the analysis, the null hypothesis tested was that the mean frequencies of a given species from the two replicates at each site were equal at all the sites where the species was found. The results are given in Table VIII. The frequency distributions of those species not identified as being significantly different were visually inspected to determine if they were rejected because of high within site variability, or consistent frequency values across the transect.

The next step in examining the distribution of the individual species was to perform Duncan's Multiple Range (DMR) on those species identified by the ANOVA as having significantly different mean frequencies. This statistical test was used to identify the sites which were significantly different from the others. The results are given in Table IX.

Both the plots of mean frequencies and DMR substantiated the community boundary between sites 3 and 4, as was seen with the community coefficients. In all cases where a species was found on both sides of the boundary, there were substantial frequency values for that species in sites belonging to one group or the other, but not both. Within the groups of sites, there existed considerable variations in patterns of frequency distribution. Except in very general terms, there did not appear to be any identifiable

## TABLE VIII

### RESULTS OF ANOVA FOR SPECIES WITH A RELATIVE FREQUENCY GREATER THAN OR EQUAL TO FIVE PERCENT

| SPECIES | SAMPLING PERIOD | | | SPECIES | SAMPLING PERIOD | | |
|---|---|---|---|---|---|---|---|
| | APR | JUN | AUG | | APR | JUN | AUG |
| AMHY | NS | NS | NS | HEPE | *** | ** | ** |
| AMPS | *** | *** | *** | LEDE | ** | * | |
| ANHA | ** | ** | ** | MEST | *** | *** | *** |
| APSK | NS | NS | | MOPU | *** | *** | |
| ARFI | *** | *** | *** | MSDG | NS | NS | NS |
| ARPU | NS | NS | NS | OPMA | *** | *** | *** |
| BIBI | NS | NS | NS | PAPE | * | NS | |
| CAGI | NS | NS | NS | PAQU | NS | NS | NS |
| CECA | NS | NS | NS | PASP | NS | NS | NS |
| CHAL | ** | NS | ** | PHYS | NS | NS | NS |
| CHLE | ** | NS | NS | QUVE | NS | NS | NS |
| CHHY | NS | NS | NS | RHAR | ** | *** | *** |
| CLTS | *** | *** | *** | SADR | NS | ** | ** |
| COMM | ** | * | * | SAKA | *** | NS | NS |
| CRGL | NS | *** | * | SCSC | *** | *** | *** |
| CRTX | ** | NS | * | SEDG | NS | NS | NS |
| ELVI | ** | | | SMBO | NS | NS | NS |
| ERAN | * | NS | NS | SMTA | NS | NS | NS |
| ERBE | NS | NS | NS | SPCR | *** | *** | *** |
| ERTR | ** | NS | NS | STSY | * | * | * |
| EUMI | NS | NS | * | SYOB | NS | NS | * |
| FEOC | NS | | | TOTL | *** | *** | *** |
| PLPU | NS | NS | | TRPU | ** | NS | * |
| GAAP | ** | | | ULAM | NS | *** | *** |
| GILO | NS | NS | NS | VIRA | ** | | |

LEGEND
```
    *        - significant at 0.10 level
   **        - significant at 0.05 level
  ***        - significant at 0.01 level
   NS        - not significant above 0.10 level
no symbol    - species was not present
```

Null hypothesis tested was that there was no difference between sites. Data from one square meter samples only.

See List of Symbols for four letter species codes.

TABLE IX

THE RESULTS OF DUNCAN'S MULTIPLE RANGE

| SPECIES | APRIL | SAMPLING PERIOD JUNE | AUGUST |
|---|---|---|---|
| AMPS | 9 4 8 5 6 7 | 9 4 5 8 6 7 | 9 4 8 5 6 3 7 |
| ANHA | 4 7 6 9 8 5 | 4 7 6 8 9 5 | 4 7 9 5 8 6 |
| ARFI | 7 5 8 6 4 9 | 7 8 5 6 4 9 | 7 8 5 6 4 9 |
| CHAL | 3 1 2 | 3 1 2* | 3 1 2 |
| CHLE | 6 9 8 4 7 5 | 6 8 9 7 4 5* | 8 6 7 4 9* |
| CLTS | 3 1 2 5 4 | 1 3 2 5 4 | 1 3 2 5 4 |
| COMM | 4 6 9 7 5 8 | 6 4 7 9 5 8 | 9 6 7 4 5 8 |
| CRGL | 4 6 5* | 4 6 5 3 | 4 5 6 3 |
| CRTX | 4 5 | 4 7 5* | 4 5 7 8 |
| ELVI | 1 2 3 | | |
| ERAN | 8 5 9 6 7 4 | 8 6 5 7 4 9* | 8 5 4 7 9 6* |
| ERTR | 7 6 4 5 8 | 7 4 6 5* | 7 6 4 5* |
| EUMI | 4 9 6 7 5 8* | 4 5 7 6 9 8* | 4 7 5 9 6 8 |
| GAAP | 1 3 2 | | |
| HEPE | 9 8 4 6 7 | 4 8 9 7 6 | 4 9 8 7 6 |
| LEDE | 8 9 5 6 7 | 6 8 5 9 7 | |
| MEST | 6 8 9 5 7 4 | 6 8 4 5 9 7 | 6 8 4 5 9 7 |
| MOPU | 5 4 7 6 8 | 5 4 7 6 | |
| OPMA | 4 5 8 9 6 | 4 5 9 8 | 4 5 8 9 6 |
| PAPE | 3 2 | 3 1 2* | |
| RHAR | 4 5 7 6 | 4 7 5 6 3 | 4 5 7 6 3 |
| SADR | 3 1 5 7* | 1 3 5 2 | 3 1 5 2 |
| SAKA | 8 9 6 | 9 8 7 5 6* | 8 9 4 5 7* |

TABLE IX (Continued)

| SPECIES | APRIL | SAMPLING PERIOD<br>JUNE | AUGUST |
|---|---|---|---|
| SCSC | 5 4 7 6 9 2 | 5 4 7 6 9 2 8 | 5 4 7 6 9 |
| SPCR | 6 8 9 7 5 4 | 8 6 9 7 5 4 | 8 6 9 7 5 4 |
| STSY | 9 5 6 | 9 5 6 | 9 5 6 |
| SYOB | 3 2 1* | 3 2 1* | 3 2 1 |
| TRPU | 4 6 9 7 5 8 | 4 9 6 5 7 8* | 4 9 6 5 7 8 |
| ULAM | 3 2 1 4* | 1 3 2 4 | 3 1 2 |
| VIRA | 3 1 4 2 6 | | |

This table contains only those species which had a relative frequency of five percent or greater at any one site, were present at more than one site and were found by ANOVA to have one or more sites significantly different from the rest. Sites are arranged in descending order of frequency. Adjacent sites which have a line over or under them are not significantly different at the 90% confidence level.

* - Sampling periods which had no significant difference between sites as determined by ANOVA, where $p = 0.10$

See List of Symbols for four letter species codes.

sets of species which could be considered as having the same pattern of frequency distribution.

CHAPTER VI

DISCUSSION

Community Coefficients

Figure 2 was constructed by plotting Jaccard's
Community Coefficient (JCC) versus consecutive pairs of
sites, e.g. 1-2, 2-3, etc.. Jaccard's Community Coeffi-
cient provides the fraction of the species shared in common
by any two sites. For example, suppose that species A, B,
C and D were found at site X, and C, D, E and F at site Y.
They would have a JCC of [2/(4+4-2)]100 or 33.3. In other
words, sites X and Y share 1/3 of their combined species in
common.

The values of the community coefficient can range from
0 to 100. Zero indicates that the sites being compared had
no species in common and 100 indicating that all the
species found at one site were present at the other. In
reality a value of 100 for a community coefficient is
unlikely because in the sampling of two stands from a
homogeneous community, or even sampling the same stand
twice, there is the probability of rare species occurring
in one sample and not the other. Even if the community
coefficient for two sites was approximately 100, it does
not mean that the two are necessarily very similar in other

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aspects. Two sites may be identical in species composition but differ greatly in density, distribution, or biomass.

Two phenomena were evident in Figure 2. The community coefficient for site pair 3-4 was much lower than that for any of the others, and the values for sites 4-5 through 8-9 were approximately equal. The low value for the site 3-4 comparison indicates that there was a sudden change in species composition from Site 3 to 4, as would be expected when changing from one physiognomic community type to another. This change was very apparent when the sites were visually compared. Site 3 was forested with Quercus marilandica, Q. stellata and Sapindus drummondii appearing to be the major species. Site 4, on the other hand, was predominantly prairie with scattered trees of Celtis reticulata, Ulmus americana and Bumelia lanuginosa, found primarily in the dune hollows. It is not inferred that the only potential community boundary is between sites 3 and 4, but rather that it is an obvious one.

The sudden drop in the value of the community coefficient can be due to a number of vegetational differences between the two sites. A simple explanation is an essentially one-to-one substitution of species from one site to the other. Another explanation is that one site has most of the species present at the other site, plus a large number of additional species. While possible, the above explanations would not be expected. A more likely explanation is a combination of species additions and

deletions, not on a one-to-one basis, which result in a change in the community coefficient due to differences in species composition and species richness. The data of Table VI and Figure 5 indicate that sites 3 and 4 share few species in common and differ distinctly in species richness.

The nearly equal community coefficient values for pairs 4-5 through 8-9 can be due to several different types of vegetational change: (1) a steady directional change in composition as would be expected along a continuous environmental gradient if the pattern of vegetational change was a continuum (Whittaker, 1956); (2) a steady nondirectional change in which species are sporadically present or absent along the gradient; or (3) a core of species shared in common, but differing in the presence of relatively rare species. All of the above could result in a rather constant value for the community coefficients.

Knowing that two sites have approximately equal community coefficients when compared to a third reveals nothing about how they compare to one another. For example, suppose site X had the species A, B, C, D and E, site Y had C, D, E, F and G, and site Z had E, F, G, H and I. Site-pairs X-Y and Y-Z would have community coefficients of 43, [3/(5+5-3)]100, but the community coefficient of site-pair X-Z would be only 11.

To better understand how all the sites differ from one another, the same method of calculating community

coefficients was used to compare all possible site pairs. Table V listed all the possible site-pair combinations. The two regions of higher community coefficient values, sites 1 through 3 and 4 through 9, support the hypothesis of a community boundary between them.

A closer examination of the calculated values for sites 4 through 9, reveals a trend of decreasing community coefficients as the distance between sites increases. However, the individual decreases did not approach the magnitude of the change from site 3 to 4. While the differences are probably not statistically significant by themselves, the consistency of the trend tends to add to its credibility.

The change in community coefficients, as seen from site 4 to 9, would be expected if the pattern of vegetational change was a continuum, with no evident community boundaries along a steadily changing environmental gradient, but as mentioned above, other factors may be influencing the observed values. It should be emphasized that communities are largely described on the basis of their major dominants. Dominance in turn is dependent on a species having sufficient numbers, biomass and distribution in order to exert a controlling effect on the community. The community coefficient does not directly take into account any of these factors.

It was somewhat unexpected to observe a maximum community coefficient of only 53.2 (site-pair 7-8) and only

two other comparisons of 50 or greater (site pairs 6-7 and
6-8). Many of the higher frequency species are present at
adjacent sites giving the appearance of greater similar-
ity. Possible contributing factors to the lower than
expected community coefficients are: (1) two dune faces do
not give a representative sample of the variation present
on the dunes of a region; (2) the sites were too widely
spaced; (3) the sites selected were not consistently the
fully stabilized vegetation type for the given area; (4)
the differences in surrounding populations produced
different potential immigrants; or (5) errors in identifi-
cation of plants.

Frequency, a measure of distribution, was the only
indicator of dominance available since density and biomass
data were not collected. An arbitrary value of five
percent relative frequency was selected as the dividing
line between more and less "important" species. In order
to see if the higher frequency species gave similar results
as those seen in Table V for sites 4 through 9, community
coefficients were calculated using only those species which
had a relative frequency of five percent or greater at
least once during the three sampling periods at any one of
the included sites. The results are seen in Figure 3.
There was no consistent trend of decreasing similarity with
increasing distance, except when Site 5 was compared to the
others.

One reason for the discrepancy between figures 2 and 3 is that Site 4 consistently had a higher community coefficient than Site 5 when compared to sites 6 through 9. Considering that: (1) most comparisons with Site 5 resulted in the lowest observed values for the community coefficient within the group of sites; and (2) only when Site 5 was compared to the other sites was there seen an inverse trend between similarity and distance; seems to indicate that the observed discrepancy was largely the result of the lower than expected similarity of Site 5, and not the greater than expected similarity of Site 4. The high similarity between sites 4 and 6, and 6 and 9 also disrupts the expected trend between similarity and distance.

These results were not expected. It seemed reasonable that if the vegetation was slowly changing in a directional manner, comparisons of species composition based on potentially dominant, widespread, dune adapted plants should give a smoother, more consistent change than comparisons based on all species present, and thus potentially containing several uncommon plants that would not be expected to be present consistently in a series of samples. There are several possible reasons for the results seen. In addition to the potential problems listed above in the discussion of the lower than expected community coefficient values, they include: (1) the vegetation was not changing in a consistent directional manner; (2) identifying important species on the basis of

high frequency values alone was not valid; (3) a sample of two replicates per site was not large enough to give results representative of the community at a given geographic location.

It is suspected that: (1) the sample size of only two replicates per site; and (2) possibly the failure to select sites which were representative of fully stabilized dunes; are the major contributing factors for the inconsistent results. The number of replicates is a probable source of error because of the high degree of variability in frequency values for some species between replicates at a geographic location. The failure to identify fully stabilized dunes is suspected because of the high frequencies of what are generally considered seral species found at some sites.

If the vegetation is not changing in a directional manner, in contradiction to the results of Curtis and McIntosh (1951), Whittaker (1956) and others, then some factor other than the expected environmental gradient of water relationships must be controlling the success and distribution of vegetation. Elevation and length of growing season change in a directional manner similar to precipitation. The soils at sites 4 through 9 are all Tivoli fine sand, so edaphic conditions should be similar, except possibly in the depth of the sand and underlying strata.

Competition, or a species failing to react consistently to the environment might result in deviations from the expected bell-shaped curve of success versus the environmental gradient. Competition between a stenoecious and an euryecious species with similar environmental optima may result in a bimodal success - environment curve for the euryecious species, among other possibilities (Whittaker, 1956). Ecotypic variation of various grasses has been described by McMillan (1956a, 1956b) and of Sporobolus cryptandrus by Quinn and Ward (1968). The possibility exists for geographically separate populations of a species to exist which differ genetically resulting in separate environmental optima. McMillan (1956a, 1956b) observed shifts in initiation of growth and flowering in relation to photoperiod in separate populations of Schizachyrium scoparium and other grasses from various locations in Nebraska. Quinn and Ward (1968) observed differences in initiation of growth, rate of growth, initiation of flowering, and morphology for populations of Sporobolus cryptandrus from Colorado, Kansas, Oklahoma and New Mexico.

## Total Frequency and Species Richness

Another means of comparing sites is to examine total frequency, the sum of the frequencies of all the individual species at a given site. Total frequency is dependent on several combined factors including; species richness,

densities and distributions. As seen in Figure 4, there was a distinct difference between sites 3 and 4, as was also the case when the community coefficients were compared.

The low total frequencies of sites 1 through 3 were probably due to several factors. Visually it appeared that the low frequencies were principally reflecting: (1) low densities due to the nearly closed canopies of these sites; and (2) uneven distributions due to clumping of species in areas receiving more sunlight.

Figure 4 also shows that, with the obvious exception of Site 9, there was a definite inverse trend between total frequency and the distance westward along the transect. Visually it appeared that decreasing total vegetative density as well as species richness may have been important factors in the decline in total frequencies. At Site 4, little bare sand could be seen between plants, but it appeared to increase further west.

The general trend of the number of species included in each sampling period for each site, Figure 5, was similar to that seen in the total frequency histogram, but the magnitude of the change was reduced. A major deviation in the similarity of the trends between the two figures was the species richness of Site 1 in June and August. It was approximately equal to that of Site 4, which consistently had the highest total frequency and was among the highest in species richness. The low frequencies but high species

richness at Site 1 probably indicate low average individual species abundance and/or uneven distributions.

There was also a sharp rise in species richness at Site 1 between the April and June sampling periods which was not seen at sites 2 or 3. The discrepancy between the sites and sampling periods may have been the result of a distinct lag in the initiation of growth in the spring at Site 1 due to low soil temperature. Comparisons of the average monthly temperatures for 1981 at the Stillwater and Guthrie weather stations, near sites 1 and 2 respectively, revealed above average monthly means during January through April (Figures 41 and 42, Appendix B). Guthrie however was 2.3 to 2.5 degrees F. warmer than Stillwater for February through April.

The considerable difference in total frequency observed for sites 3 and 4 was partly the result of differences in species richness and not entirely density related. It is evident that the changes in species richness were responsible in part for some of the observed trends in the community coefficients, and may have been a major factor in the observed decrease in total frequency observed for sites 4 through 9.

The mean frequency for all species given in Figure 6 indicates that density and/or distribution factors, and not simply species richness, influenced the observed total frequency. As a general rule the lowest mean frequencies were those of sites 1 through 3, and the highest were from

sites 4 and 9. Site 7 consistently had the lowest mean frequency of the prairie sites, but had essentially the same species richness as Site 6. When compared to Site 8 however, Site 7 had distinctively higher species richness, but very similar mean frequencies. This seems to indicate a change in species' responses to the environment from Site 6 to 8. Comparing sites 6 and 7, species richness remained very similar, but the average frequency per species decreased. This may have been the result of a drop in the abundance of individual species. Comparing Site 7 to 8 however, the average frequency per species increased slightly, but the species richness dropped considerably. This seems to indicate that instead of species' freqeuncies continuing to drop, some species were competitively excluded. Densities are probably being affected by the climatic gradient and competition. Additionally, species' distribution on the dune may be changing. The observed frequencies may be indicating: (1) a change in the number of individuals present with little change in distribution; (2) the number if individuals remaining relatively constant, but changes in their distribution (ie. a species being widespread on a dune at one end of the gradient and restricted to largely the lower portion of the slope at the other end of the gradient); or (3) a combination of the above. Also, assuming that species richness increases as the climax condition is approached, Site 8 may have represented an earlier seral condition than Site 7.

## Analysis of Individual Species

Species which had a relative frequency value of five percent or greater at one or more sites for any sampling period were selected for further examination. Initially, for each species, an ANOVA was run on the observed frequency value at each site for each of the three sampling periods. This test determined if a significant difference existed between the observed frequency values, and thus identified species which might be instrumental in defining potential species groups. If the frequency values were determined to be significantly different, Duncan's Multiple Range (DMR) was used to identify similar groups of sites for each species.

When the results of the DMR were compared, no discernable pattern(s) between groups of several species were obvious, except for the distinct break between sites 1 through 3 and sites 4 through 9. Essentially, each species had its own pattern of similarity for frequency values from site to site. No similar groups of species could be identified as would be expected if the vegetation was changing in a series of distinct communities. Rather, the changes in species frequency appeared to be individualistic in nature.

Problems arise when the individual patterns of species frequency distribution are characterized as supporting Gleason's individualistic theory of vegetational change.

If the sites are: (1) comparable in soil types; (2) in equilibrium with the long term environment; (3) exposed to a gradually changing climate across the gradient; and (4) indicating the vegetation is not capable of significantly altering the physical environment; then what would be expected is a number of bell-shaped curves, one for each species, each of which differs in location, breadth, and/or magnitude when plotted along the gradient of a determinant factor. Bell-shaped frequency distribution curves were seen for a few species. More common were very general trends of increasing, decreasing, or irregular curves. An increasing or decreasing trend may have been the result of intercepting the species in the mid-range of its environmental limits.

Particularly in the case of annuals, these irregular frequency distributions may have been the direct result of between-site weather variations. Typically in western Oklahoma, a large precentage of the precipitation comes from thunderstorms which characteristically result in extremely variable distributions and amounts of rainfall, a high percentage of runoff, and long dry periods. It is tempting to explain the observed irregular frequency distributions on between-site variation, and the higher than expected total frequency and species richness values at Site 9, on the basis of an abnormally wet or otherwise climatically favorable year. Irregular curves may also result from an inadequate number of replicates at each

geographic location  and/or the selection of sites that are
not equal in stability with the environment.

If within site variation, differences  between  repli-
cates, was a major problem affecting  the  results  of  the
statistical analysis, then  visually  inspecting  the  mean
frequency distributions for general  trends  identified  as
not significantly different by the statistical analysis may
give some insight to how species are  reacting  across  the
environmental  gradient.  The distributions of some of  the
higher  frequency  species are described in  the  following
paragraphs.

Celtis species  were  an  important  component  of the
understory in  all  of  the  first  three  sites.  Their
distribution continued out into  the eastern prairie sites,
but with drastically lower  frequencies.  Smilax bona-nox
also was common at the first three  sites, with a very high
frequency at Site 2. Sites 1 and 3 differed  from  2  in  a
number of other ways.  Sapindus drummondii had frequencies
equivalent to Celtis species at sites  1  and  3,  but  was
almost nonexistent at  2.  Similar  distributions were seen
for  Chenopodium  album,  Galium  aparine  and  Viola
rafinesquii.  Site  2 differed in having a higher frequency
of  Cercis  canadensis, and to a  lesser  extent  Juniperus
virginiana.  Both of these were present only in the  August
one square meter sample indicating potentially low seedling
survival  from  one  growing  season to the  next.  Celtis
species and Sapindus drummondii had  correspondingly  lower

frequencies in April than June or August. Site 1 differed from the other two in having <u>Elymus</u> <u>virginicus</u> present with high frequency. There was a trend of decreasing frequency from Site 1 to 3 for <u>Cyperus</u> species, and <u>Symphoricarpos</u> <u>orbiculatus</u>. <u>Parthenocissus</u> <u>quinquefolia</u>. <u>Paretaria</u> <u>pennsylvatica</u> generally increased in frequency from Site 1 to 3.

The overstory of Site 1, sampled with the five square meter quadrats, contained high frequencies of small <u>Celtis</u> species and <u>Sapindus</u> <u>drummondii</u> trees, accompanied by <u>Cornus</u> <u>drummondii</u>, <u>Juniperus</u> <u>virginiana</u> and <u>Gymnocladus</u> <u>dioica</u>. Large trees with low frequencies included, <u>Quercus</u> <u>stellata</u>, <u>Q</u>. <u>macrocarpa</u>, <u>Q</u>. <u>muehlenbergii</u>, <u>Ulmus</u> <u>americana</u>, <u>Sapindus</u> <u>drummondii</u>, <u>Gymnocladus</u> <u>dioica</u> and <u>Bumelia</u> <u>lanuginosa</u>. At Site 2, <u>Celtis</u> species continued to be an important small tree, but <u>Sapindus</u> <u>drummondii</u> and <u>Gymnocladus</u> <u>dioica</u> were replaced by <u>Cercis</u> <u>canadensis</u>, <u>Ulmus</u> <u>rubra</u>, and <u>Quercus</u> <u>velutina</u>. Large trees included, <u>Quercus</u> <u>macrocarpa</u>, <u>Q</u>. <u>velutina</u>, <u>J</u>. <u>virginiana</u>, <u>U</u>. <u>americana</u>, <u>B</u>. <u>lanuginosa</u>, and <u>Juglans</u> <u>nigra</u>. <u>Celtis</u> species continued to have the highest frequency for small trees at Site 3. <u>Sapindus</u> <u>drummondii</u> was present again, but at a lower frequency than at Site 1, and <u>Juniperus</u> <u>virginiana</u> was present at a lower frequency than Site 2. Large trees were primarily <u>Quercus</u> <u>stellata</u>, <u>Q</u>. <u>marilandica</u>, <u>B</u>. <u>lanuginosa</u>, and <u>S</u>. <u>drummondii</u>.

Sites 1 through 3 were far from being a homogeneous group. Site 3 was fairly characteristic of Duck and Fletcher's (1945) Post oak-Blackjack vegetation type. Sites 1 and 2 appeared to be some type of intergrade between the Post oak-Blackjack and Oak-Hickory vegetation types of Duck and Fletcher. They included species described by Bruner (1931) as dominants of upland and of floodplain sites of the oak-hickory association. The primary cause for the dicrepancies in the species compositions of sites 1 through 3 was probably differences in the soils and physiography. Site 1 was the most mesic site because of its sandy loam soil and proximity, in elevation, to the river, in addition to the climatic factors. Site 2 had a less xeric soil than site 3 because of its physical composition and the apparently shallower sandy soil. If the sites were edaphically more similar, it is suspected that they would have been less distinct, and more like that expected of a continuum. In a study of 208 upland forest stands throughout Oklahoma, Rice and Penfound (1959) described a vegetational continuum with no identified dominant species achieving their maximum development in the same stand as another.

The pattern of vegetational change for sites 4 through 9 was composed largely of widespread species with varied frequency distributions. In order to simplify classification of each site and to place more emphasis on perennials and long-lived annuals, the top 12-15 species at

each site were ranked according to their summed frequencies for all three sampling periods.

Based on this comparison, the five highest frequency species at Site 4 were; _Euphorbia missurica_, _Croton glandulosa_, _Ambrosia psilostachya_, _Triplasis purpurea_, and _Helianthus petiolaris_. Of these, only _A. psilostachya_ is a perennial. The ten highest ranked species contain three more perennials, _Rhus aromatica_ (sixth), _Andropogon hallii_ (eighth), and _Opuntia macrorhiza_ (ninth). Site 4 did not appear to have been heavily grazed or otherwise disturbed, as indicated by the presence of _Schizachyrium scoparium_ with frequencies of over 30 percent, the low frequency of _Artemisia filifolia_, and no sizeable areas of bare sand. However, the high frequencies of the above annuals and _Opuntia macrorhiza_ could be considered as indicating recent disturbance. The high frequencies of the annuals may also have been the result of a favorable growing season.

The first five species at Site 5 consisted of: _Schizachyrium scoparium_, _Croton glandulosa_, _Artemisia filifolia_, _Monarda punctata_, and _Euphorbia missurica_. Three of the five highest frequency species at Site 4 dropped dramatically in importance at Site 5. _Triplasis purpurea_ dropped to twelfth. _Ambrosia psilostachya's_ frequency fell to less than ten percent, and _Helianthus petiolaris_ was not present at Site 5. _Schizachyrium scoparium_ and _Monarda punctata_ were present at Site 4 with relatively high frequencies, ranked thirteenth and

fourteenth respectively. _Artemisia_ _filifolia_ had a frequency of less than ten percent at Site 4. Site 5 also differed from the others in that it was the only site which _Chrysopsis_ _villosa_, _Gilia_ _longiflora_ and _Aphanostephus_ _skirrhobasis_ were present in abundance.

_Sporobolus_ _cryptandrus_, _Mentzelia_ _stricta_, _Paspalum_ _setaceum_, _Croton_ _glandulosa_ and _Chenopodium_ _leptophyllum_ had the five highest ranked frequencies at Site 6. _Sporobolus_ _cryptandrus_ was sixth overall at Site 5, and had a frequency of approximately 20 percent at Site 4. _Mentzelia_ _stricta_ and _Paspalum_ _setaceum_ were also at sites 4 and 5, but with much lower frequencies. _Artemisia_ _filifolia_ was ranked eleventh at Site 6. This reduction was at least partly due to periodic herbicide spraying at Site 6 which is directed primarily as a control on _Artemisia_ _filifolia_. Prior to the June, 1981 sampling, adjacent areas to Site 6 were sprayed. _Artemisia_ _filifolia_ on the site had some wilting and die-back on the branch ends, but did not appear seriously affected. Forbs also did not seem to be seriously affected. With the exception of _Chenopodium_ _leptophyllum_, the higher frequency forbs did not have a substantial drop in frequency for the August sampling period. _Chenopodium_ _leptophyllum_ also had a large drop in frequency from April to June, and June to August at Site 9, and smaller drops in frequency from June to August at the other sites. Therefore, the spraying at Site 6 was

probably not entirely responsible for the observed drop in frequency.

The species with the five highest summed frequencies at Site 7 were; _Artemisia filifolia_, _Sporobolus cryptandrus_, _Eragrostis trichodes_, _Aristida purpurea_ and _Euphorbia missurica_. _Eragrostis trichodes_ was present with frequencies of 30 percent or greater at sites 4 through 6. _Aristida purpurea_ was also found on sites 4 through 6, but at very low frequencies.

_Sporobolus cryptandrus_ and _Artemisia filifolia_ are again the two highest ranked species at Site 8. They were joined by _Chenopodium leptophyllum_, _Eriogonum annuum_ and _Helianthus petiolaris_. _Chenopodium leptophyllum_ had been present at sites 4 through 8, but its frequency had oscillated greatly. _Helianthus petiolaris_ had a very distinctly bimodal frequency distribution. It was ranked fifth at Site 4 and then was absent or had very low frequencies for sites 5, 6 and 7. _Eriogonum annuum_ was common on sites 4 through 7, with frequencies between approximately 20 and 50 percent.

_Ambrosia psilostachya_, _Sporobolus cryptandrus_, _Helianthus petiolaris_, _Triplasis purpurea_ and _Cyperus schweinitzii_ were the first five species at Site 9, ranked by summed frequencies. _Ambrosia psilostachya_, like _Helianthus petiolaris_, was distinctly bimodal, also having a high frequency value at Site 4. It differs from _H. petiolaris_ in that it had a low frequency at Site 8.

Triplasis purpurea had been steadily decreasing in frequency from a maximum at Site 4 to a very low frequency at Site 8. Cyperus schweinitzii was also present on sites 4, 6, 7, and 8, where its frequency oscillated between approximately 15 and 60 percent.

Based on these comparisons, it seems reasonable to place sites 4 through 9 in four broad vegetational groups, described by the highest frequency perennial grass and woody perennial, except for Site 9. These are: (1) Site 4, Andropogon hallii-Rhus aromatica; (2) Site 5, Schizachyrium scoparium-Artemisia filifolia; (3) sites 6-8, Sporobolus cryptandrus-Artemisia filifolia; and (4) Site 9, Sporobolus cryptandrus-Ambrosia psilostachya. These groups represent the sites with maximum frequency values of the mentioned species, and not distinct communities. The frequency distributions of the other species do not support these boundaries, and are instead individualistic in nature.

Environmental Factors

The high frequencies of annuals, especially at Site 4, were unexpected for sites supposedly in equilibrium with the long term environment. However, if soil moisture is a limiting factor then the dominants may be distributed in such a way that there appears to exist "open space" above ground between individuals. Pound and Clements (1898) reported one to three meters between individuals in the open communities of the stabilized sand hills of Nebraska

in the blue-stem formation. Spacing of this extent was not observed in the sites selected for this study. Densities did appear to be much less than would be expected in prairie sites on more mesic soils. This wide spacing may be necessary for individuals to obtain sufficient moisture during dry years. Thus even though there appears to be "open space" above ground, the firmly established perennials may be very effectively controlling the availability of soil moisture in these areas by the action of their roots. As the soil moisture declines the annuals and newly established perennials would be expected to be the least successful.

During periods of higher soil moisture, the area required to meet the physiological demands of the individuals would be reduced and so in effect the area controlled by the dominants would decrease. This in turn would result in newly available space within the community. Earlier seral species might then be expected to be the best adapted to initially take advantage of such a situation. The wide spacing of the dominants would reduce their effectiveness in controlling the environment of the community through alternative factors, such as shading of the soil surface.

If the wet cycle continues, then the seral species would be gradually replaced by the dominants, with the result of an increase in their density. It is probable that before a new equilibrium is established, the climate would swing back towards a dry year, or series of years,

thus perpetuating the wide spacing of the dominants. Seral and dominant propagules would continue to germinate in the "open areas" but generally would not be expected to become established.

This continual fluctuation may explain why species such as Calamovilfa gigantia, generally considered a pioneer, would continue to be an important component of sand hill vegetation. The "open areas" of wet years may also explain why it is possible for there to be literal explosion of annuals on the sand hills during years of optimal growth conditions. Hulett, et al. (1966) described erratic development of annuals as characteristic of the sand dunes of Saskatchewan. The openness of the community, in addition to the physical nature of sand, would also explain why even stabilized dunes are very susceptible to blow-outs. The death or reduced success of a single individual dominant could potentially open up a relatively large area that would then be more suceptible to erosion.

The high frequency of the seral species, specifically at Site 4, is not easily explained simply by precipitation. Based on monthly precipitation, 1981 did not seem to be a highly favorable year for annuals (Figure 50, Appendix C). The precipitation for March was slightly above normal, but April and May were approximately 1.5 inches per month below average. June was above average by about one inch, and July was slightly below. Whether or not these

variations were significant enough to cause noticeable changes in "average" species abundances is debatable.

The precipitation distributions for 1980 near Site 4 were drastically different from normal (Figure 51, Appendix C). April and May received more than twice the average monthly precipitation while June through September received less than half the norm. It is possible that the high frequency of annuals at Site 4 during an "average" year, 1981, may be more of a response to a potentially good reproductive year for spring annuals, and a poor year for the warm season grasses during 1980. It is not immediately evident why *Ambrosia* *psilostachya* had such high frequencies based simply on precipitation. Annuals, such as *Helianthus* *petiolaris* which was observed flowering in May, may have avoided the potential moisture stress during the summer in 1980. Site 5 had a similarly dry summer in 1980 (Figure 53, Appendix C), but received approximately half as much precipitation in May. Whether or not this difference is sufficient to explain the lower frequencies of annuals in 1981 at Site 5 when compared to Site 4 is debatable, especially since Site 5 had significantly more precipitation in May of 1981 than Site 4 (Figures 50 and 52, Appendix C).

The monthly precipitation received during 1981 at Range, near Site 9, by itself does not explain the higher total frequencies observed at Site 9 when compared to sites 6 through 8. Depending on the month and sites compared,

Site 9 may have been somewhat more favorable in terms of the amount of precipitation received compared to the norm (Figures 60 and 61, Appendix C). In general terms however, sites 6 through 9 all had a wet March followed by an average to slightly dry April and May, a distinctly dry June, and a slightly above average to normal July. There were also no distinct differences between sites in the pattern or extent of monthly temperature departures from the norm (Figure 43, Appendix B).

An interesting shift was noticed in the normal monthly precipitation patterns for sites 4 through 9 (Appendix C). At sites 4 through 7 the monthly precipitation amounts are distributed over the year in an approximately bell-shaped curve with the highest monthly precipitation occurring in May. The curve remains bell-shaped for sites 8 and 9, but the month receiving the greatest amount of rainfall changes. June is just slightly higher than May and July at Beaver, near Site 8. At Goodwell, near Site 9, the month with the maximum amount of rainfall is clearly July. With July being normally the hottest month at all the sites, this difference in precipitation distribution may be an important factor in determining the distribution and success of several species, particularly those that bloom during the summer months. Thus it may be partially responsible for the higher observed total frequencies and species richness observed at Site 9.

There appears to be a linear relationship for the total frequencies (Figure 4) of sites 4 through 8. When the total frequency for a site was plotted against the average annual precipitation for that site, the relationship becomes more obvious (Figure 7). Sites 1 through 3 and probably 9 show no linear relationship with the other sites. Correlation coefficients were calculated for sites 1 through 9, 4 through 9, and 4 through 8 using total frequencies for each sampling period and also mean total frequency for all three sampling periods. There was found a linear relationship with a confidence level of 90% or greater for sites 4 through 8 for the all three sampling periods. There was a linear relationship with a confidence level of 95% for sites 4 through 9 for the June sampling period. The other comparisons were found not to be linear at confidence levels of 90% or greater.

Similar, but not necessarily statistically significant, results were obtained when precipitation effectiveness indices, and length of growing season were plotted against total frequency, and also for pan evaporation, elevation and wind movement, but with opposite slopes. When the number of species per site was substituted for total frequency again similar results were obtained. The sites were not selected with the objective of keeping any one of these factors constant while investigating the others. Therefore it cannot be determined if any one was a limiting factor along the

length of the transect, or if one or  more factors replaced

another as the position along the transect changed.

# CHAPTER VII

## SUMMARY

The objective of this study was a description of the patterns of vegetational change on sand dunes along a climatic and physiographic environmental gradient in north-central and northwestern Oklahoma as determined by single factor, frequency, data. Potential community boundaries, if present, were to be identified and related to environmental changes.

The nine sites can be divided into two general physiognomic groups, deciduous forest and grass/shrub. This was readily evident when visiting the sites and was supported by the low community coefficients of sites from opposite sides of the community boundary. This apparently distinct community boundary between sites 3 and 4 may be the result of a edaphic conditions. Site 3 is on Eufaula fine sand, which is higher in organic matter than the Tivoli fine sand found at sites 4 through 9.

Within the grass/shrub sites, there was a general inverse trend between similarity of species composition and distance between sites. However, this trend does not remain when only species with a relative frequency of five percent or greater at any one site are used to calculate

community coefficients. If there is a vegetational continuum across the grass/shrub section of the study area, as indicated by individual species distributions, then frequency alone may not give an accurate representation of species importance.

The potentially interrelated community attributes, total frequency and species richness, have similar trends across the study area. Total frequencies were lowest in the forested sites, as would be expected because of the size and spacing of the dominant trees in relation to the quadrat size, and the apparent low understory densities. Total frequency was greatest at Site 4, the eastern-most grass/shrub site, generally decreased to Site 8, and then increased at Site 9. The same general trend was observed for species richness, but the magnitudes of the differences were reduced. Species richness declined slightly from Site 4 to Site 7, while the total frequency decreased markedly, resulting in a decreasing mean frequency per species. The mean frequency per species increased from Site 7 to Site 9 as the result of decreased species richness and/or increased total frequency. A linear relationship was found between mean total frequency and precipitation for sites 4 through 8. This relationship does not prove precipitation was the major factor influencing total frequency because other environmental factors are changing simultaneously. Also competition is changing as species frequencies and composition change.

Frequency distributions of individual species revealed wide variation in patterns of species' success, as measured by frequency, across the environmental gradient. With the exception of the community boundary between sites 3 and 4, Duncan's Multiple Range test in conjunction with analysis of variance, and inspection of frequency histograms failed to identify other definite community boundaries on the basis of several species sharing similar distributional patterns.

The deciduous forest sites, 1 through 3, formed a heterogeneous group. _Quercus_ spp., _Celtis_ spp., _Sapindus drummondii,_ _Bumelia_ _lanuginosa_ and _Ulmus_ _americana_ in various combinations were the major dominants. _Celtis_ spp. and _Ulmus_ _americana_ seedlings, _Smilax_ _bona-nox_, _Parthencissus_ _quinquefolia_ and _Symphoricarpos_ _orbiculatus_ were important woody species in the understory. Differences in edaphic conditions were probably a major factor in making these sites relatively distinct from one another.

The grass/shrub sites, 4 through 9, can be placed into four groups based on two perennial species with high frequencies and their physiognomies: (site 4) _Andropogon hallii_ - _Rhus aromatica_; (site 5) _Schizachyrium scoparium_ - _Artemisia filifolia_; (sites 6-8) _Sporobolus cryptandrus_ - _Artemisia filifolia_; and (site 9) _Sporobolus cryptandrus_ - _Ambrosia psilostachya_. The other species generally did not exhibit frequency distribution patterns which support these

potential community boundaries. Site 5, located at Little Sahara State Park, was unique in being the only site with the species _Chrysopsis villosa_, _Gilia longiflora_ and _Aphanostephus skirrhobasis_ present in abundance.

# LITERATURE CITED

Adams, D. E. and R. C. Anderson. 1980. Species response
     to a moisture gradient in central Illinois forests.
     Amer. J. Bot. 67(3):381-392.

Alizai, H. U., and L. C. Hulbert. 1970. Effects of soil
     texture on evaporative loss and available water in
     semi-arid climates. Soil Science. 110(5):328-338.

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1980.
     Terrestrial Plant Ecology. Menlo Park, CA: Benjamin-
     Cummings Publ. Co., Inc. 604 pp.

Blair, W. F. and T. H. Hubbell. 1938. The biotic
     districts of Oklahoma. Amer. Midl. Nat. 20:425-454.

Bruner, W. E. 1931. The vegetation of Oklahoma. Ecol.
     Monogr. 1:99-188.

Chadwick, H. W. and P. D. Dalke. 1965. Plant succession
     on dune sands in Fremont county, Idaho. Ecology.
     46(6):765-780.

Clements, F. E. 1916. Plant succession: an analysis of
     the development of vegetation. Washington D.C.:
     Publ. Carnegie Inst. No. 242. 512 pp.

Cowles, H. C. 1899. The ecological relations of the
     vegetation on the sand dunes of Lake Michigan.
     Bot. Gaz. 27:95-117, 167-202, 281-308, 361-391.

Curtis, J. T. 1955. A prairie continuum in Wisconsin.
     Ecology. 36(4):558-566.

Curtis, J. T. and R. P. McIntosh. 1951. An upland forest
     continuum in the prairie-forest border region of
     Wisconsin. Ecology. 32(3):476-495.

Daley, R. H. 1972. The native sand sage vegetation of
     eastern Colorado. (Unpub. M.S. thesis, Colorado
     State University).

Dix, R. L. and J. E. Butler. 1960. A phytosociological
     study of a small prairie in Wisconsin. Ecology.
     41(2):316-327.

70

Duck, L. G. and J. B. Fletcher. 1945. A Survey of the
    Game and Furbearing Animals of Oklahoma. Pittman-
    Robertson Series No. II. State Bulletin No. 3.
    144 pp.

Gleason, H. A. 1917. The structure and development of
    the plant association. Bull. Torrey Bot. Club.
    43:463-481.

Hulett, G. K., R. T. Coupland, and R. L. Dix. 1966. The
    Vegetation of dune sand areas within the grassland
    regions of Saskatchewan. Canadian J. Bot.
    44:1307-1331.

Hyder, D. N., C. E. Conrad, P. T. Tueller, L. D. Calvin,
    C. E. Poulton, and F. A. Sneva. 1963. Frequency
    sampling in sagebrush-bunchgrass vegetation. Ecology.
    44(4):740-746.

Jaccard, P. 1902. Lois de distribution florale dans la
    zone alpine. Bull. Soc. Vaud Sci. Nat. 38:69-130.
    (as cited in: Barbour, M. G., J. H. Burk and W. D.
    Pitts. 1980. Terrestrial Plant Ecology. Menlo Park,
    CA: Benjamin/Cummings Publ. Co., Inc. 604 pp.)

Kershaw, K. A. 1973. Quantitative and Dynamic Plant
    Ecology. 2nd ed. New York: American Elsevier.
    308 pp.

Kumler, M. L. 1969. Plant succession on the sand dunes
    of the Oregon coast. Ecology. 50(4):695-704.

McMillan, C. 1956a. Nature of the plant community. I.
    Uniform garden and light period studies of five grass
    taxa in Nebraska. Ecology. 37(2):330-340.

McMillan, C. 1956b. Nature of the plant community. II.
    Variation in flowering behavior within populations of
    Andropogon scoparius. Amer. J. Bot. 43:429-436.

Morrison, R. G. and G. A. Yarranton. 1974. Vegetational
    heterogeneity during a primary sand dune succession.
    Can. J. Bot. 52:397-410.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and
    Methods of Vegetation Ecology. New York: John Wiley
    and Sons. 547 pp.

Pool, R. J. 1914. A study of the vegetation of the sand-
    hills of Nebraska. Minn. Bot. Studies. 4:189-312.

Pound, R. and F. E. Clements. 1898. The vegetational
    regions of the prairie province. Bot. Gaz.
    25(6):381-395.

Quinn, J. A. and R. T. Ward. 1968. Ecological differentiation in sand dropseed (Sporbolus cryptandrus). Ecol. Monogr. 39(1):61-78.

Rice, E. L. and W. T. Penfound. 1959. The upland forests of Oklahoma. Ecol. 40(4):593-608.

Sherwood, R. T. B. 1980. Vegetation of the Woods county, Oklahoma sand dunes. (Unpub. Ph.D. thesis, University of Oklahoma).

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16:284-307.

Taylor, H. M. 1960. Moisture relationships of some range-land soils of the southern Great Plains. J. Range Mgt. 13:77-80.

Thornthwaite, C. W. 1931. The climates of North America. Geogr. Rev. 21:633-655.

U.S. Dept. of Agriculture Soil Conservation Service. 1959. Soil Survey. Beaver County, Oklahoma. Washington D.C.: U.S. Govt. Printing Office.

U.S. Dept. of Agriculture Soil Conservation Service. 1959. Soil Survey. Kingfisher County, Oklahoma. Washington D.C.: U.S. Govt. Printing Office.

U.S. Dept. of Agriculture Soil Conservation Service. 1960. Soil Survey. Logan County, Oklahoma. Washington D.C.: U.S. Govt. Printing Office.

U.S. Department of Commerce. 1981. Climatological data. Oklahoma. Annual summary 1981. Vol. 90, No. 13.

Van Denack, J. M. 1961. An ecological analysis of the sand dune complex in Point Beach State Forest, Two Rivers, Wisconsin. Bot. Gaz. 122:155-174.

Waterfall, U. T. 1972. Keys to the Flora of Oklahoma. Stillwater, OK: published by author. 246 pp.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26(1):1-80.

Yarranton, G. A. and R. G. Morrison. 1974. Spatial dynamics of a primary succession: Nucleation. J. Ecology. 62:417-428.

APPENDIX A


FREQUENCY DISTRIBUTIONS
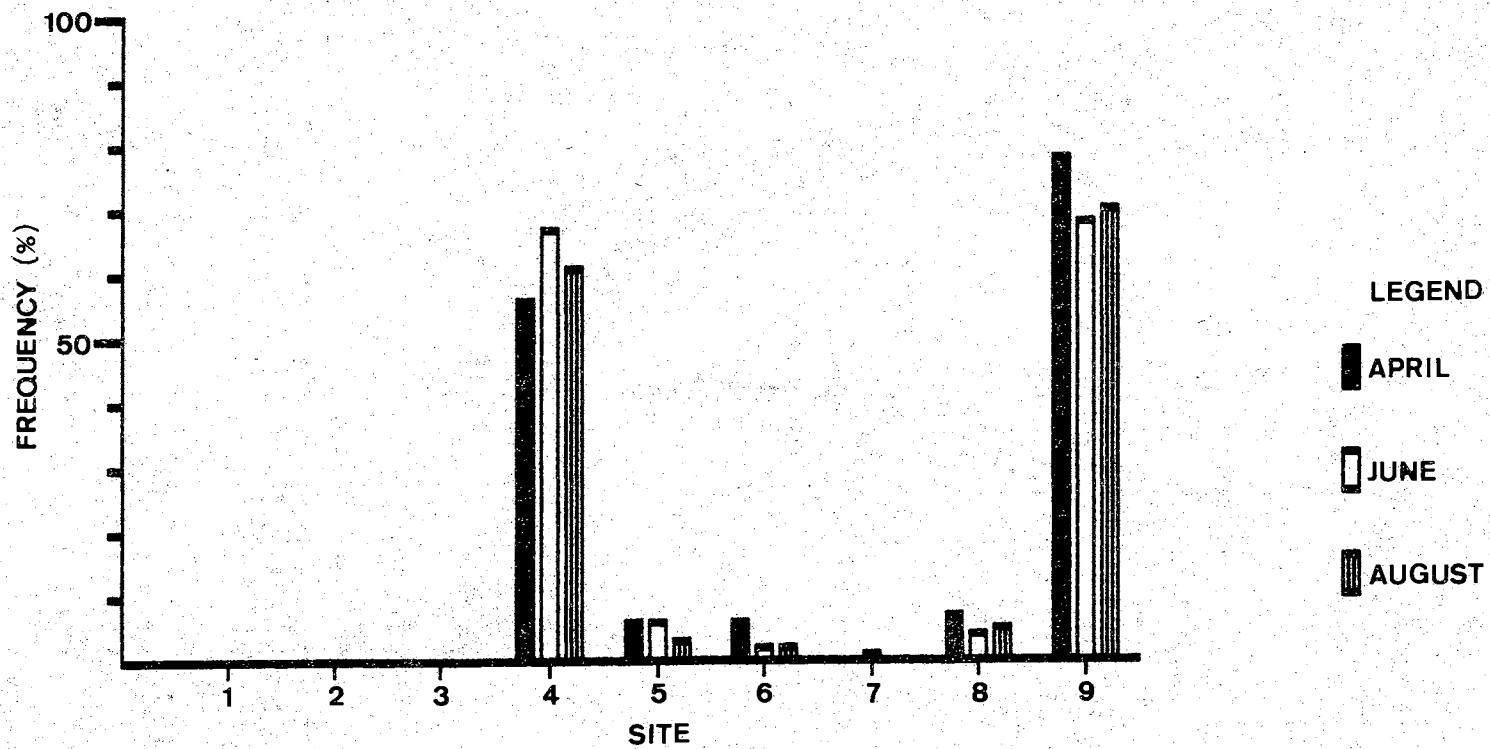
Figure 8.   Mean Frequency Distributions for _Ambrosia_
             _psilostachya_ for All Sites and Sampling
             Periods
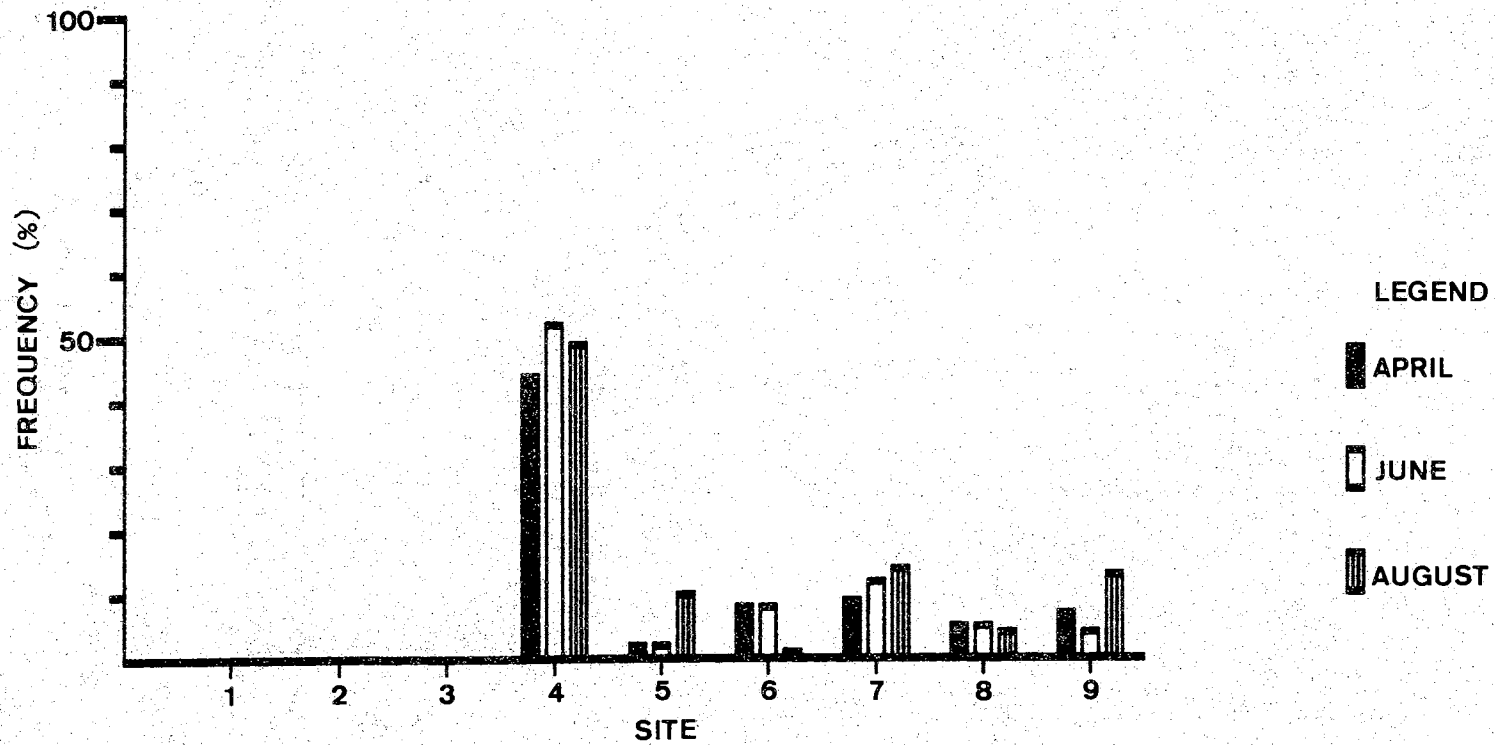
Figure 9.  Mean Frequency Distributions for <u>Andropogon</u>
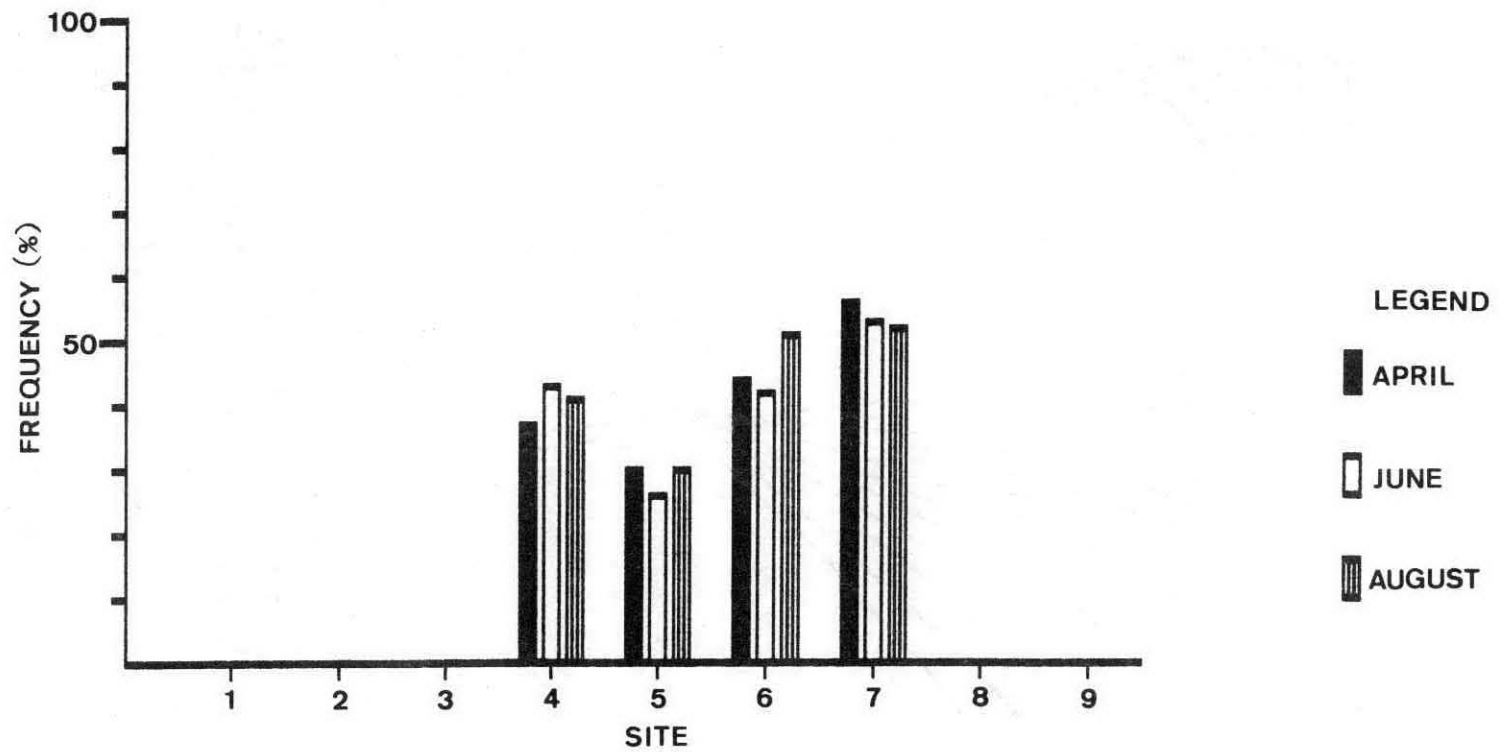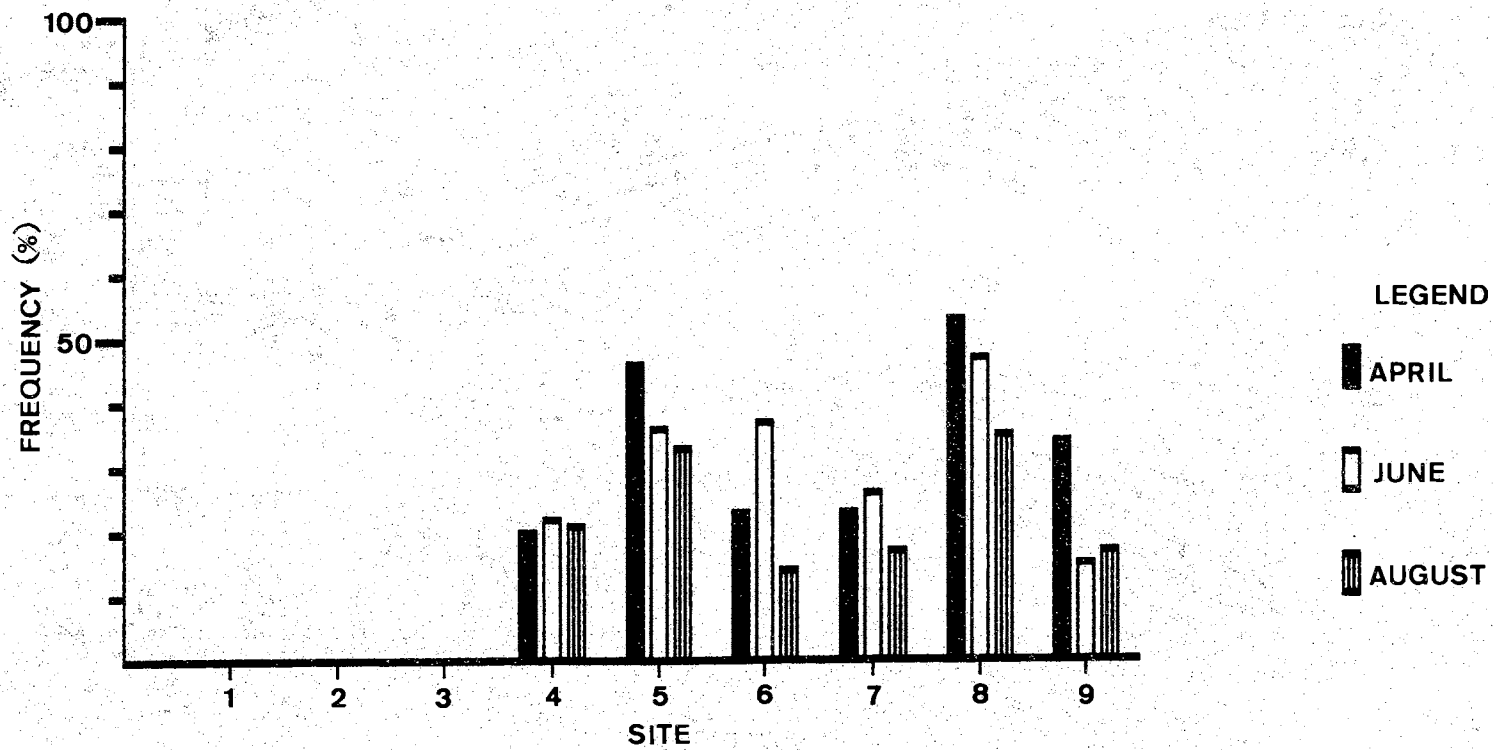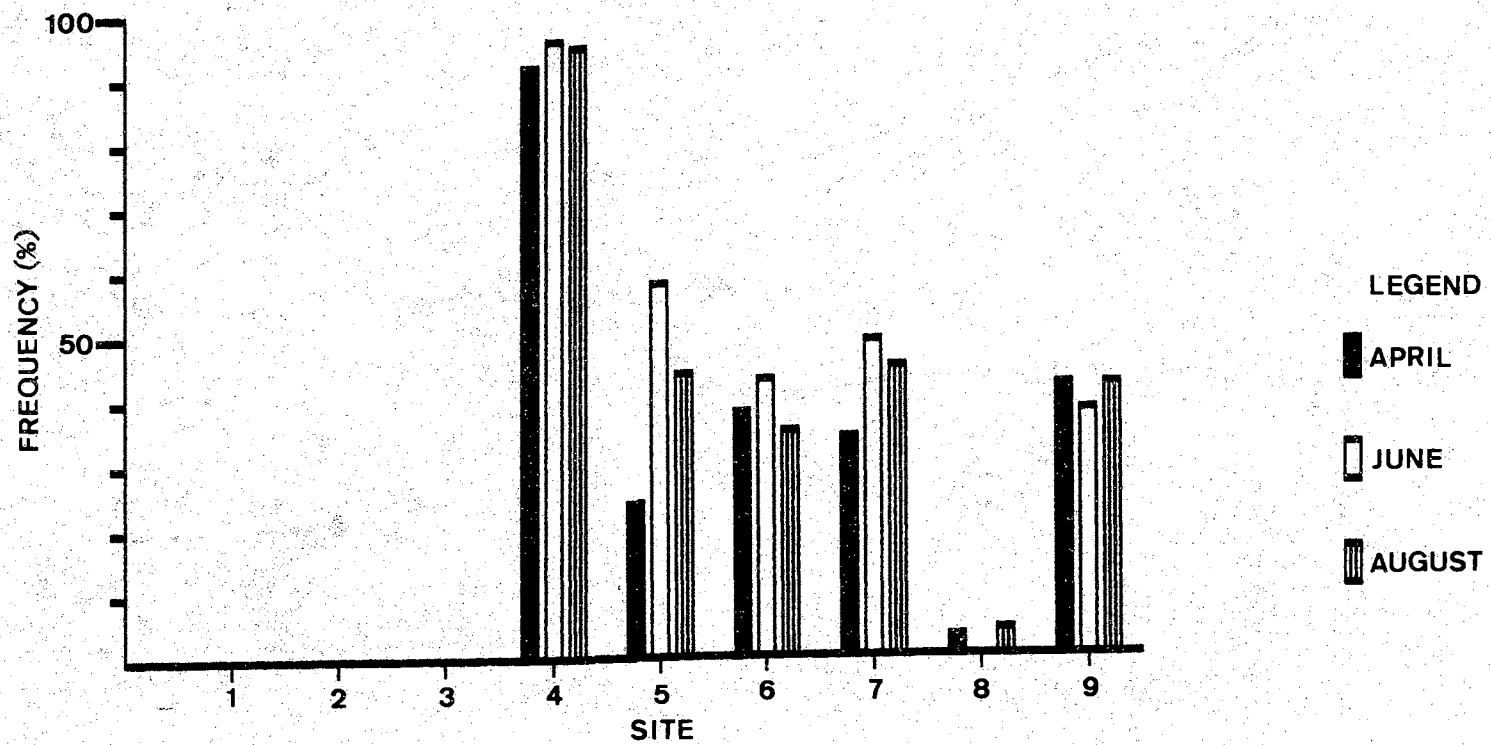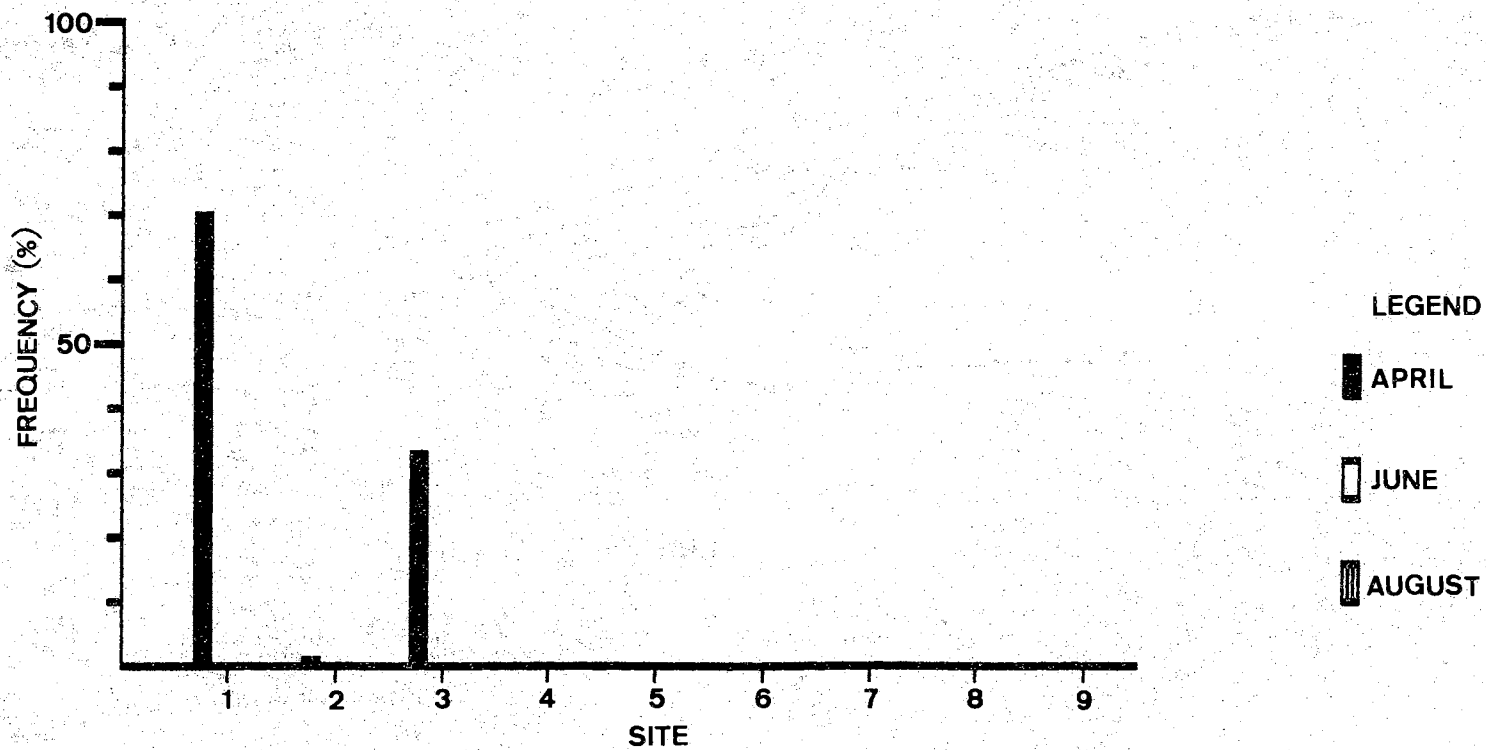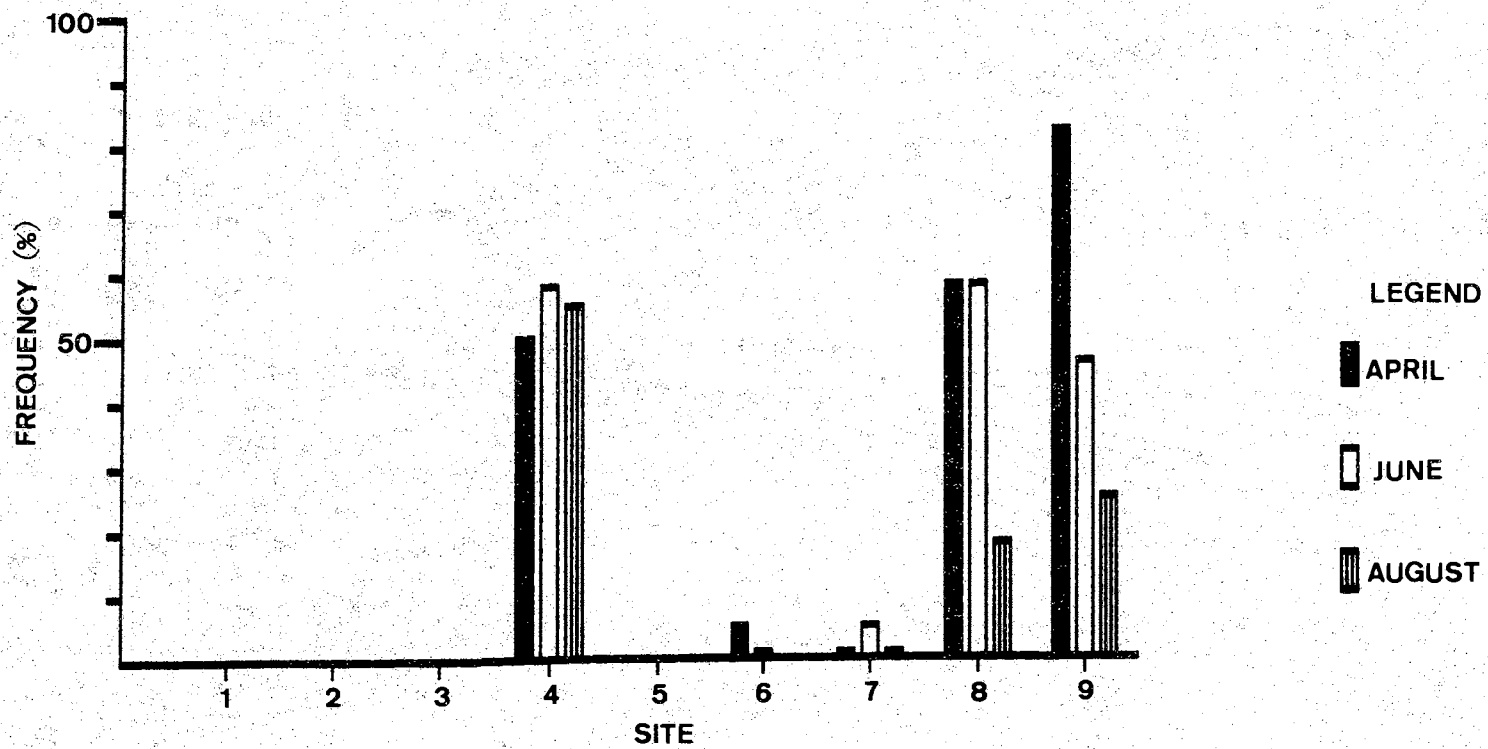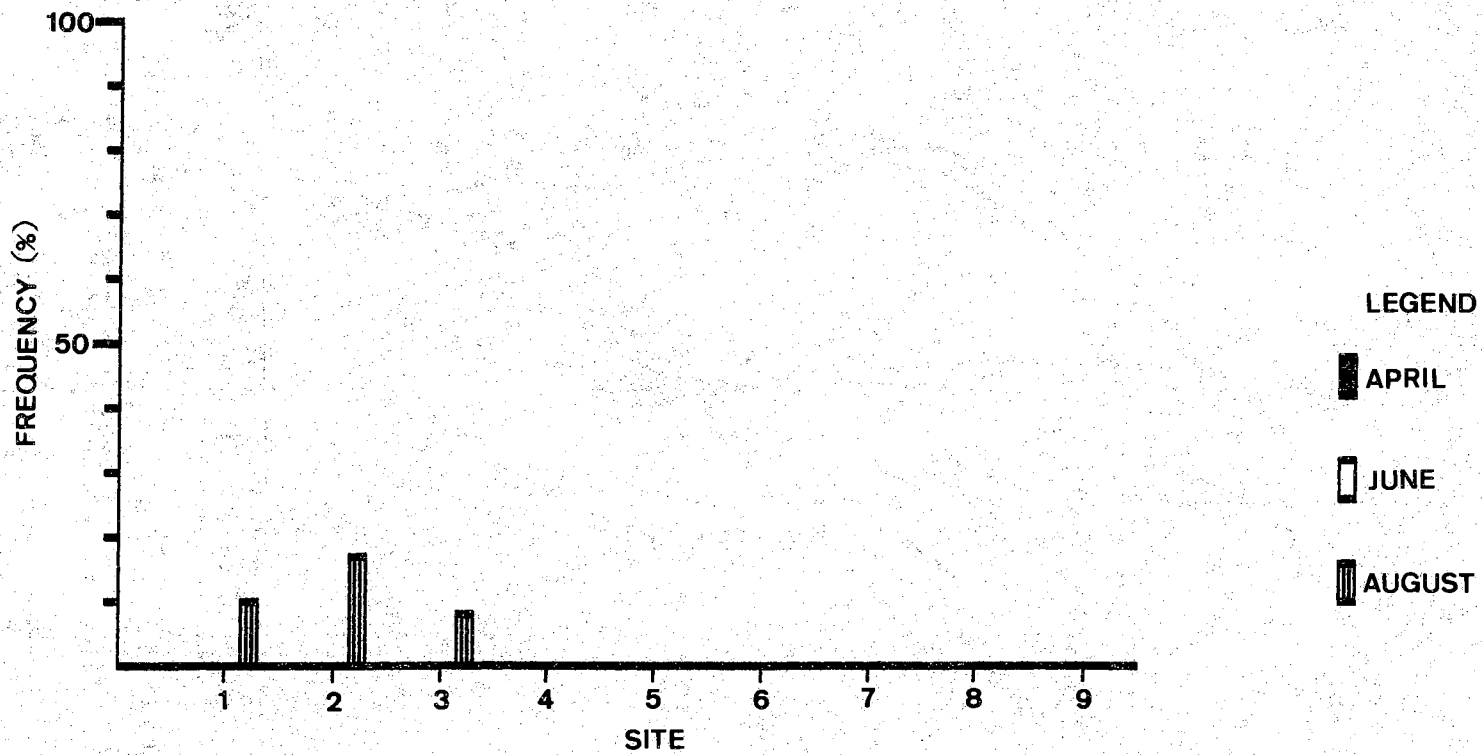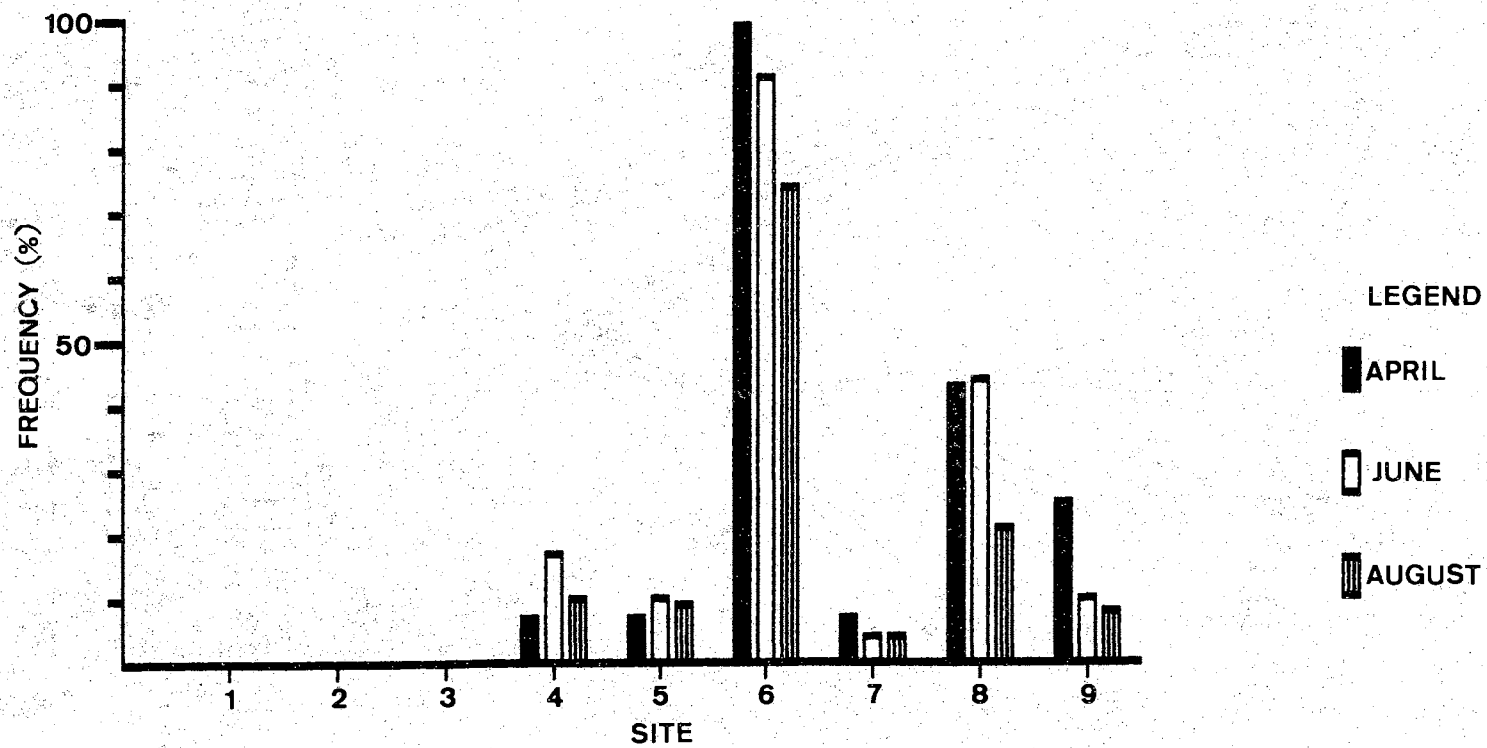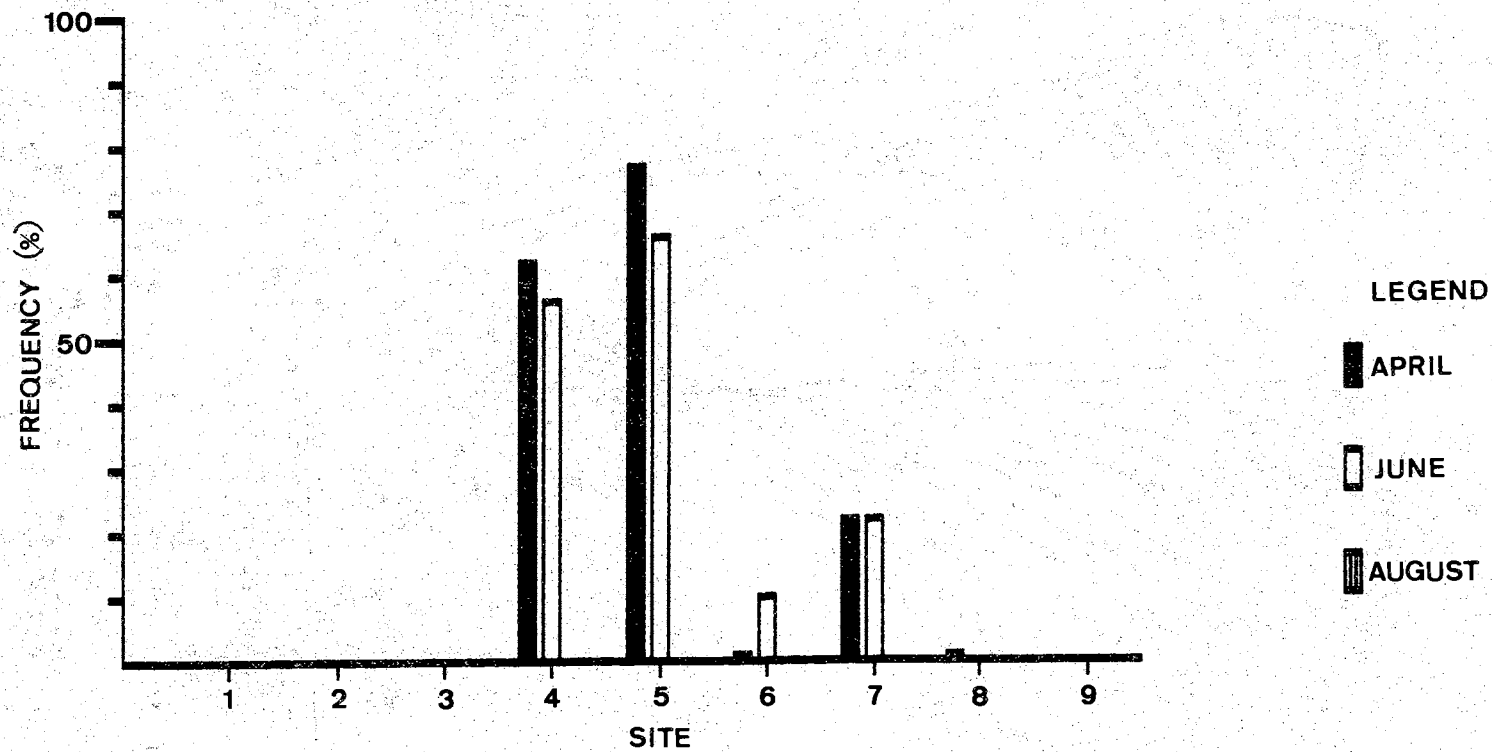<u>hallii</u> for All Sites and Sampling Periods
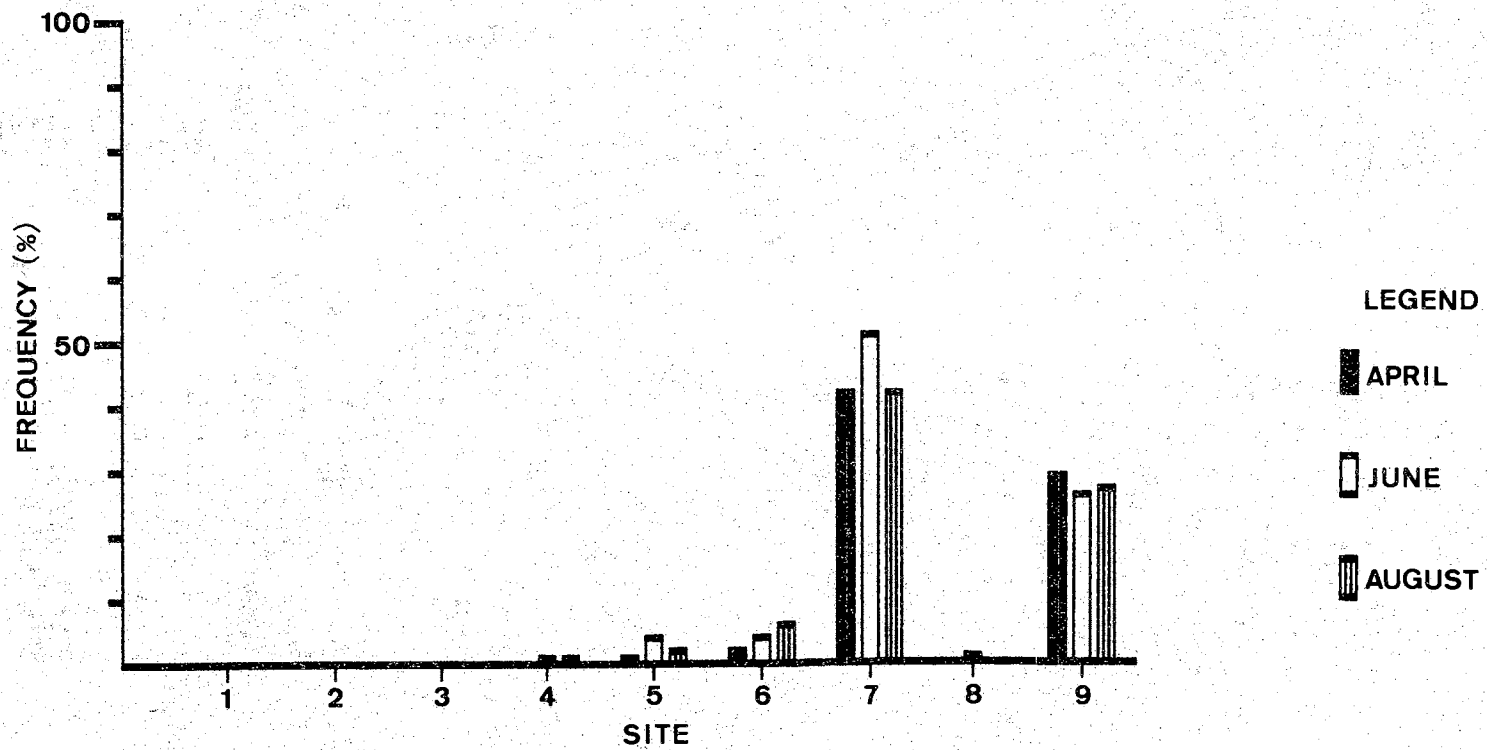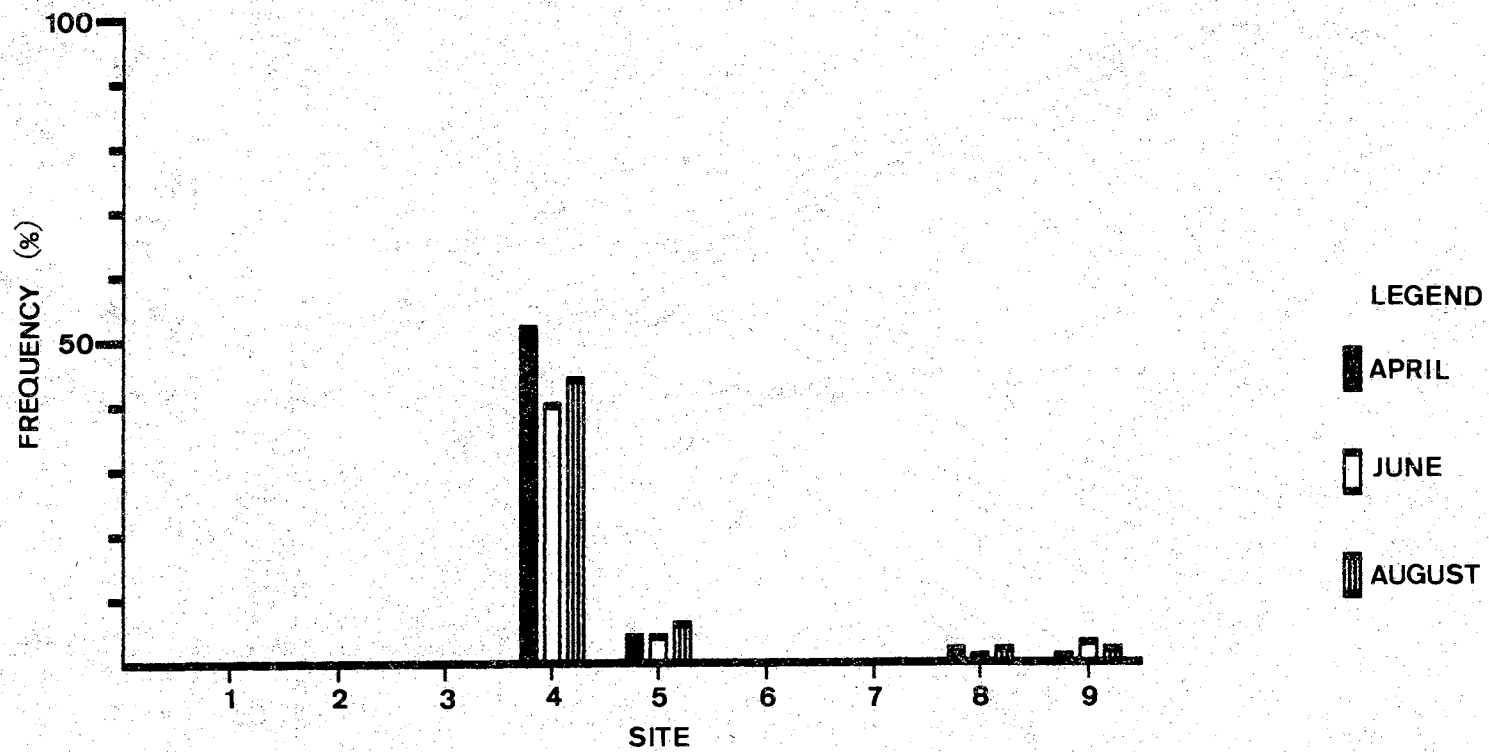
Figure 10. Mean Frequency Distributions for <u>Aristida</u>
<u>purpurea</u> for All Sites and Sampling
Periods
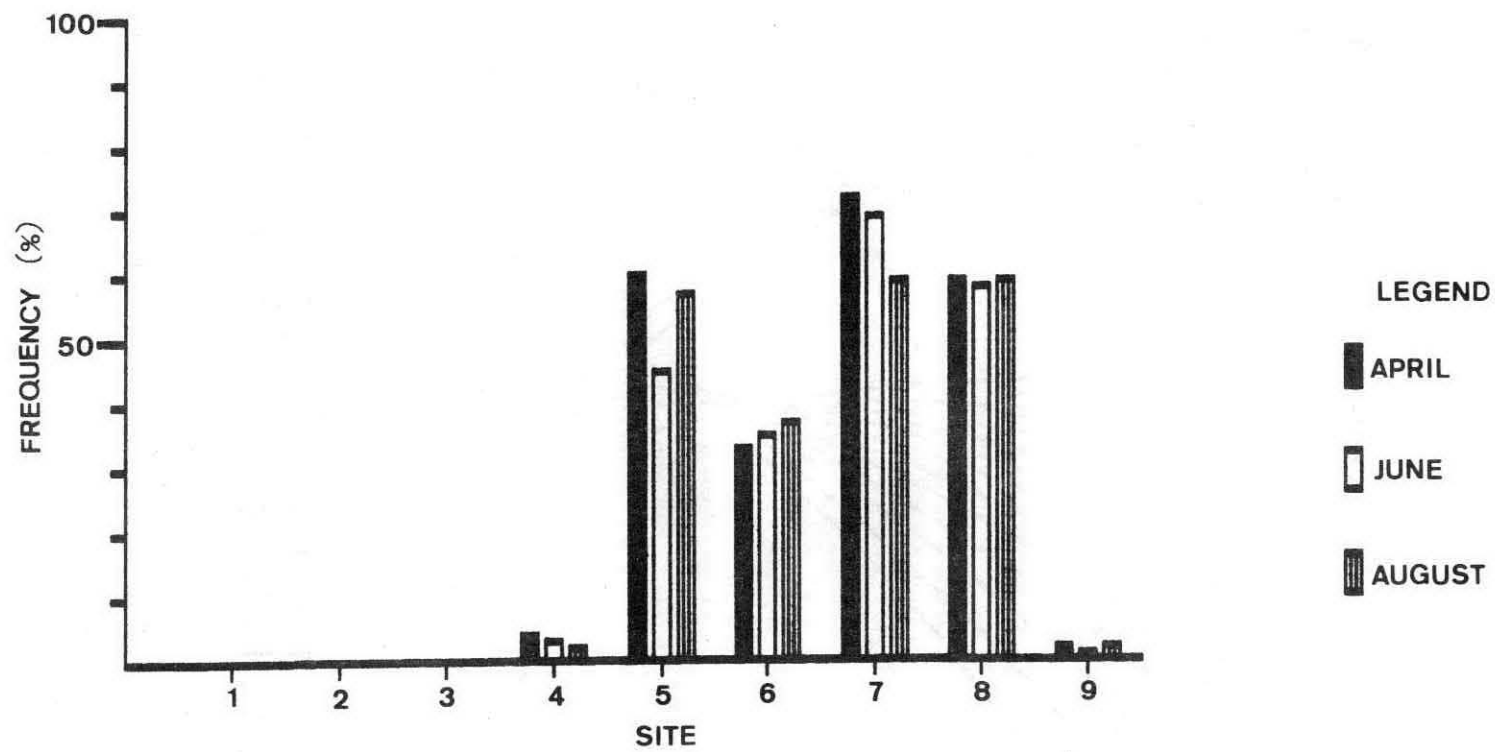
Figure 11.  Mean Frequency Distributions for _Artemisia
filifolia_ for All Sites and Sampling Periods
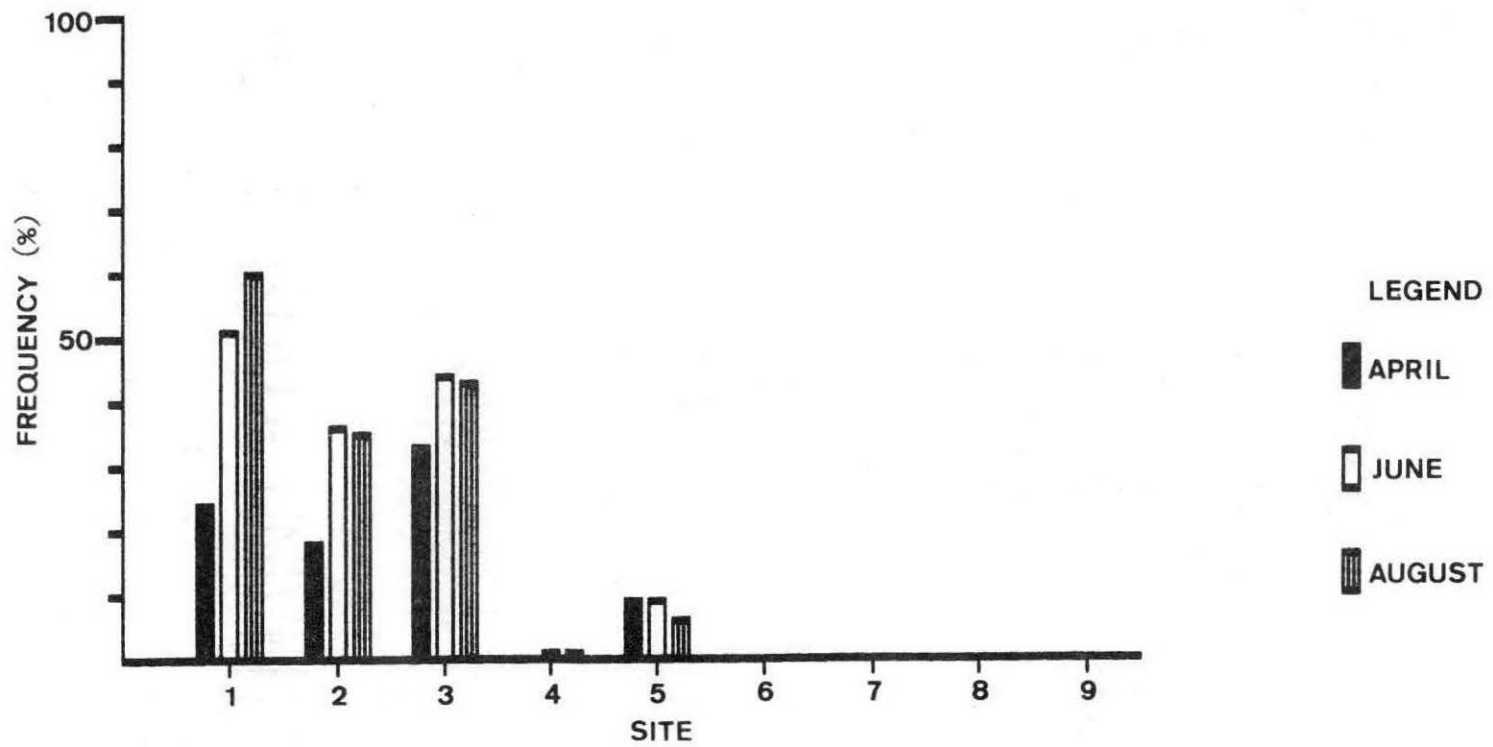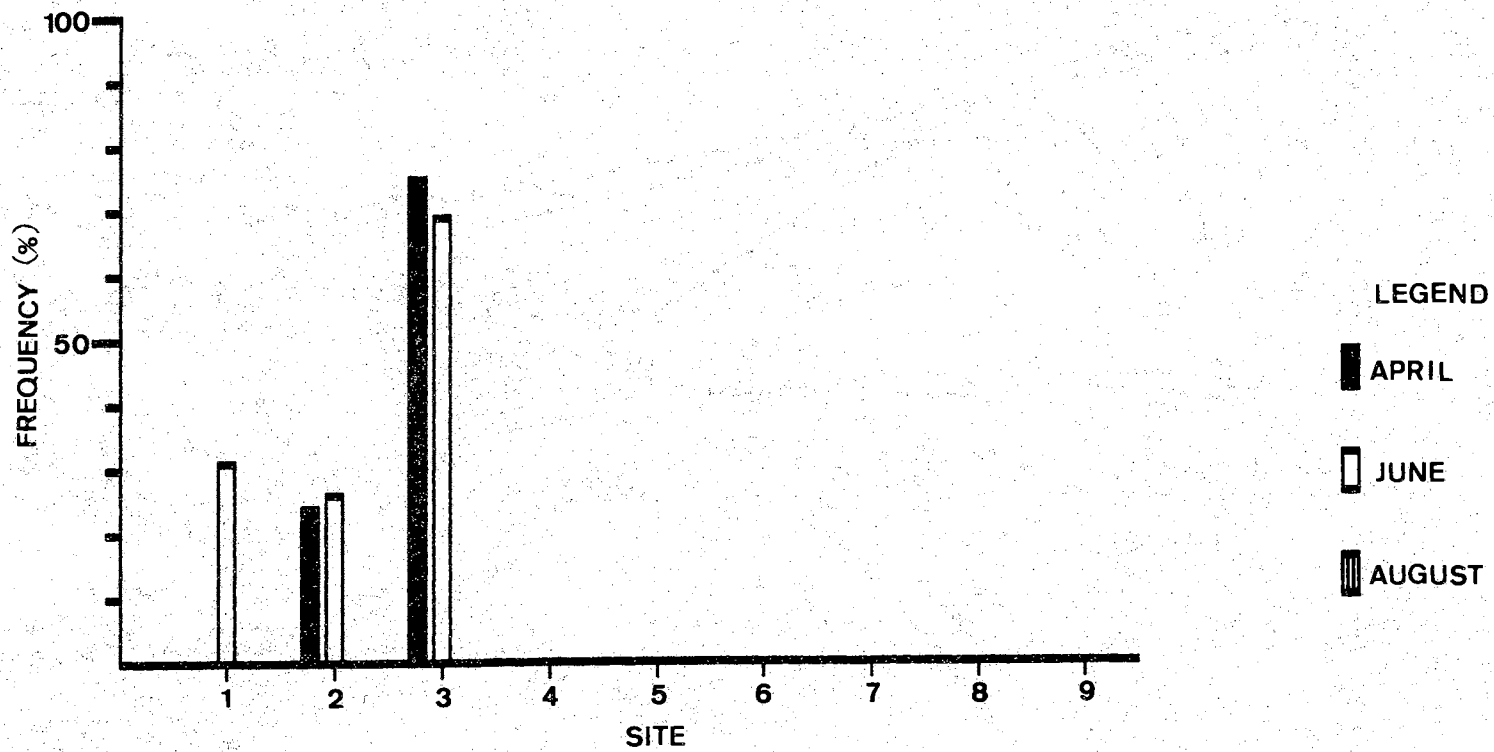
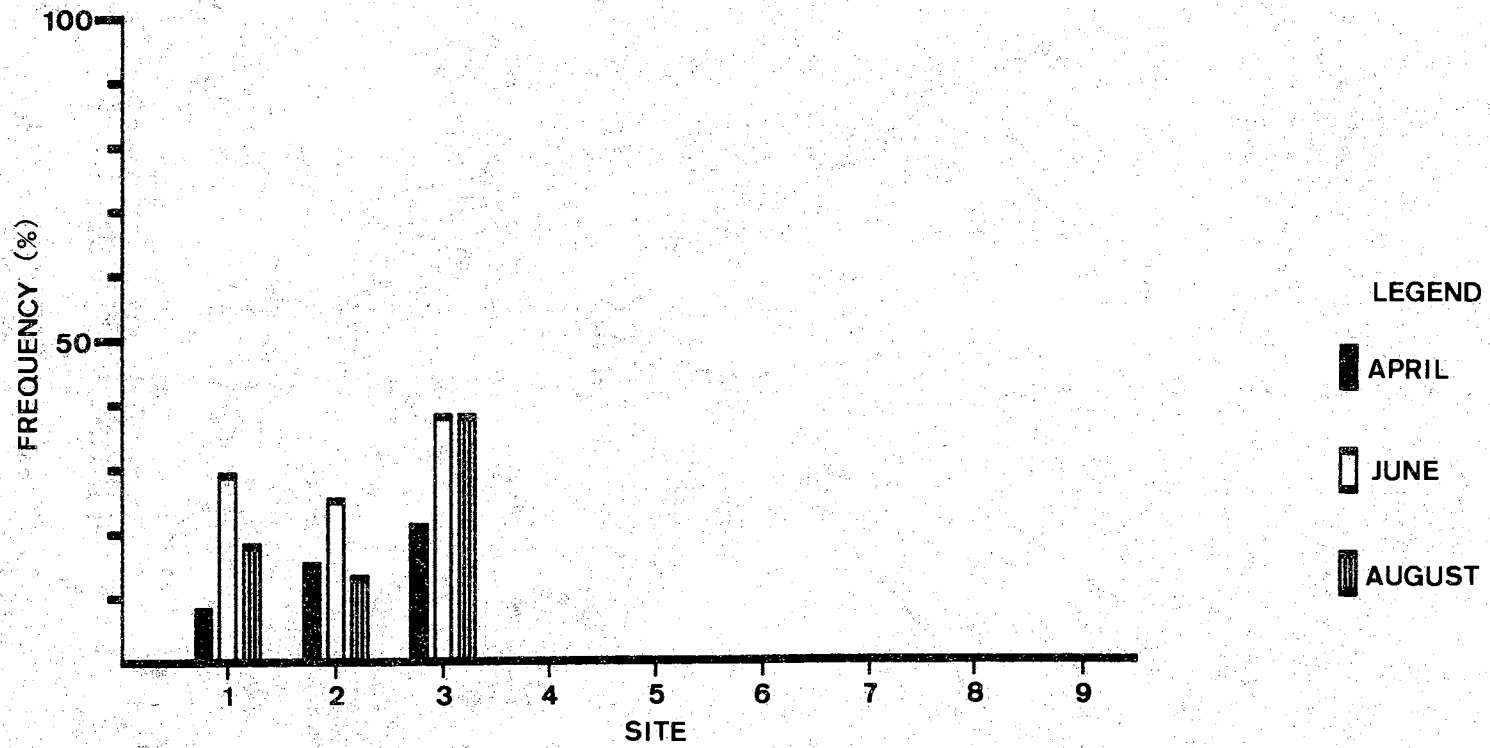Figure 12. Mean Frequency Distributions for Celtis spp. for All Sites and Sampling Periods
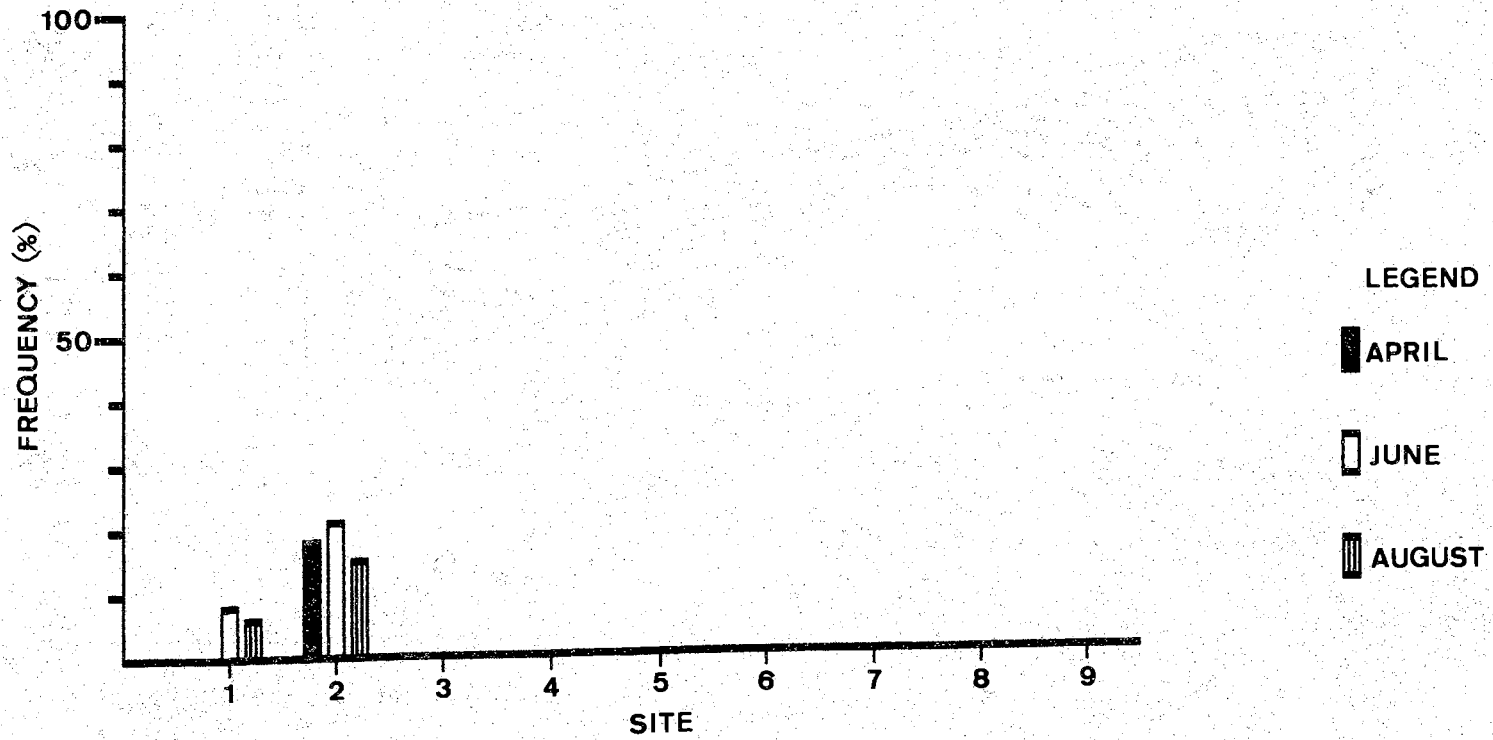
Figure 13. Mean Frequency Distributions for _Cercis canadensis_ for All Sites and Sampling Periods
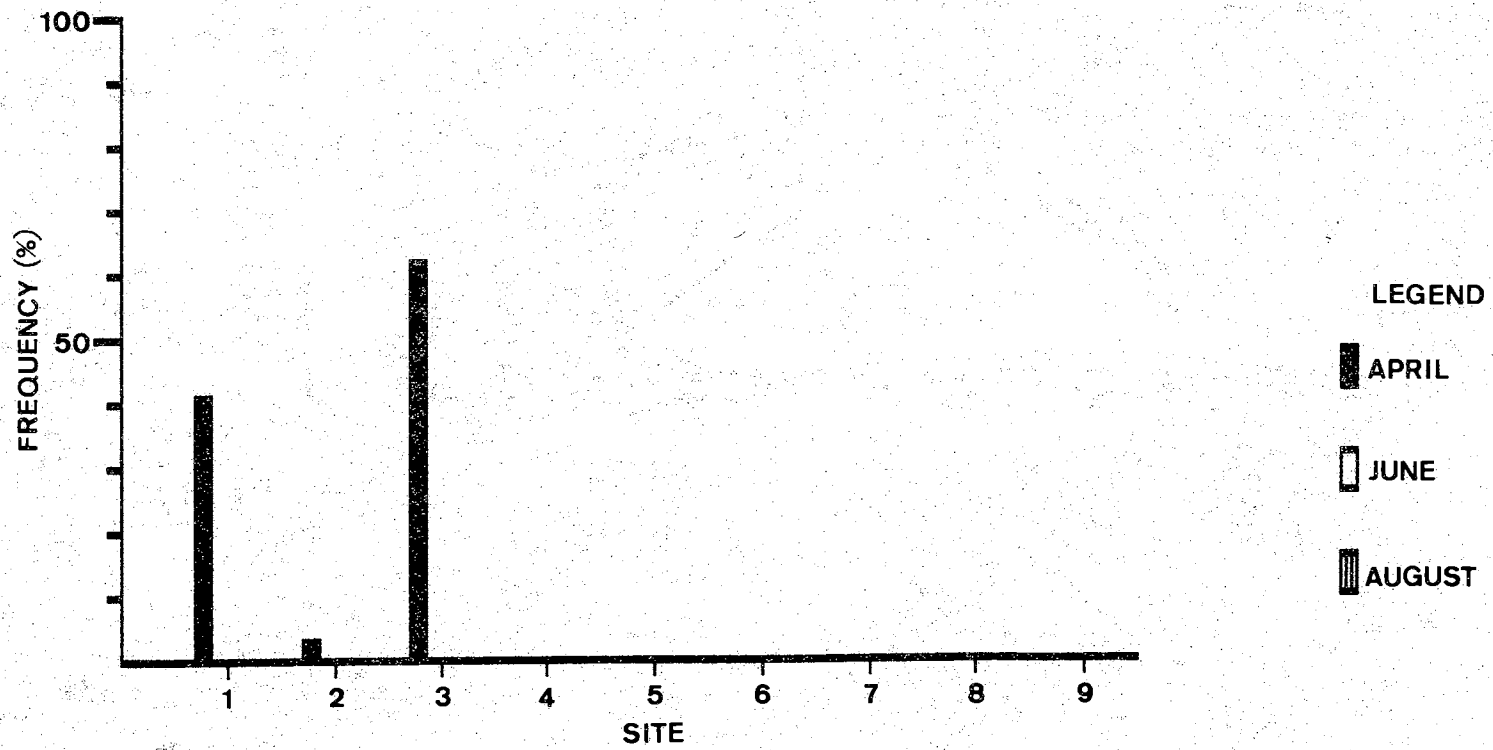
Figure 14.  Mean Frequency Distributions for Chenopodium
album for All Sites and Sampling Periods
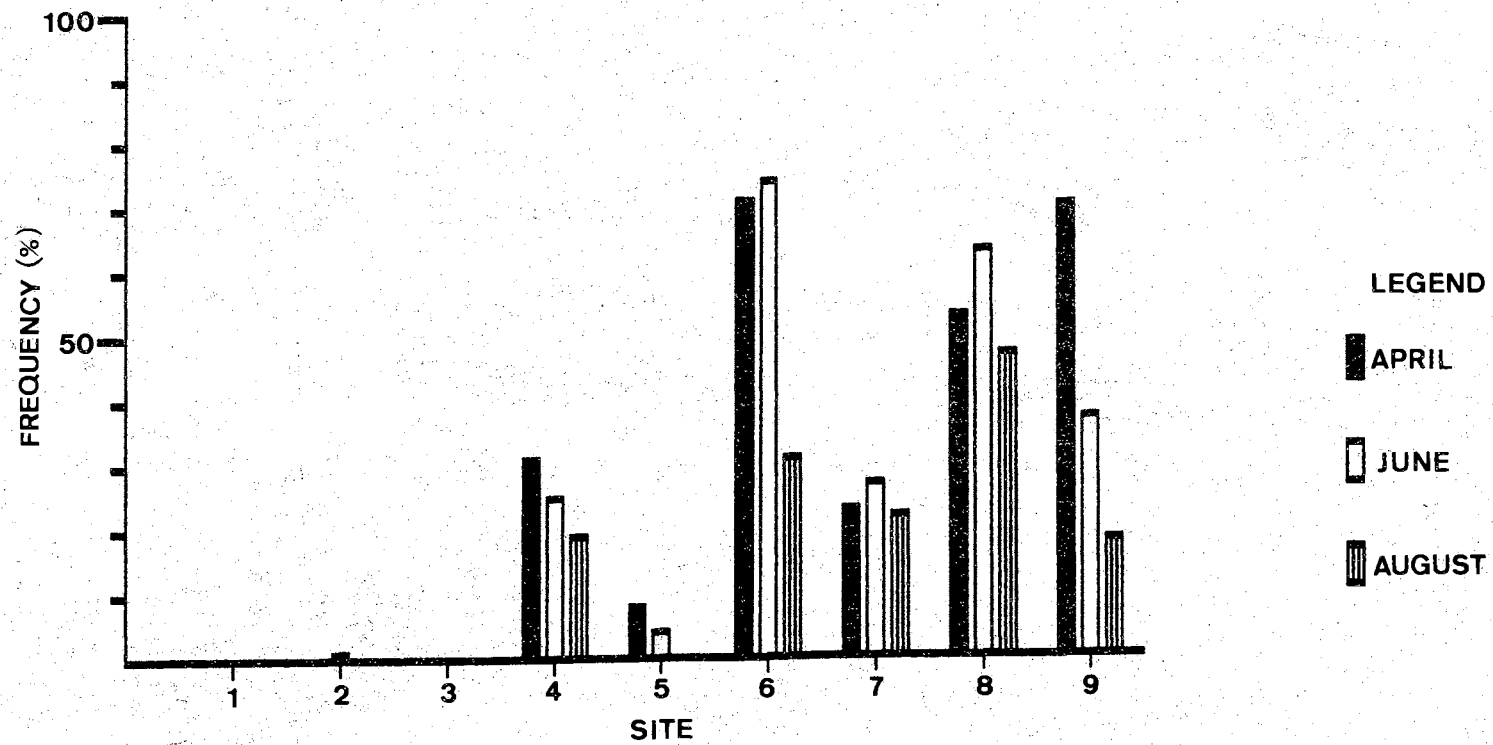
Figure 15. Mean Frequency Distributions for <u>Chenopodium</u>
<u>leptophyllum</u> for All Sites and Sampling
Periods
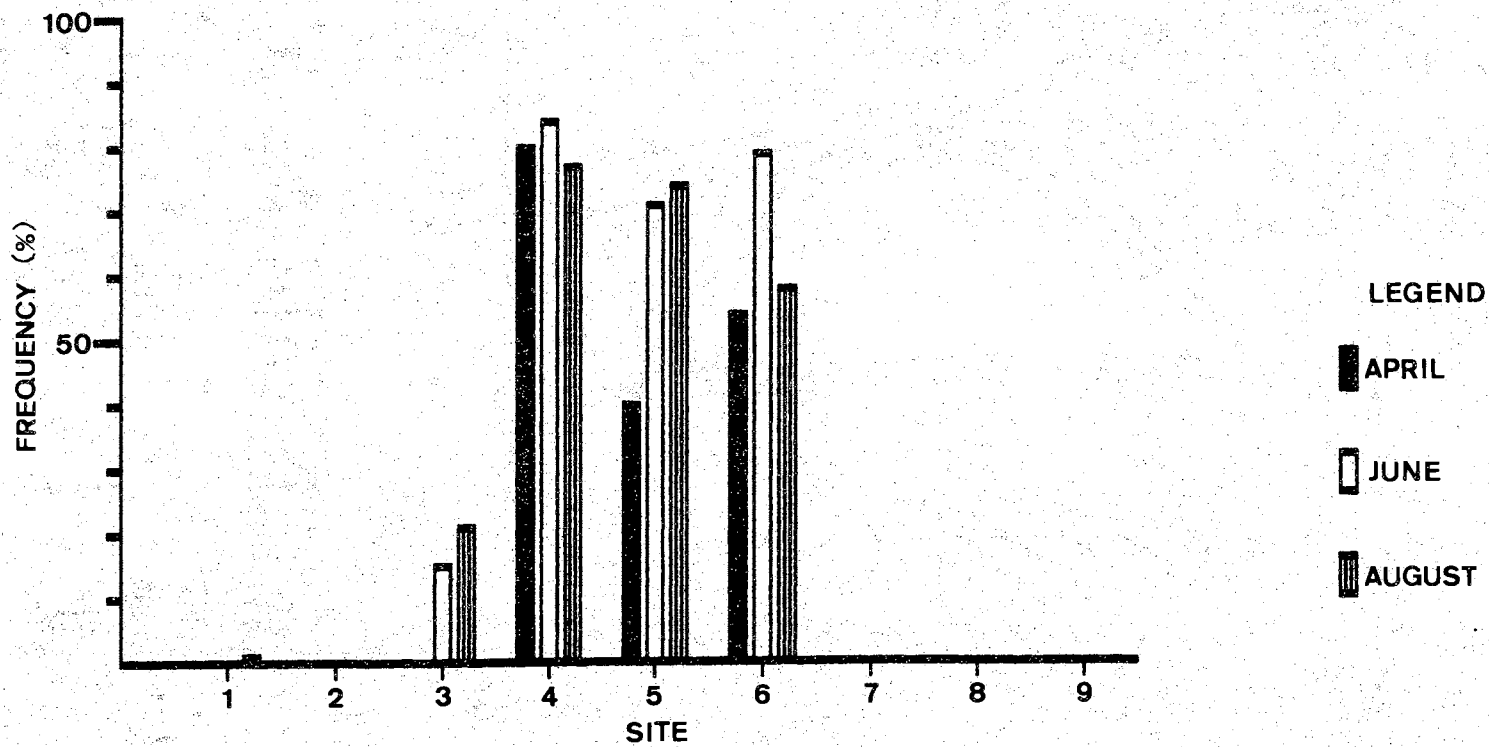
Figure 16.   Mean Frequency Distributions for Croton
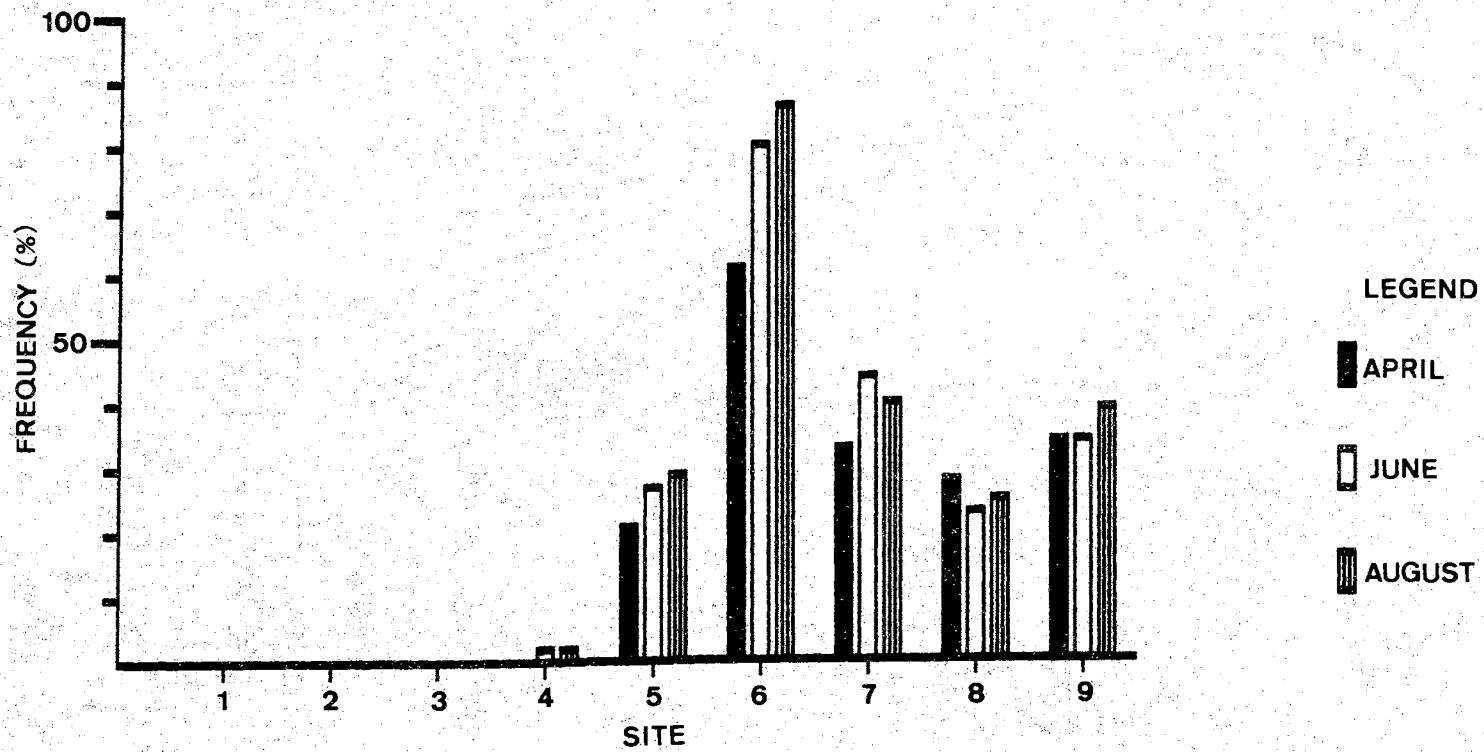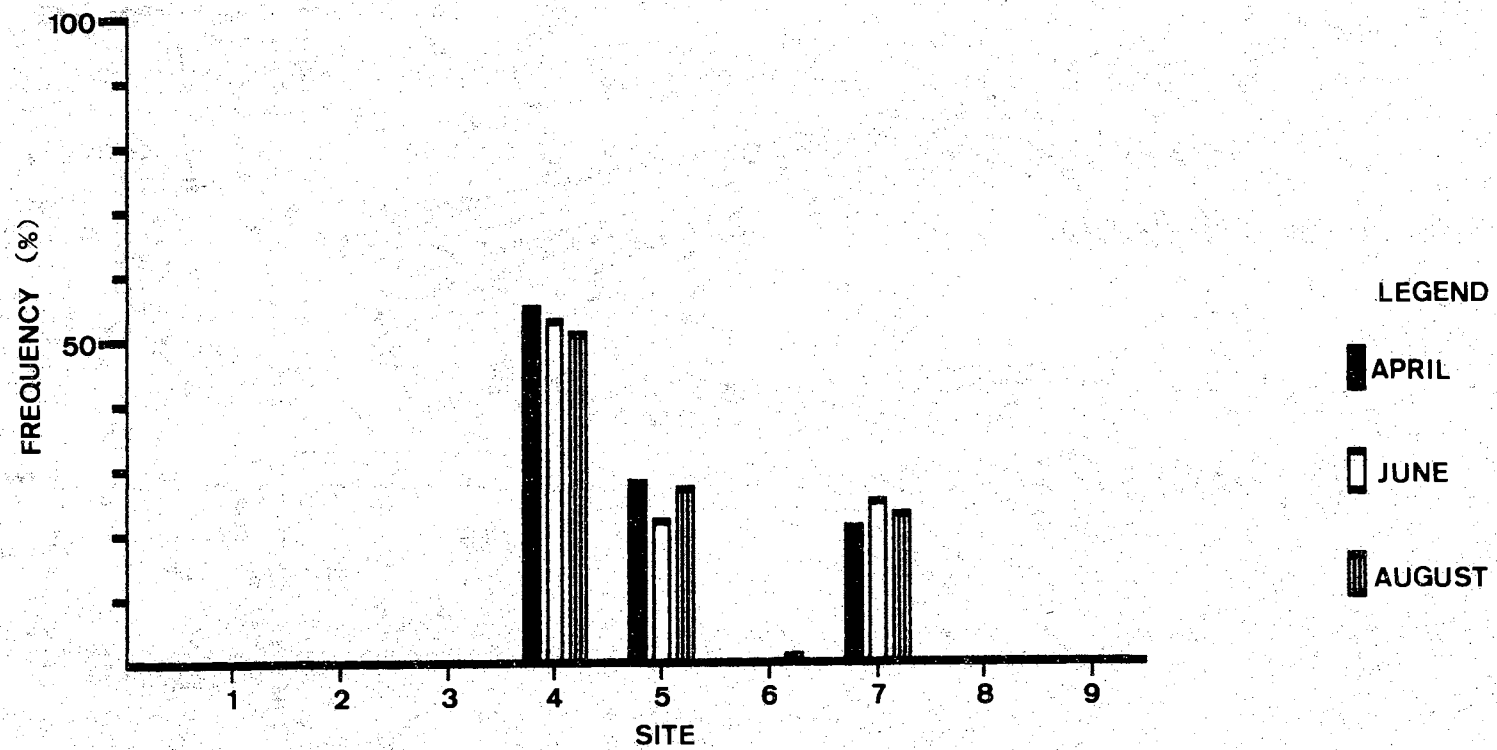             glandulosa for All Sites and Sampling
             Periods
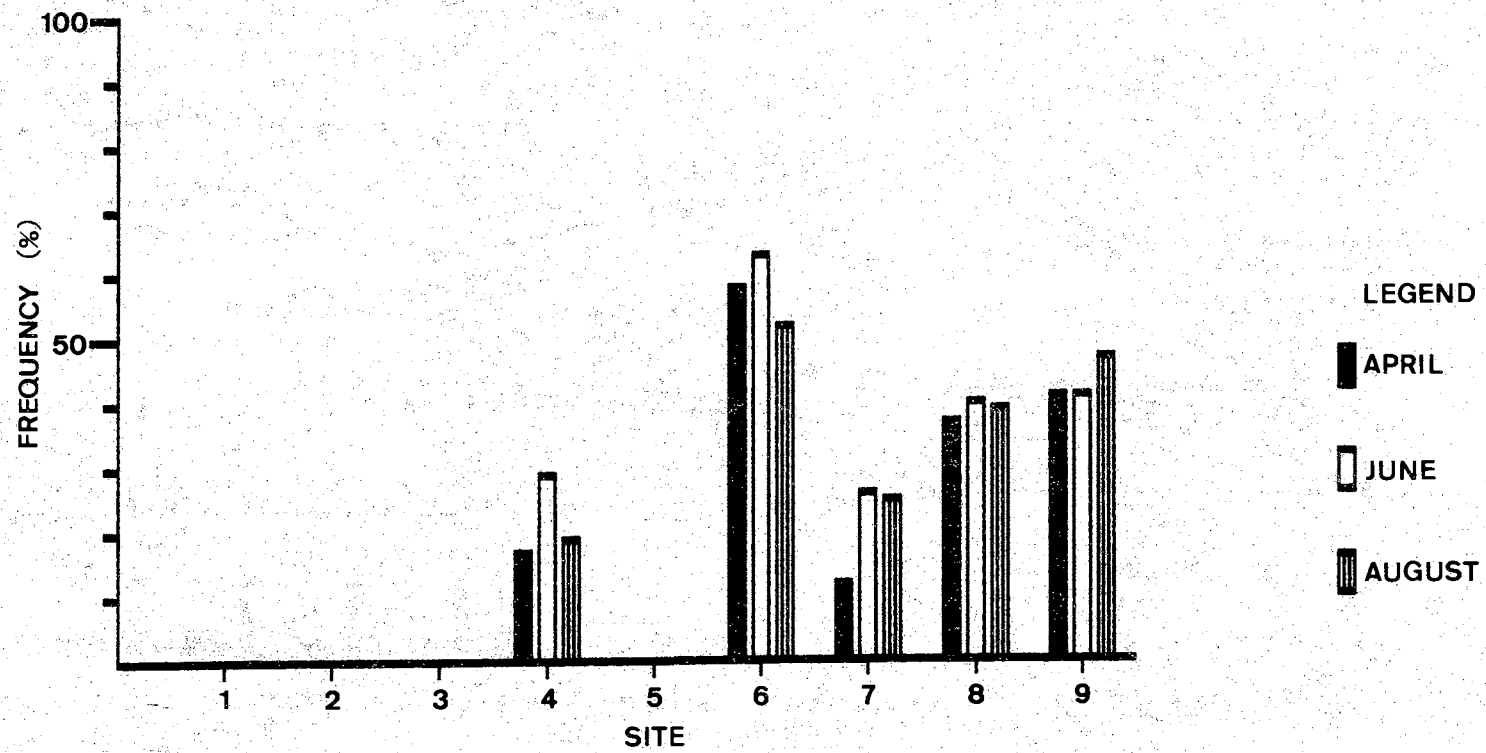
Figure 17. Mean Frequency Distributions for Cyperus
schweinitzii for All Sites and
Sampling Periods
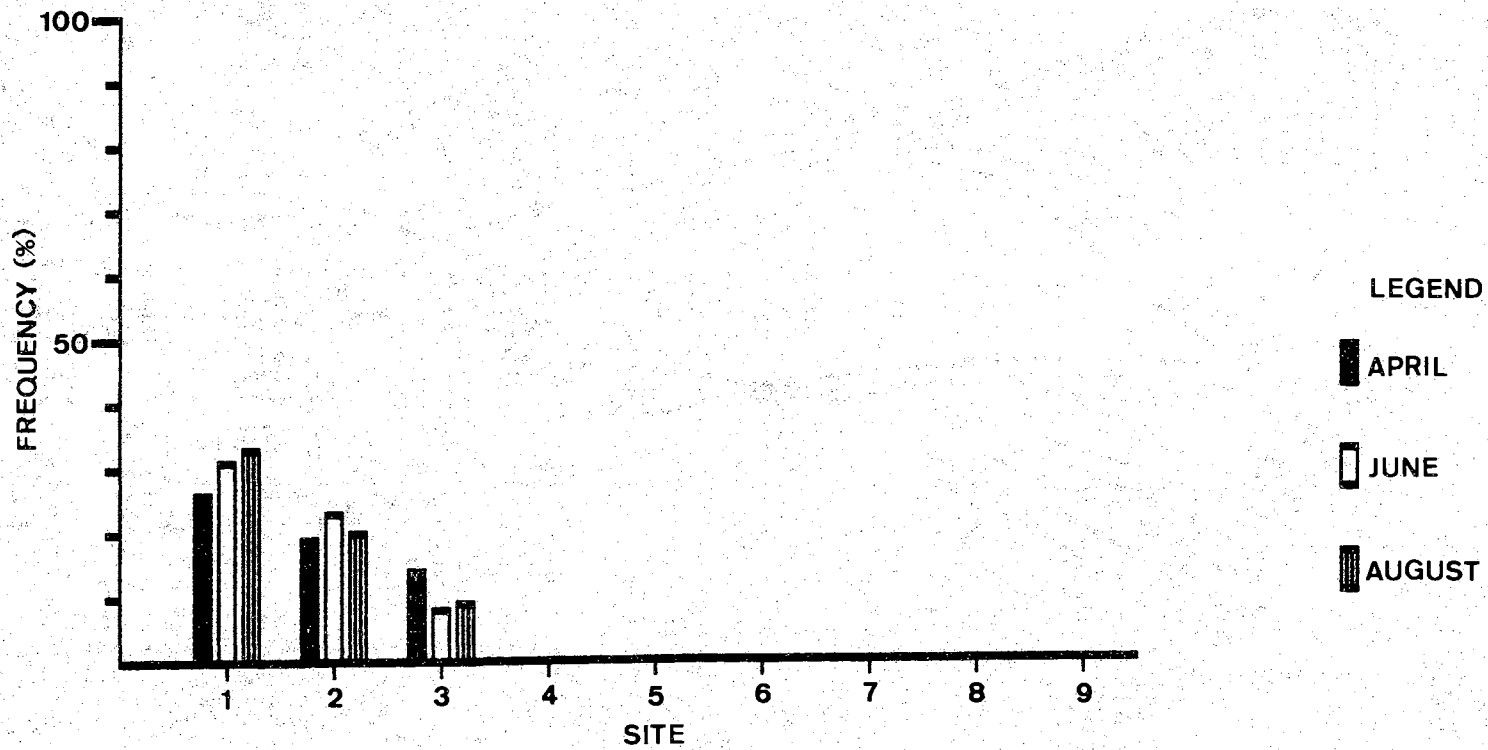
Figure 18. Mean Frequency Distributions for Cyperus spp. for All Sites and Sampling Periods
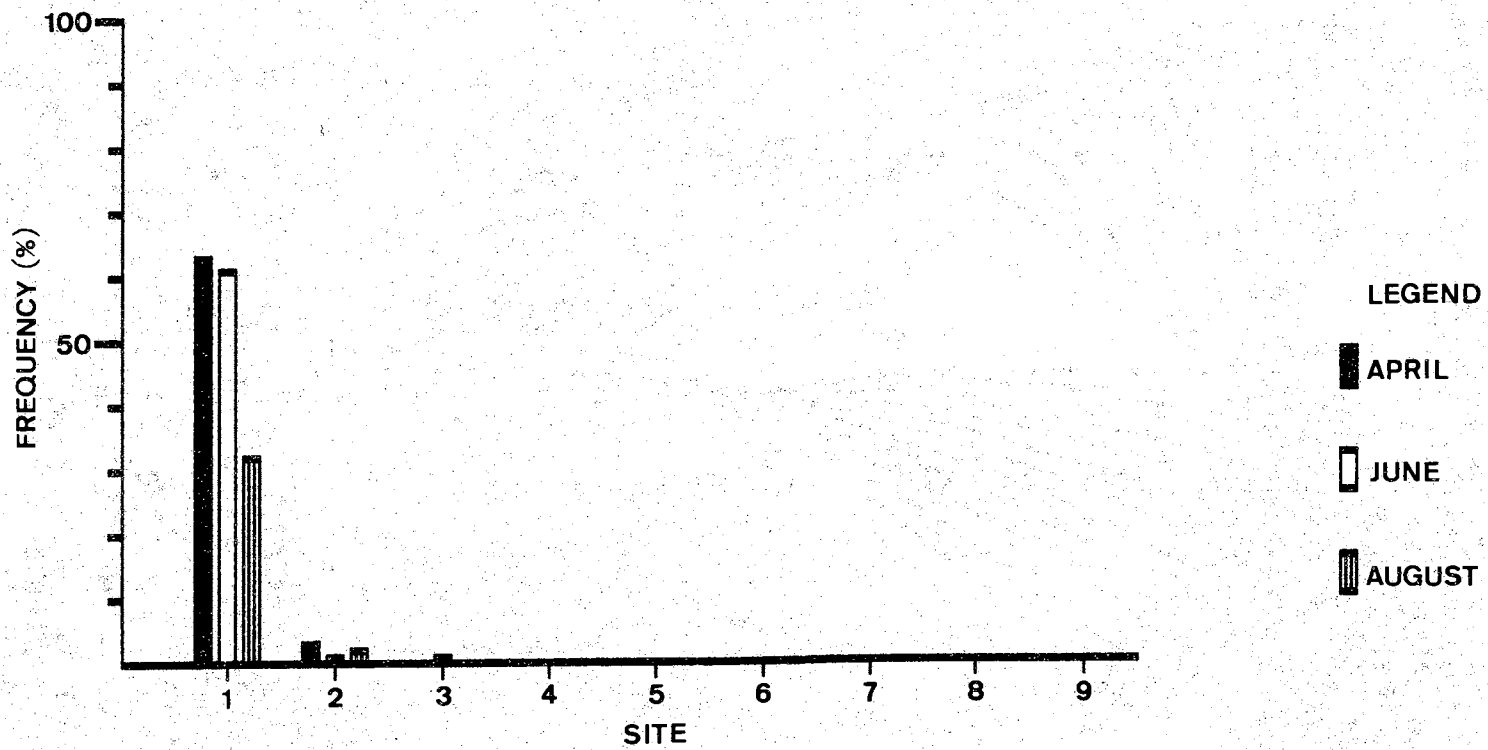
Figure 19. Mean Frequency Distributions for Elymus
virginicus for All Sites and Sampling
Periods

Figure 20. Mean Frequency Distributions for _Eragrostis trichodes_ for All Sites and Sampling Periods

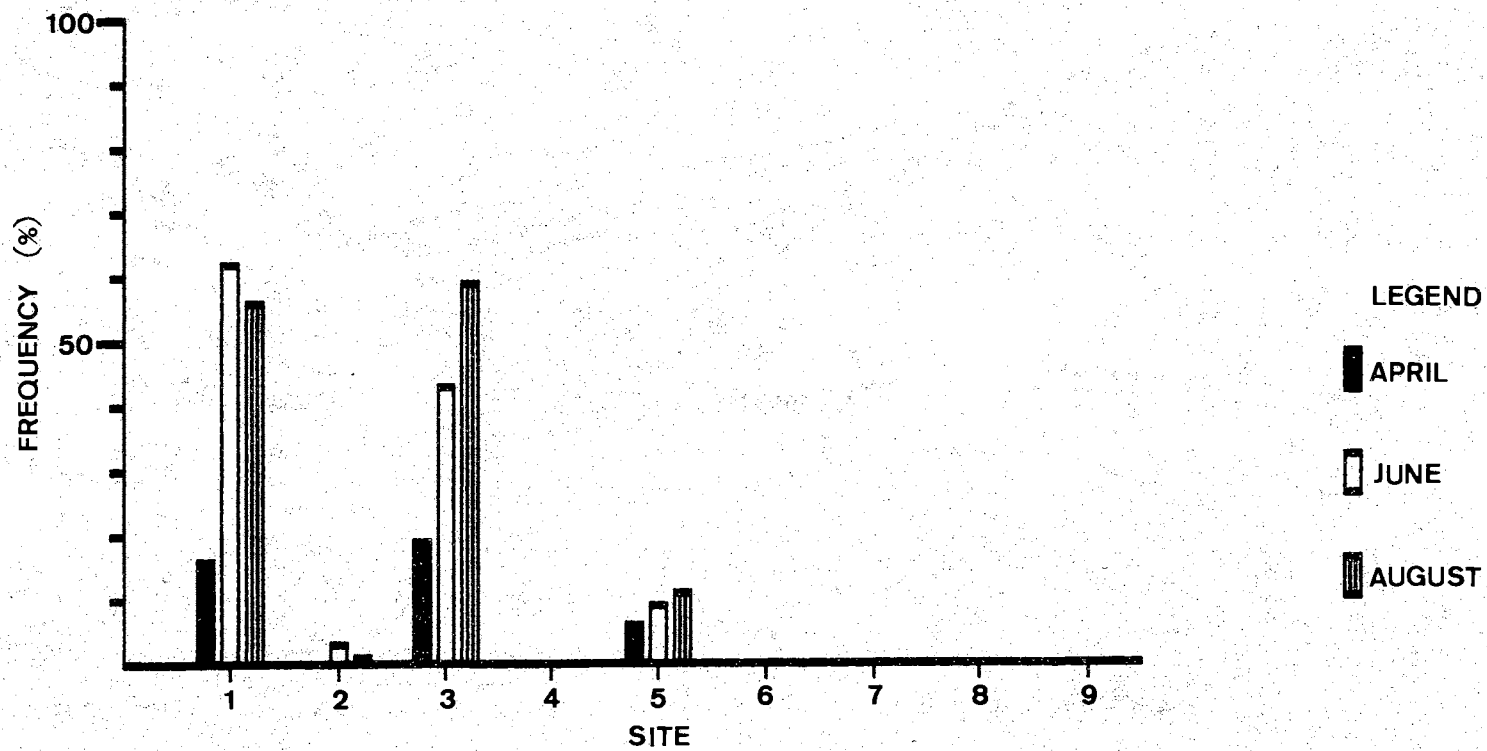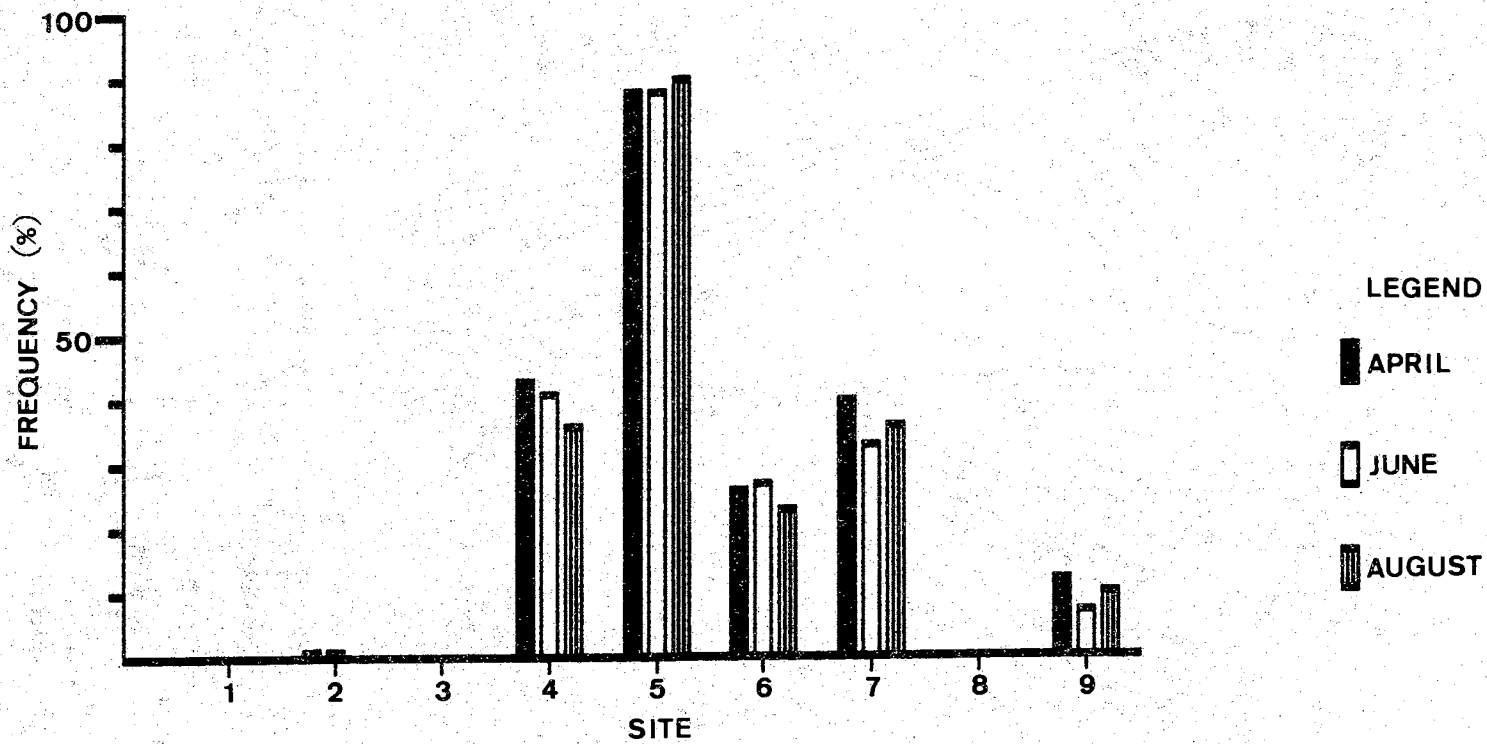Figure 21.   Mean Frequency Distributions for *Eriogonum annum* for All Sites and Sampling Periods

Figure 22. Mean Frequency Distributions for Euphorbia missurica for All Sites and Sampling Periods

Figure 23.   Mean Frequency Distributions for _Galium aparine_ for All Sites and Sampling Periods

Figure 24.  Mean Frequency Distributions for Helianthus
petiolaris for All Sites and Sampling
Periods

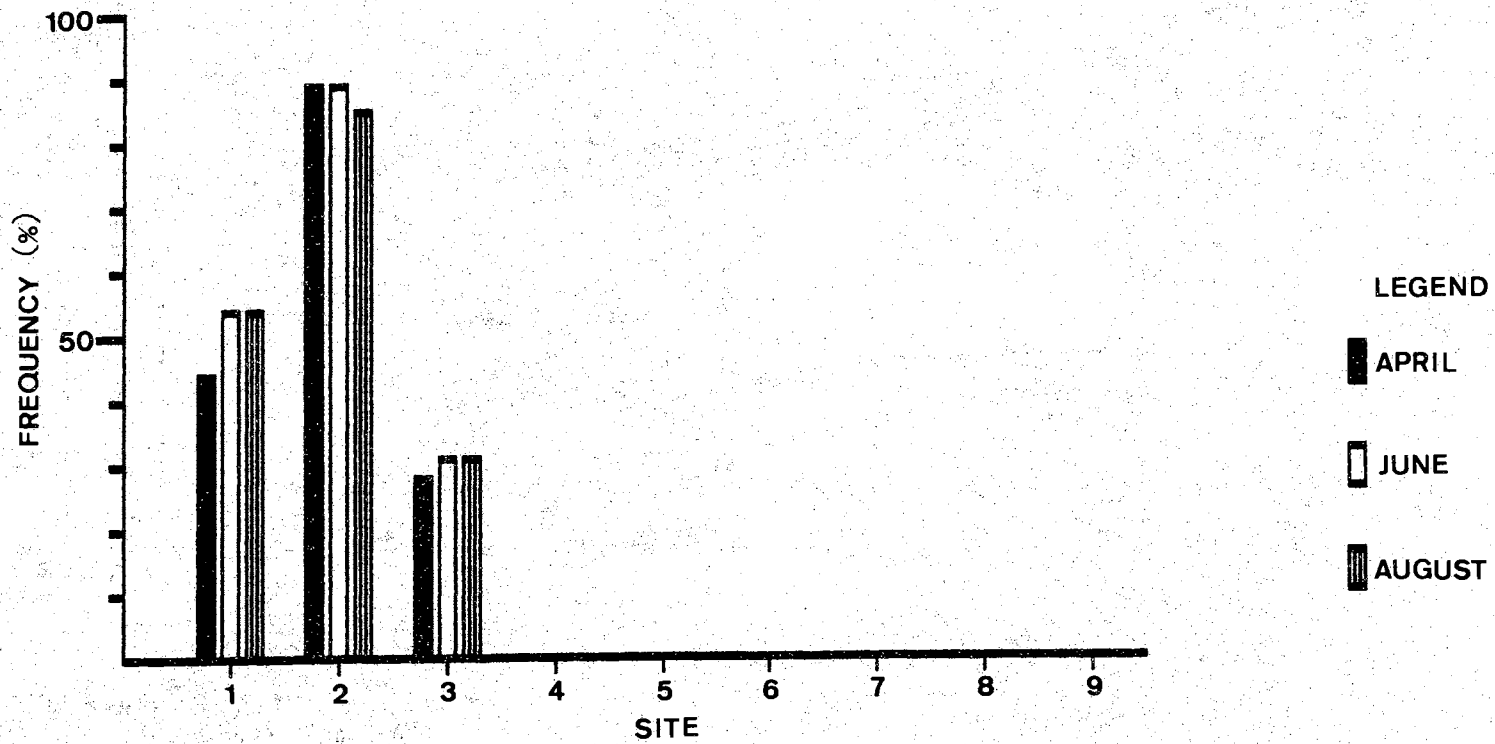Figure 25.   Mean Frequency Distributions for _Juniperus_
             _virginiana_ for All Sites and Sampling
             Periods

Figure 26. Mean Frequency Distributions for _Mentzelia stricta_ for All Sites and Sampling Periods

Figure 27. Mean Frequency Distributions for _Monarda_
_punctata_ for All Sites and Sampling
Periods

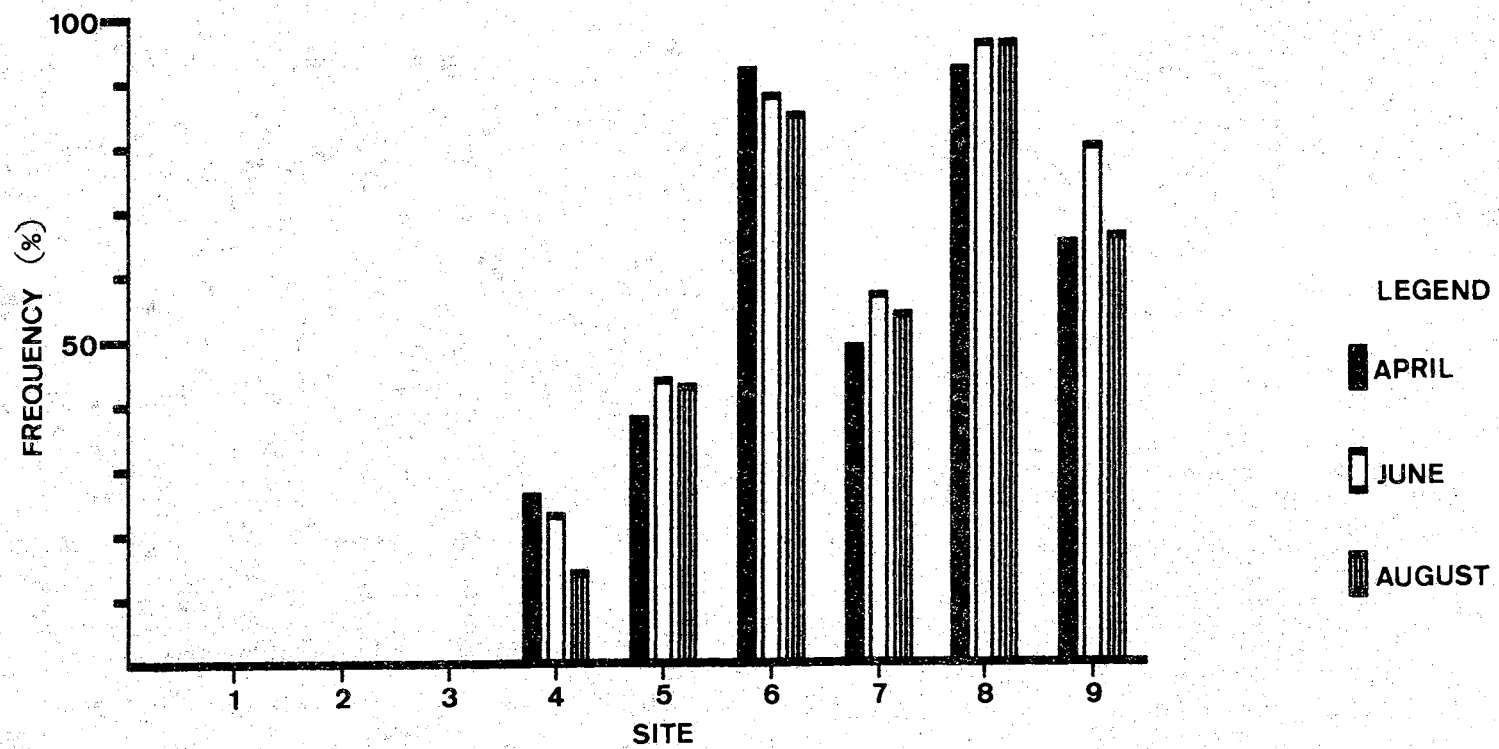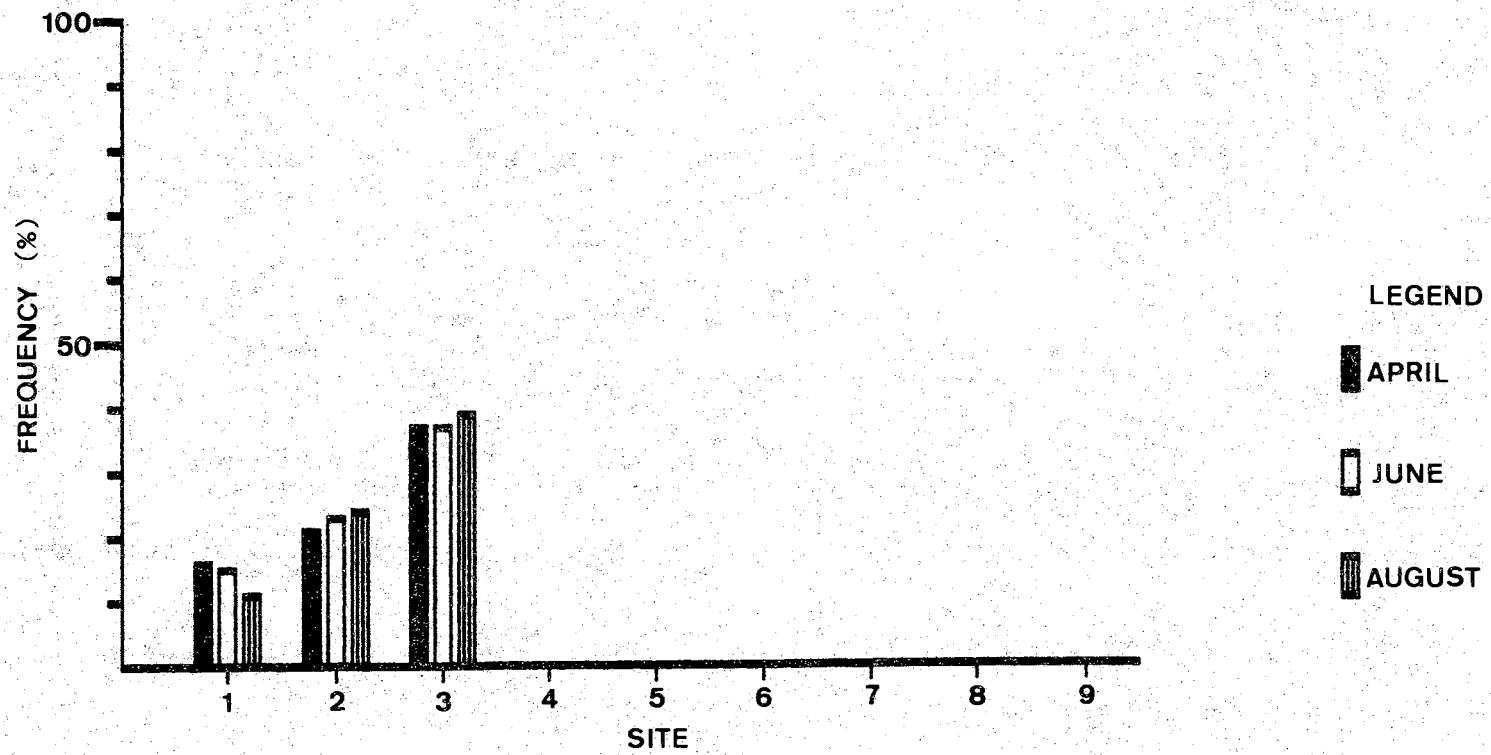Figure 28. Mean Frequency Distributions for _Opuntia_
_macrorhiza_ for All Sites and Sampling
Periods

Figure 29.  Mean Frequency Distributions for _Parietaria_
_pensylvanica_ for All Sites and Sampling
Periods

Figure 30. Mean Frequency Distributions for _Parthenocissus_
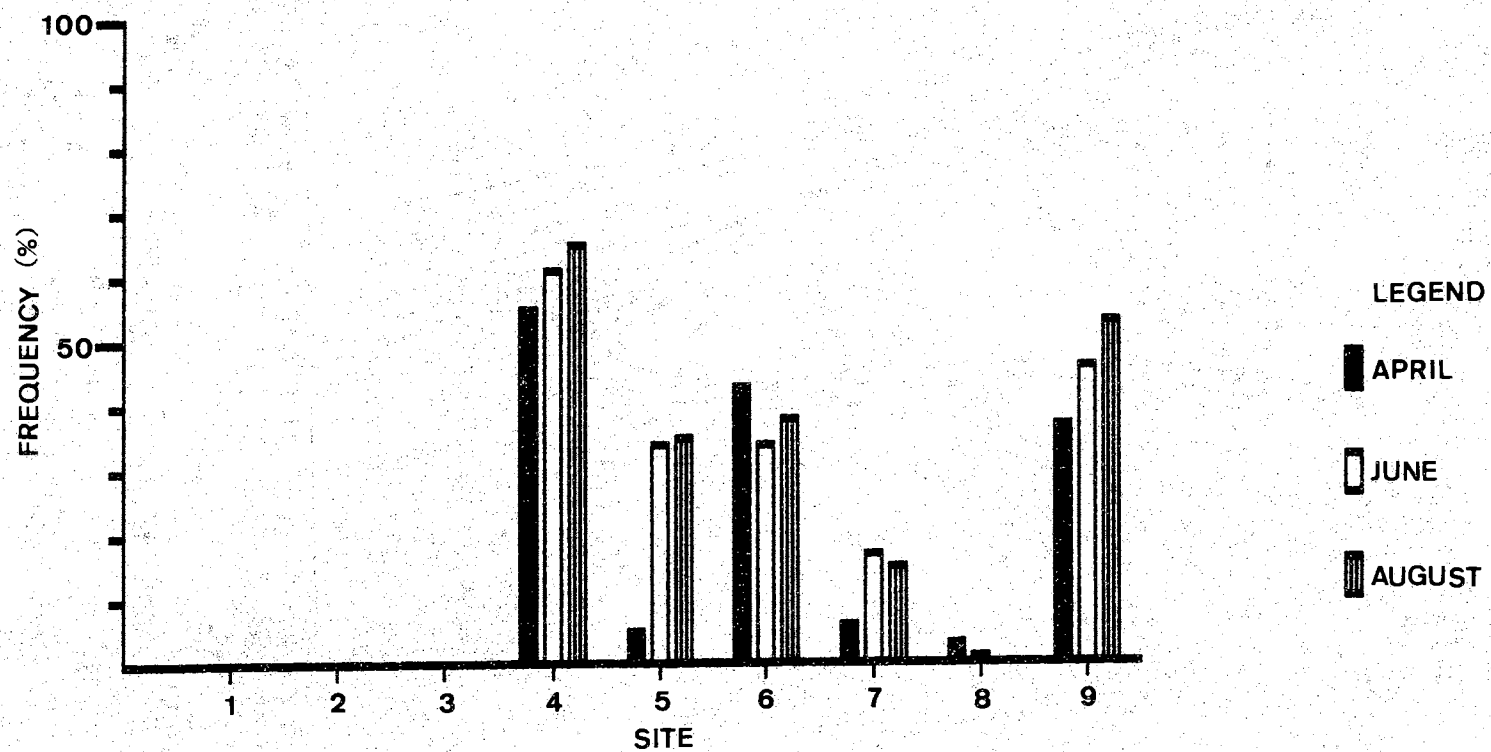_quinquefolia_ for All Sites and Sampling
Periods

Figure 31. Mean Frequency Distributions for Paspalum
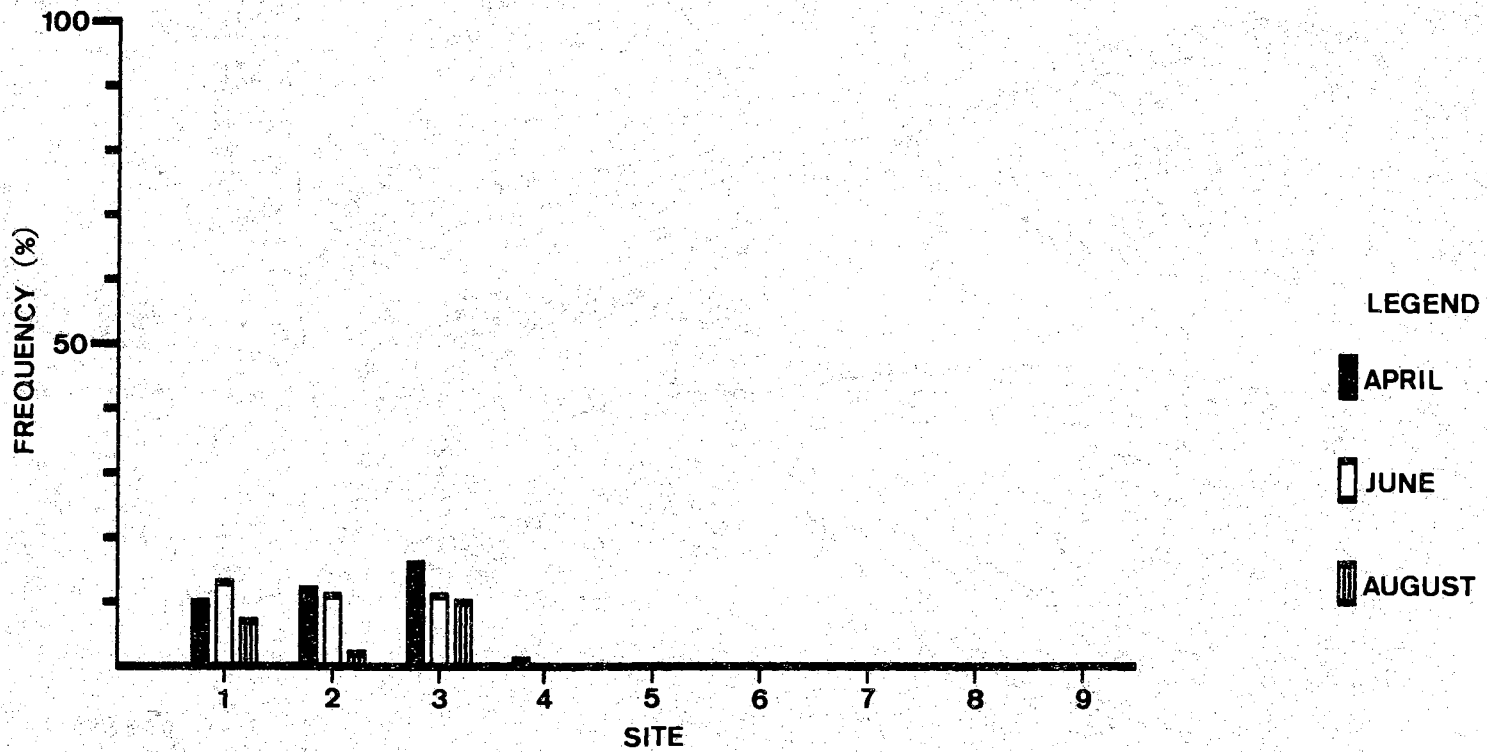setacium for All Sites and Sampling
Periods

Figure 32.   Mean Frequency Distributions for _Rhus_ _aromatica_ for All Sites and Sampling Periods

Figure 33.  Mean Frequency Distributions for Sapindus
            drummondii for All Sites and Sampling
            Periods

Figure 34.   Mean Frequency Distributions for Schizachyrium
scoparium for All Sites and Sampling Periods

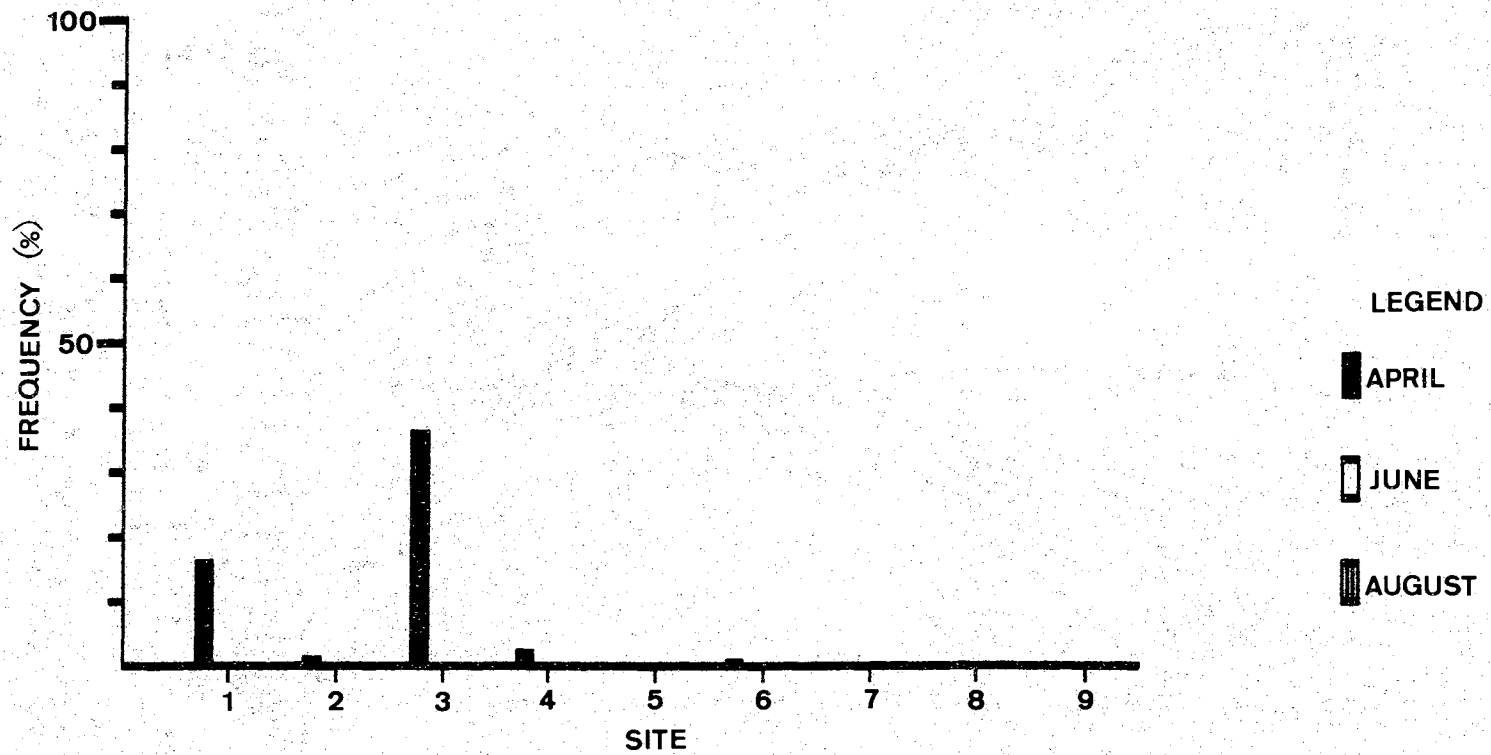Figure 35. Mean Frequency Distributions for *Smilax bona-nox* for All Sites and Sampling Periods

Figure 36.   Mean Frequency Distributions for Sporobolus
             cryptandrus for All Sites and Sampling
             Periods

Figure 37. Mean Frequency Distributions for Symphoricarpos
orbiculatus for All Sites and Sampling Periods

Figure 38. Mean Frequency Distributions for <u>Triplasis</u> <u>purpurea</u> for All Sites and Sampling Periods

Figure 39. Mean Frequency Distributions for Ulmus
americana for All Sites and Sampling
Periods

Figure 40. Mean Frequency Distributions for <u>Viola</u>
<u>rafinesquii</u> for All Sites and
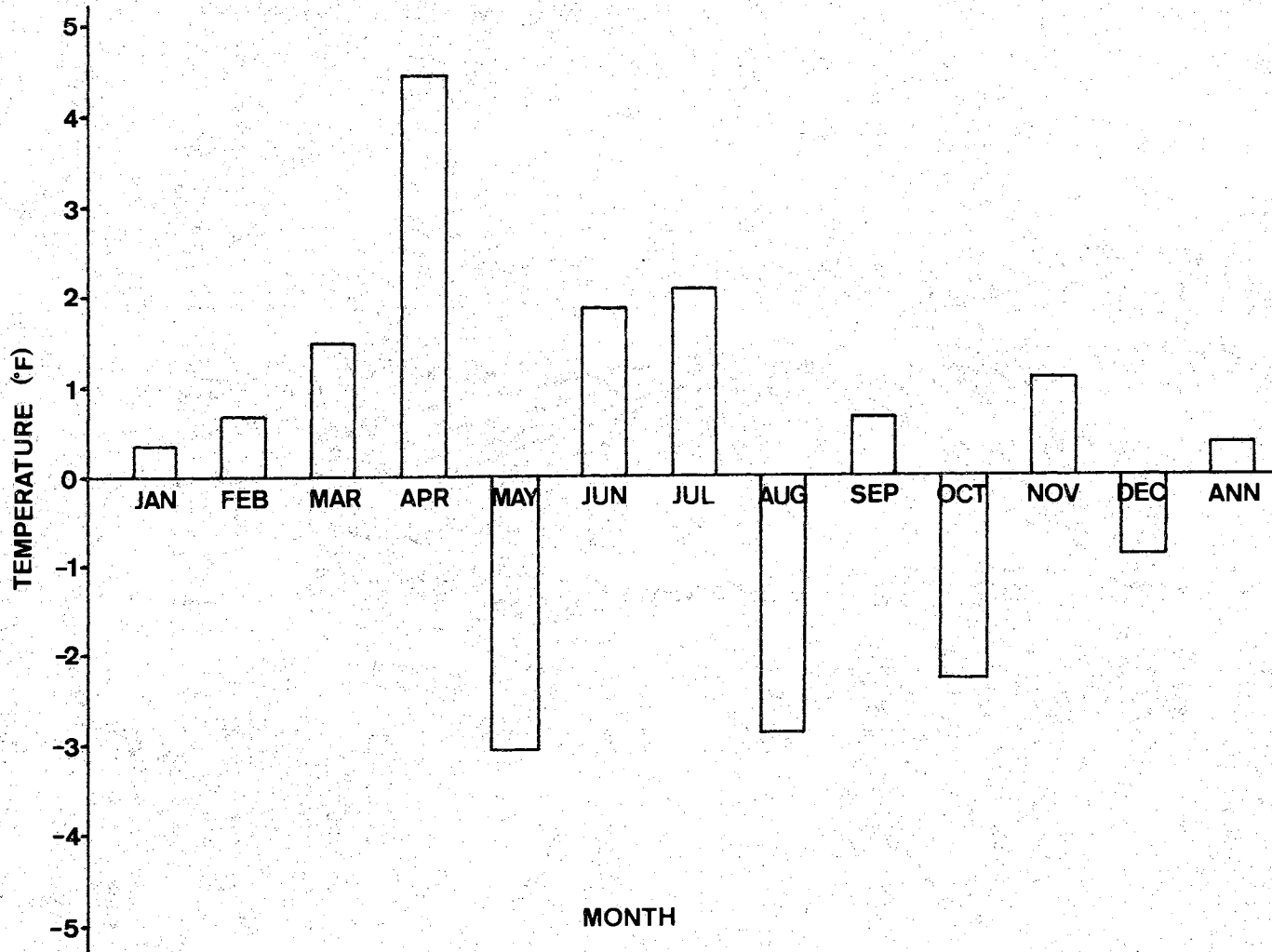Sampling Periods

APPENDIX B


TEMPERATURE DEVIATIONS

Figure 41.   1981 Monthly Temperature Deviations from Normal at Stillwater (Site 1)
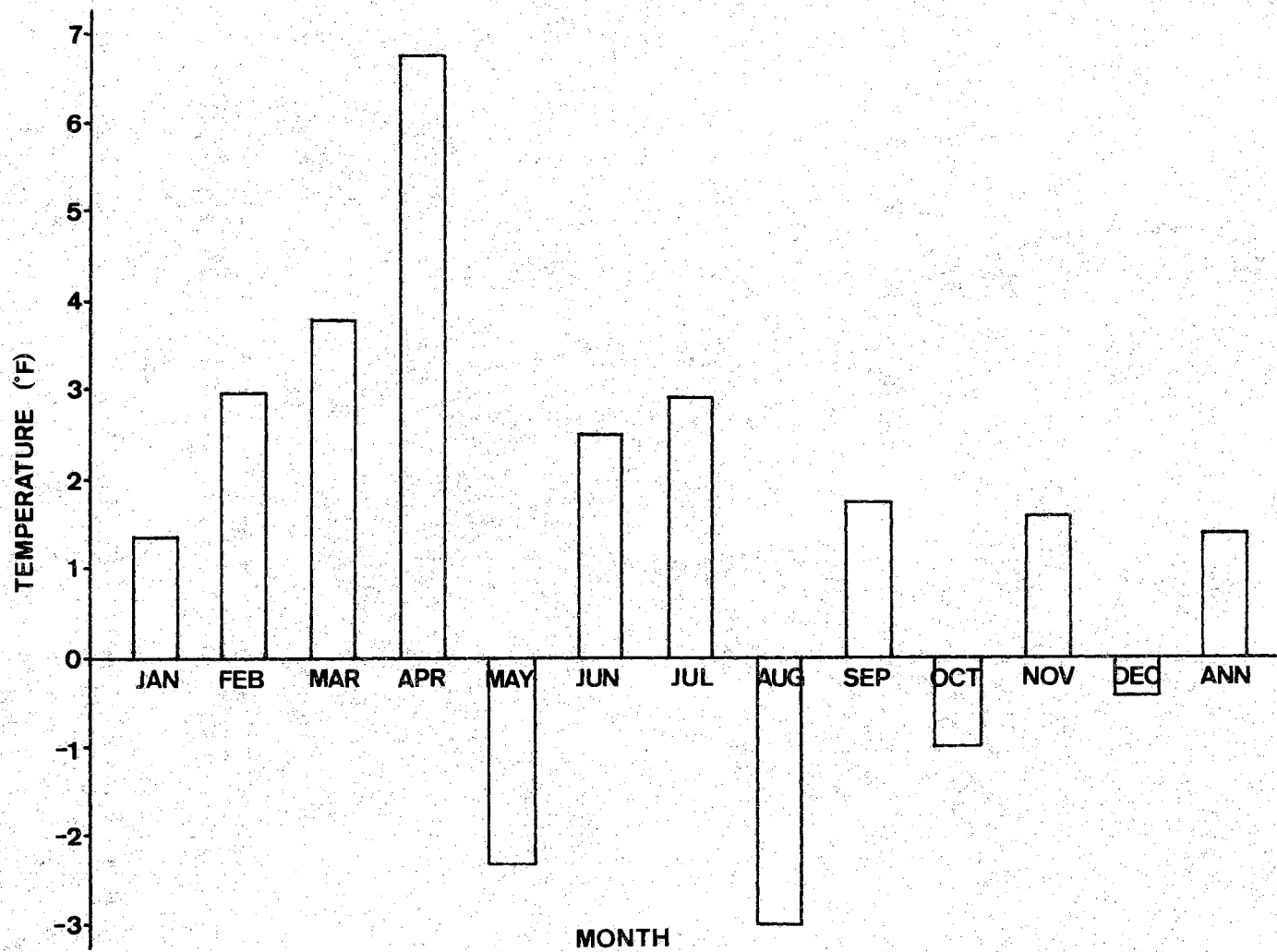
Figure 42.   1981 Monthly Temperature Deviations from Normal
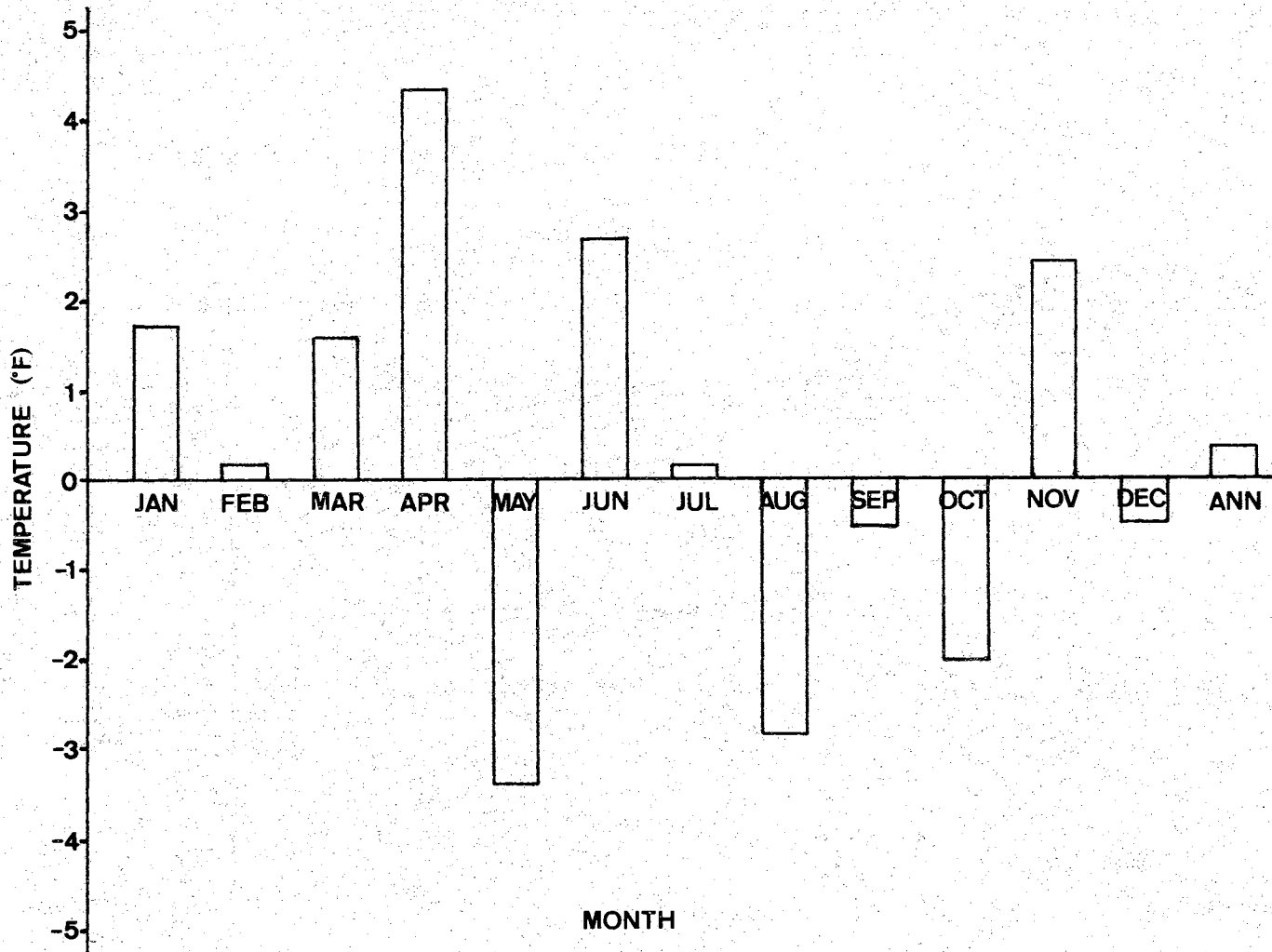at Guthrie (Site 2)

Figure 43. 1981 Monthly Temperature Deviations from Normal at Goodwell (Site 9)

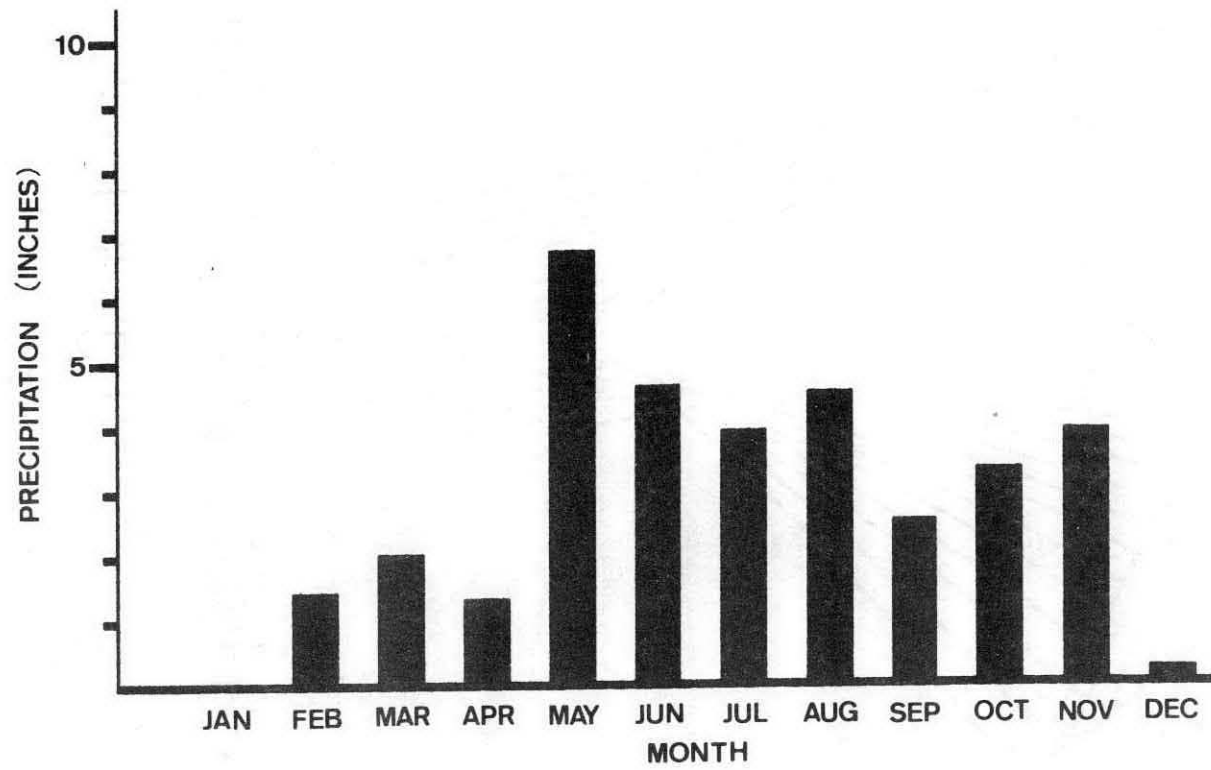APPENDIX C


MONTHLY PRECIPITATIONS

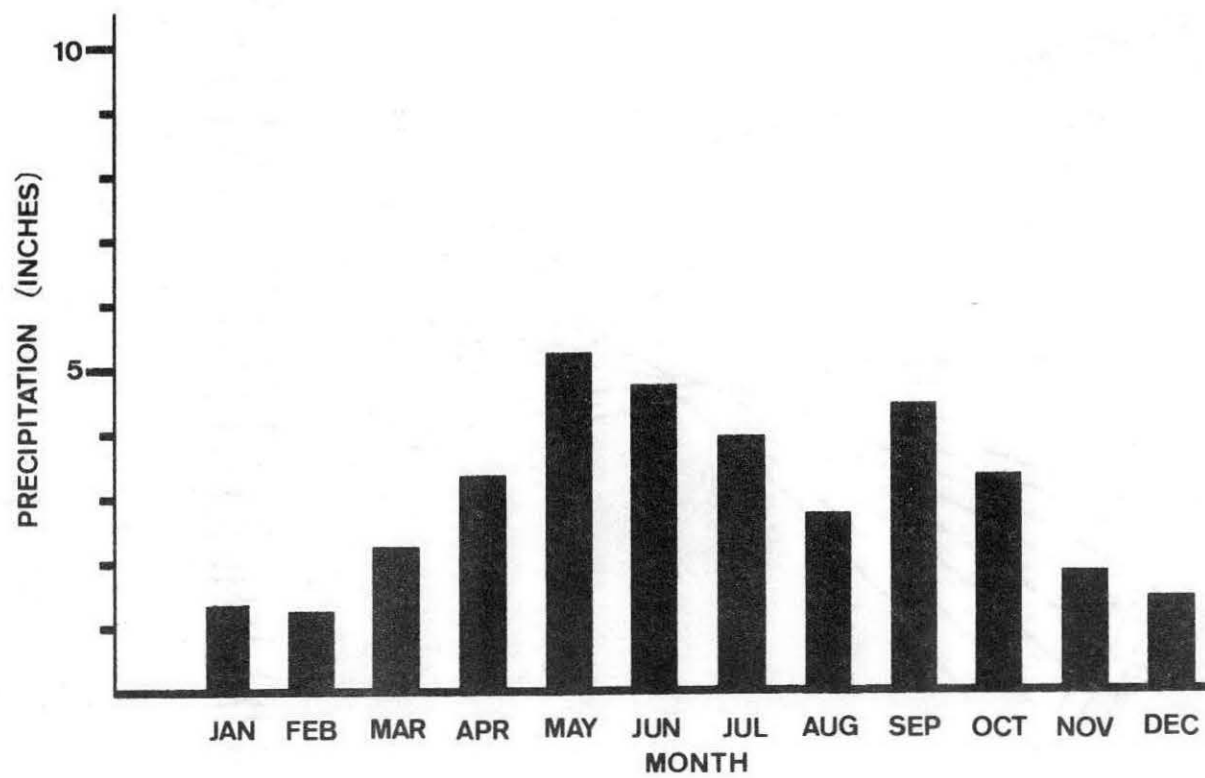Figure 44.  1981 Monthly Precipitation at Perkins (Site 1)

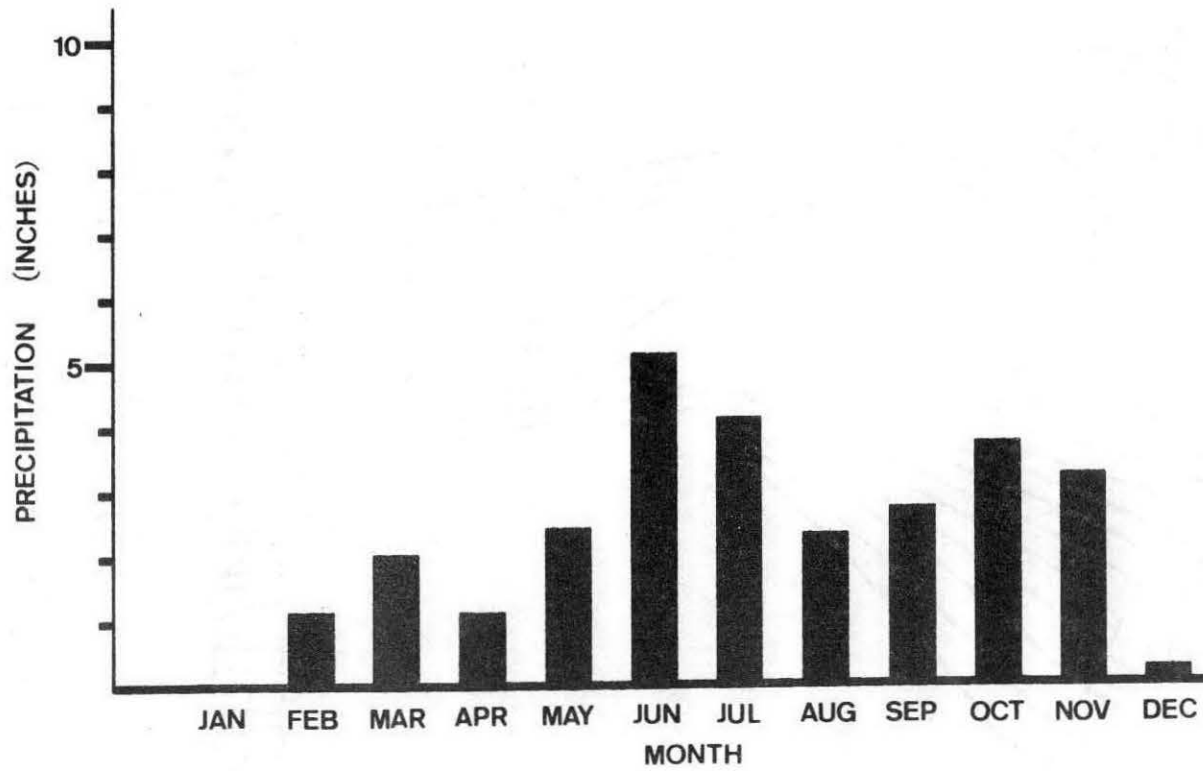Figure 45.  Monthly Normal Precipitation at Perkins (Site 1)

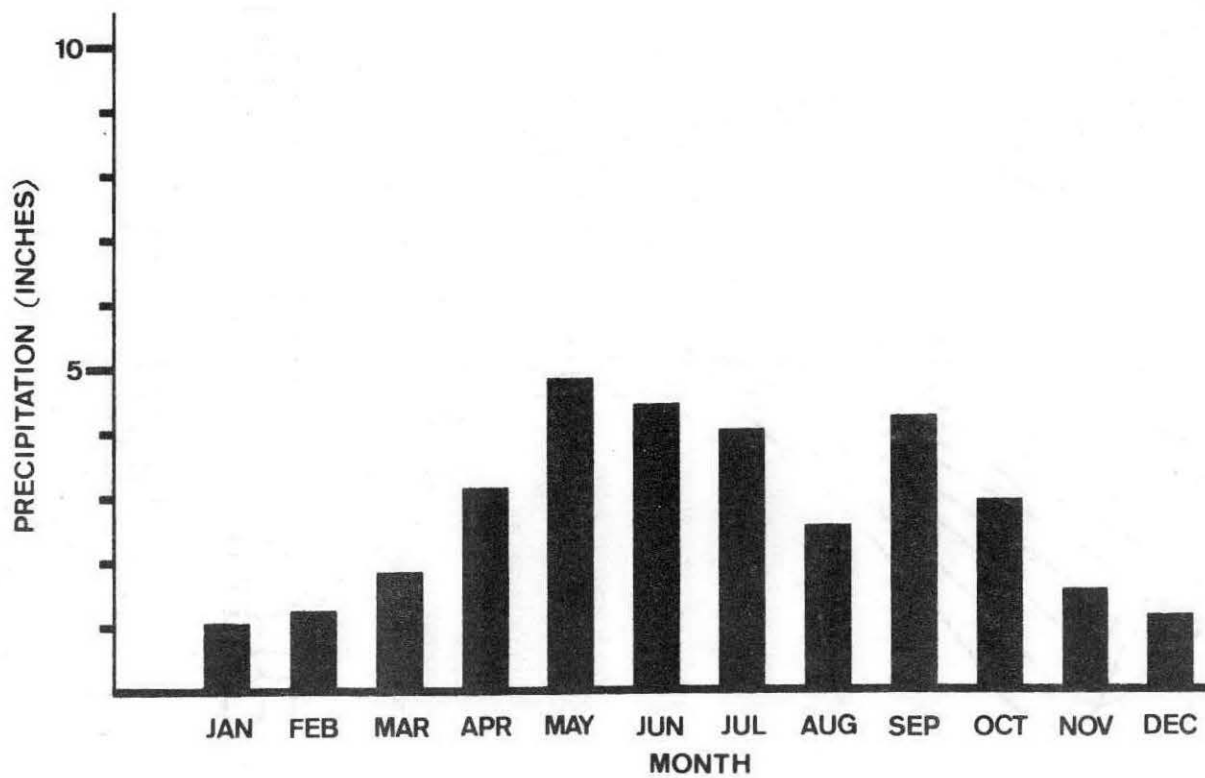Figure 46.  1981 Monthly Precipitation at Guthrie (Site 2)

Figure 47.  Monthly Normal Precipitation at Guthrie (Site 2)
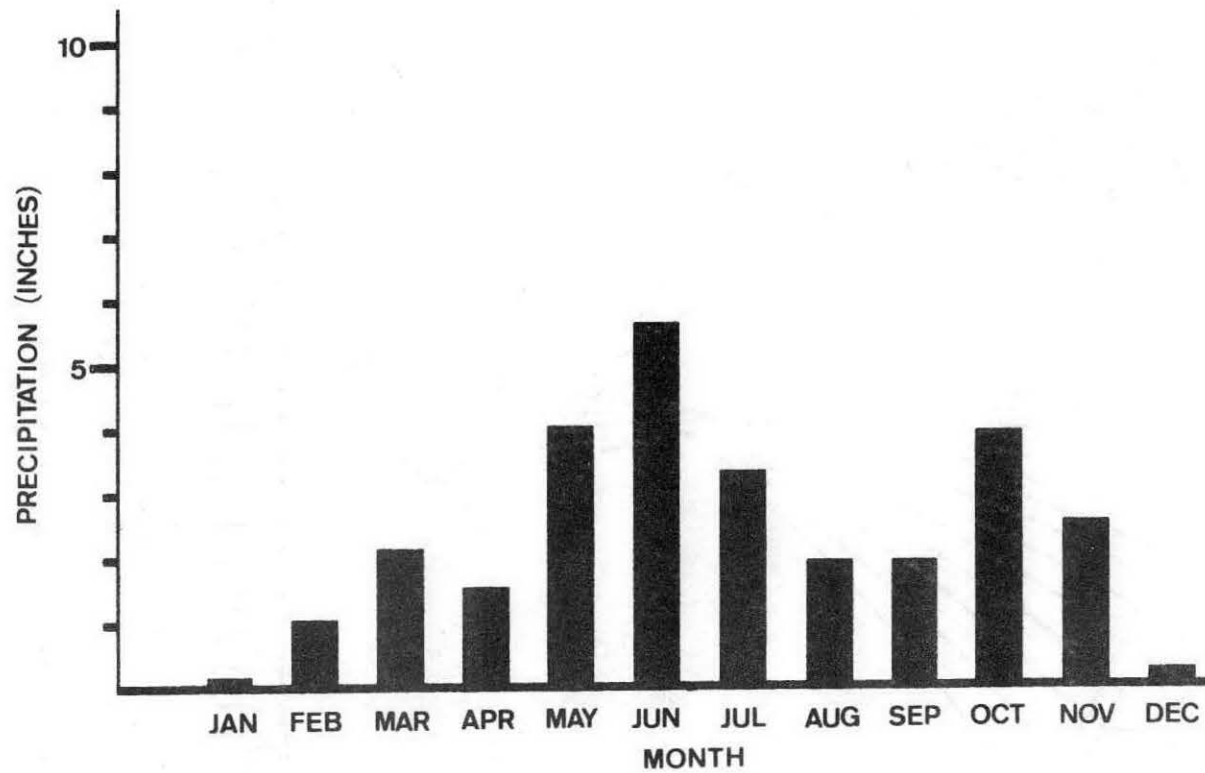
Figure 48.   1981 Monthly Precipitation at Hennessey (Site 3)
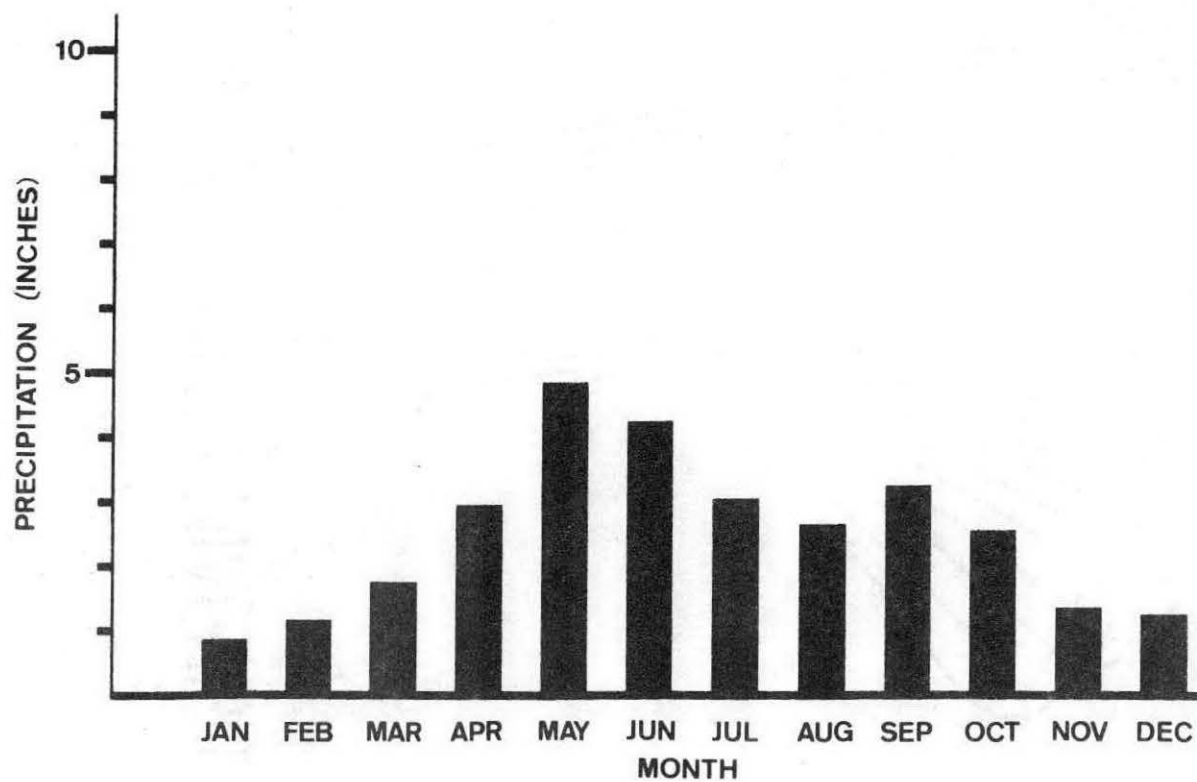
Figure 49. Monthly Normal Precipitation at Hennessey (Site 3)
(20 year average not available from Ames, Site 4.
Hennessey next closest station.)

Figure 50.   1981 Monthly Precipitation at Ames (Site 4)

Figure 51.  1980 Monthly Precipitation at Ames (Site 4)

Figure 52. 1981 Monthly Precipitation at Waynoka (Site 5)

Figure 53.   1980 Monthly Precipitation at Waynoka (Site 5)

Figure 54.  Monthly Normal Precipitation at Waynoka (Site 5)

Figure 55.    1981 Monthly Precipitation at Fort Supply (Site 6)
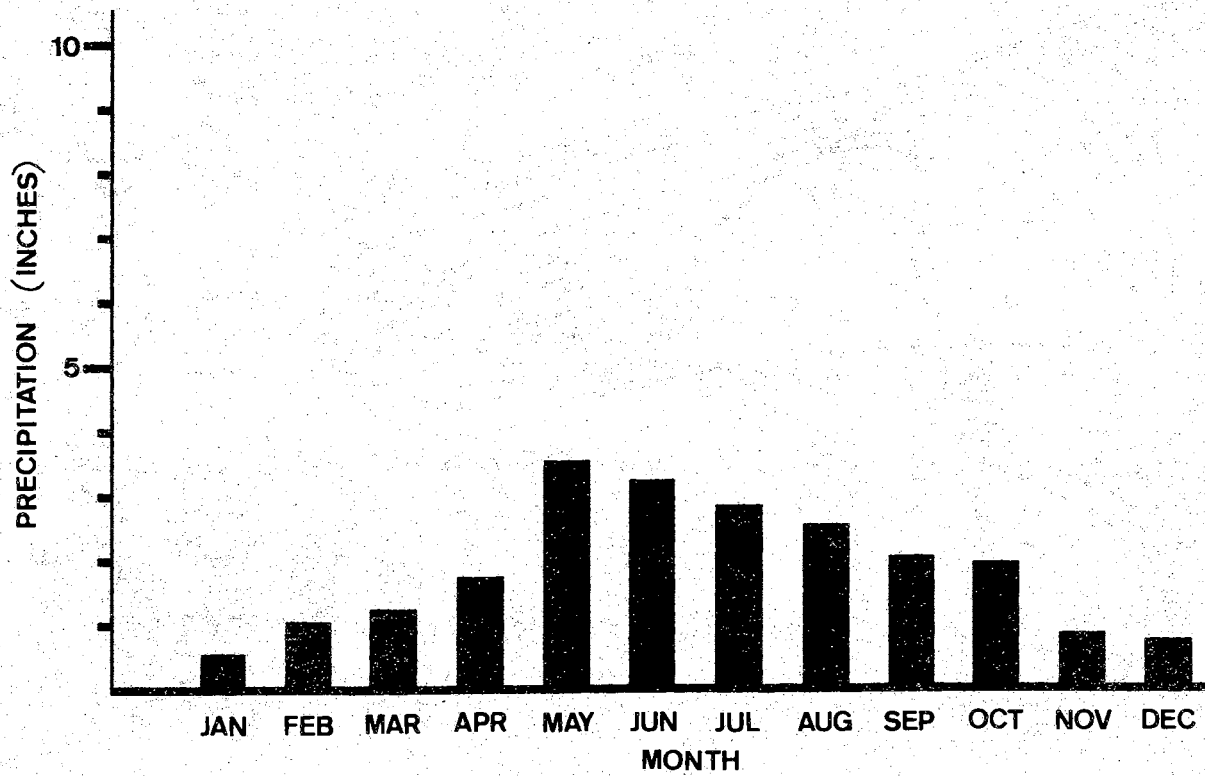
Figure 56.   Monthly Normal Precipitation at Fort Supply (Site 6)
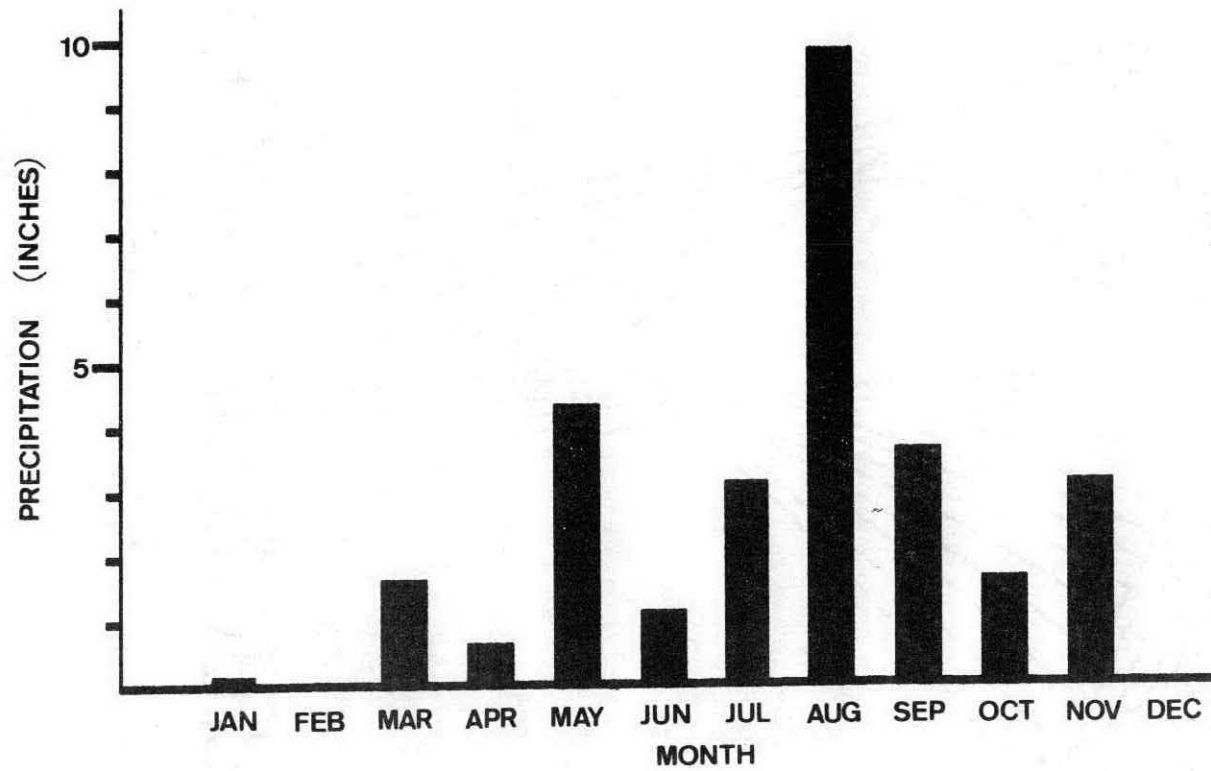
Figure 57. 1981 Monthly Precipitation at Gate (Site 7)
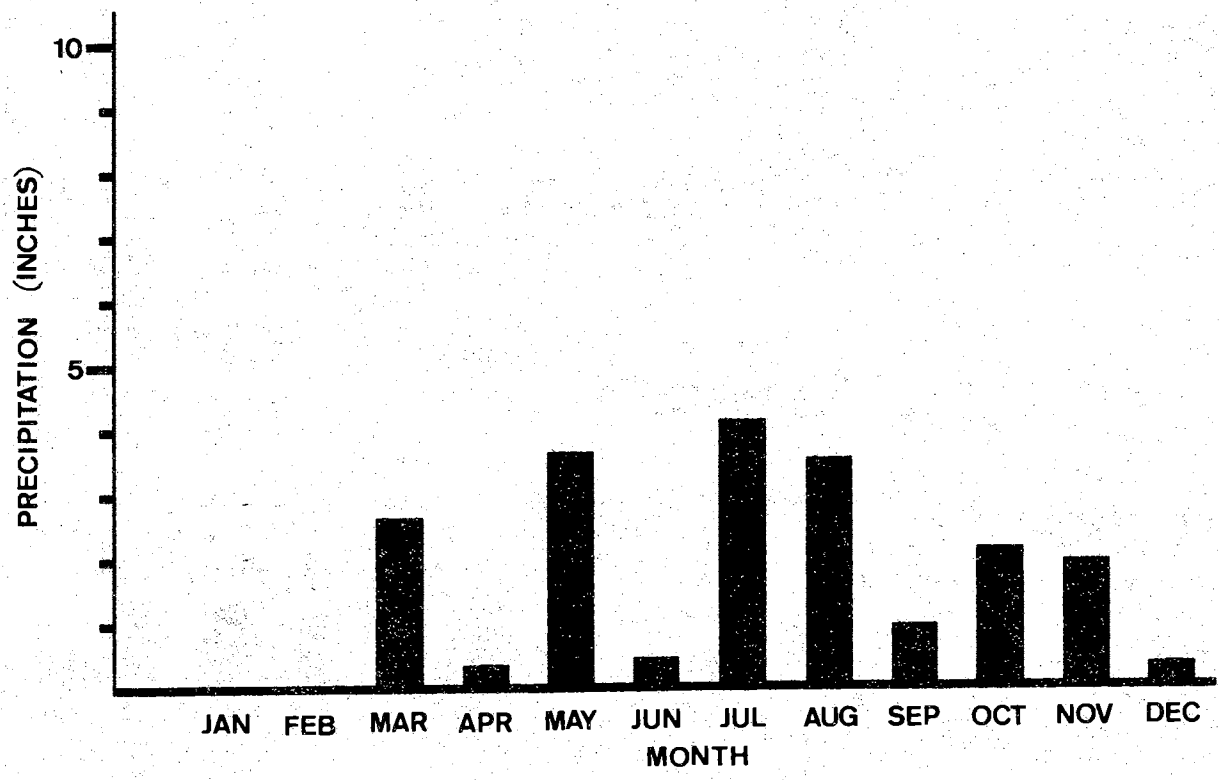
Figure 58.   1981 Monthly Precipitation at Beaver (Site 8)
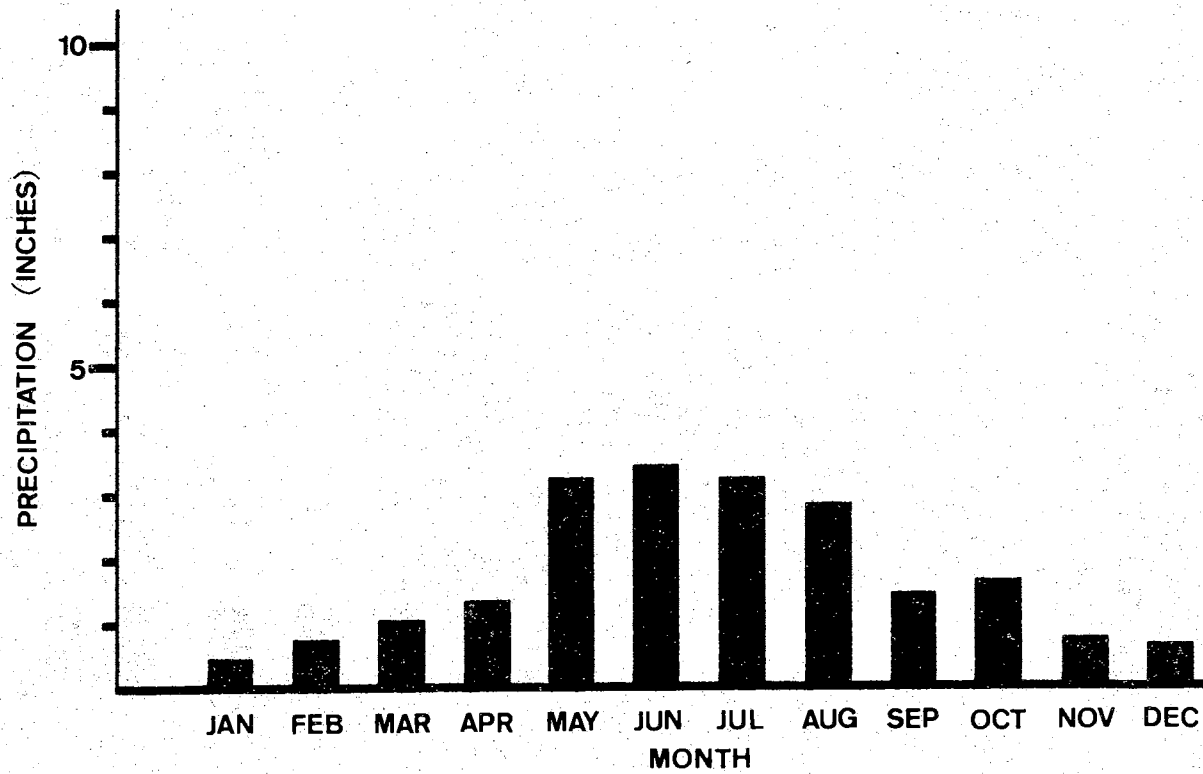
Figure 59.  Monthly Normal Precipitation at Beaver (Site 8)
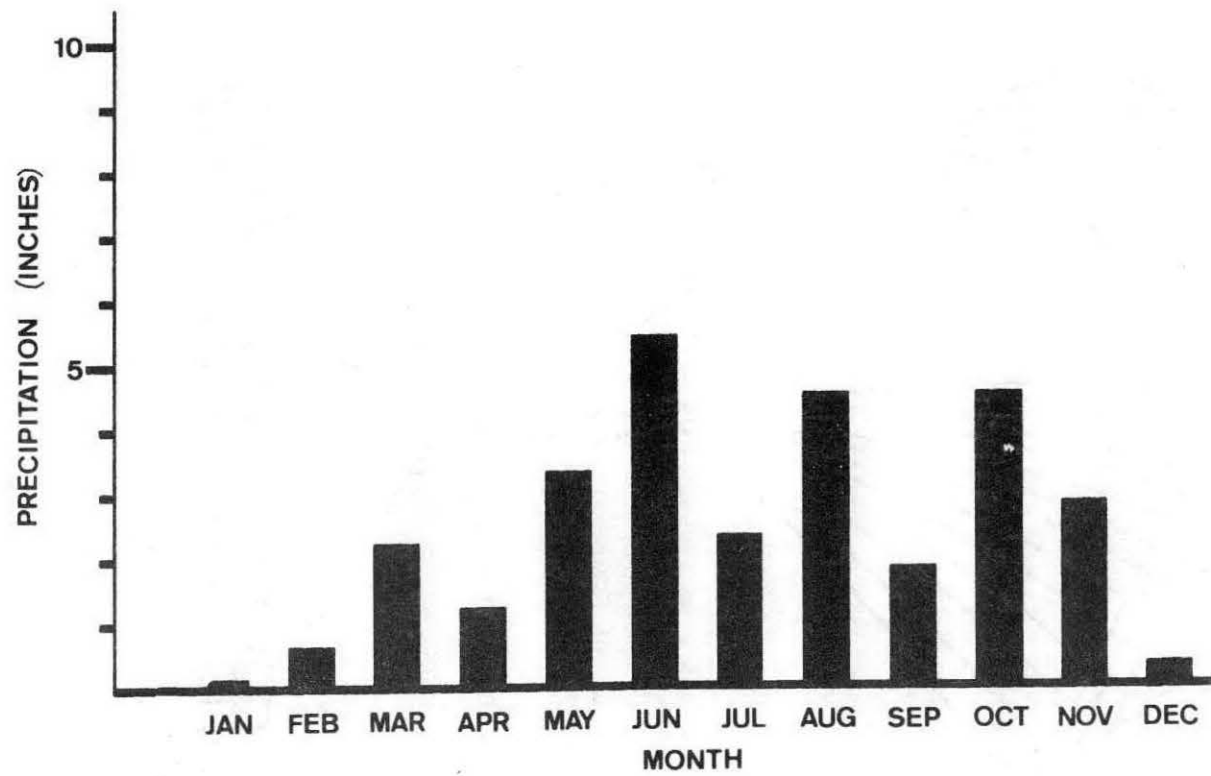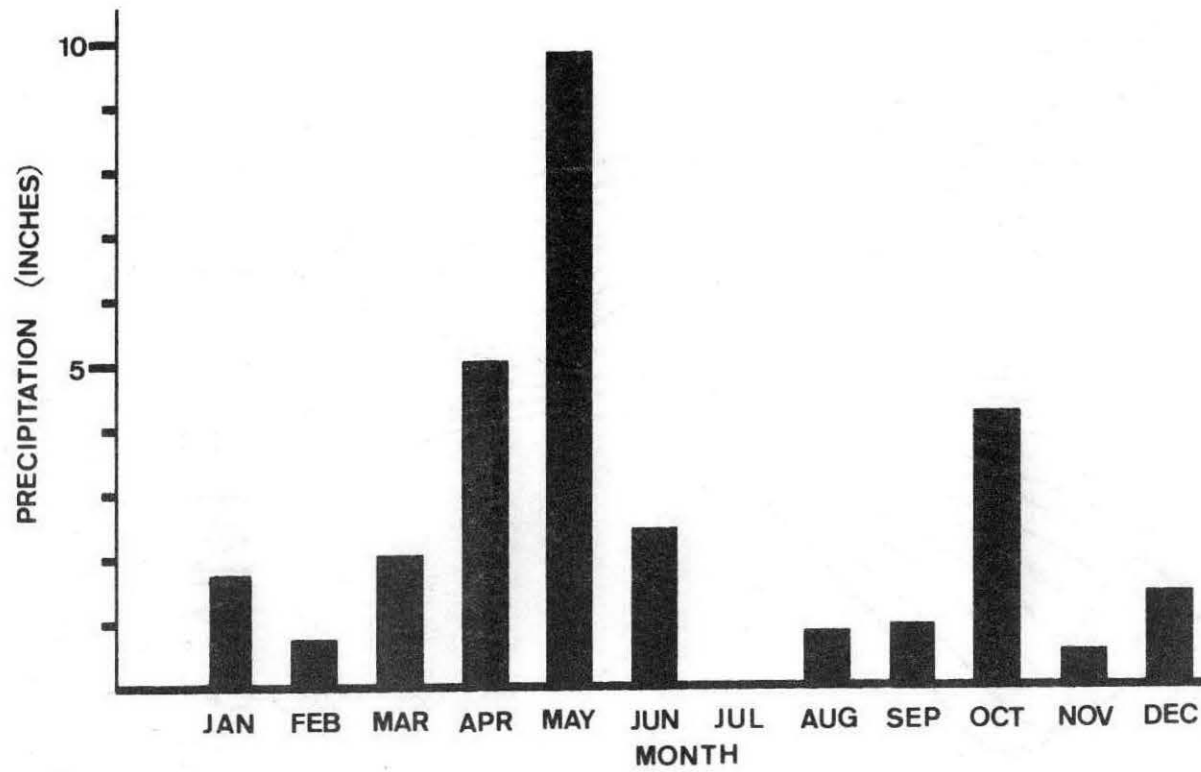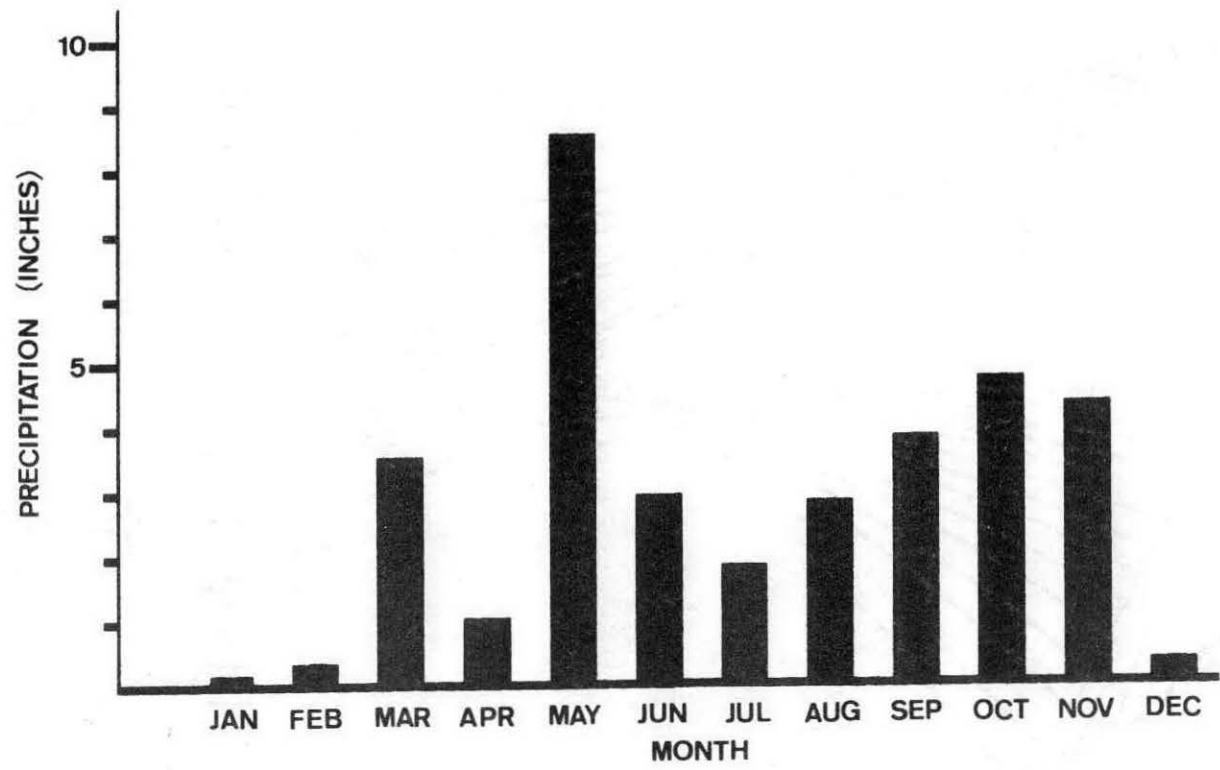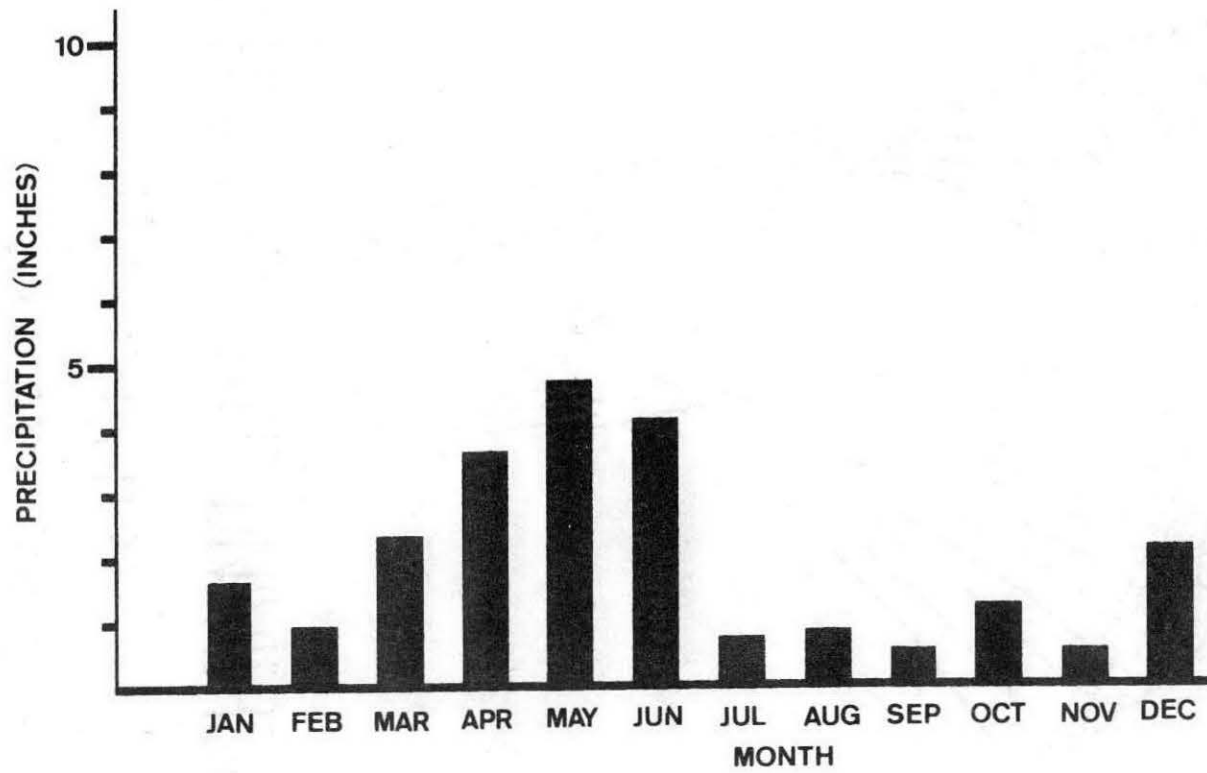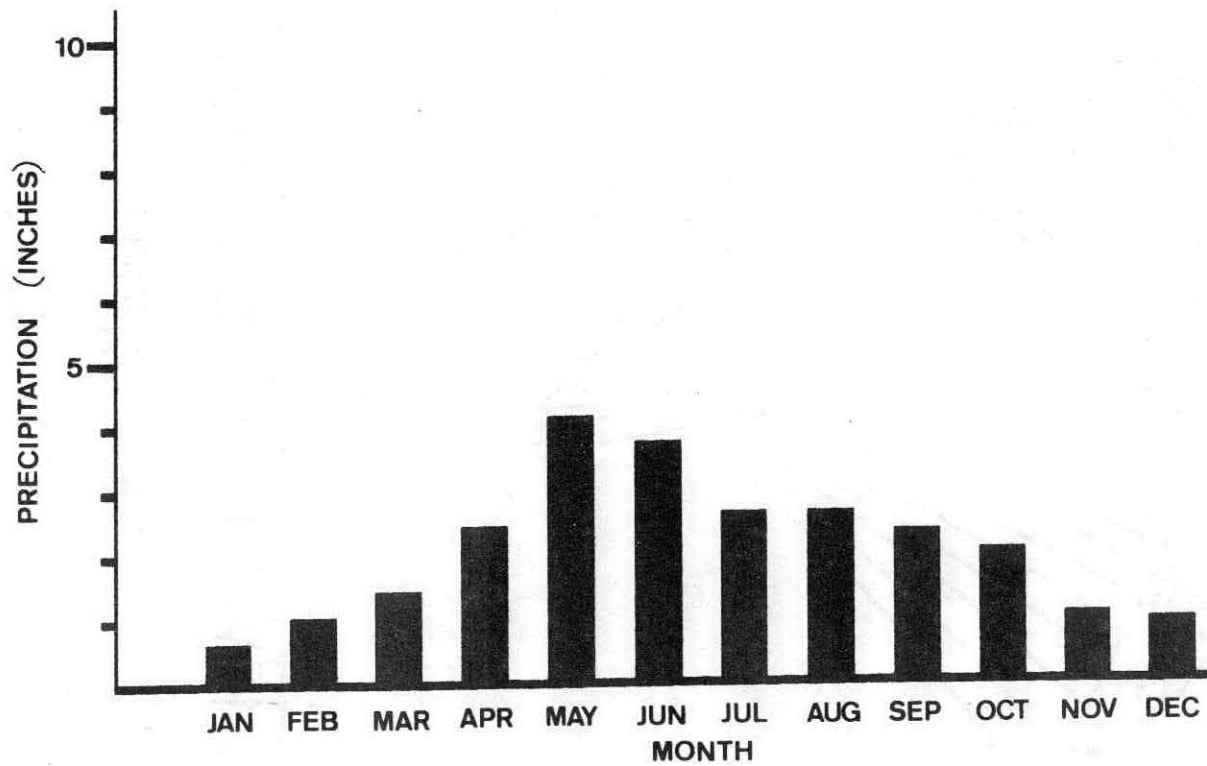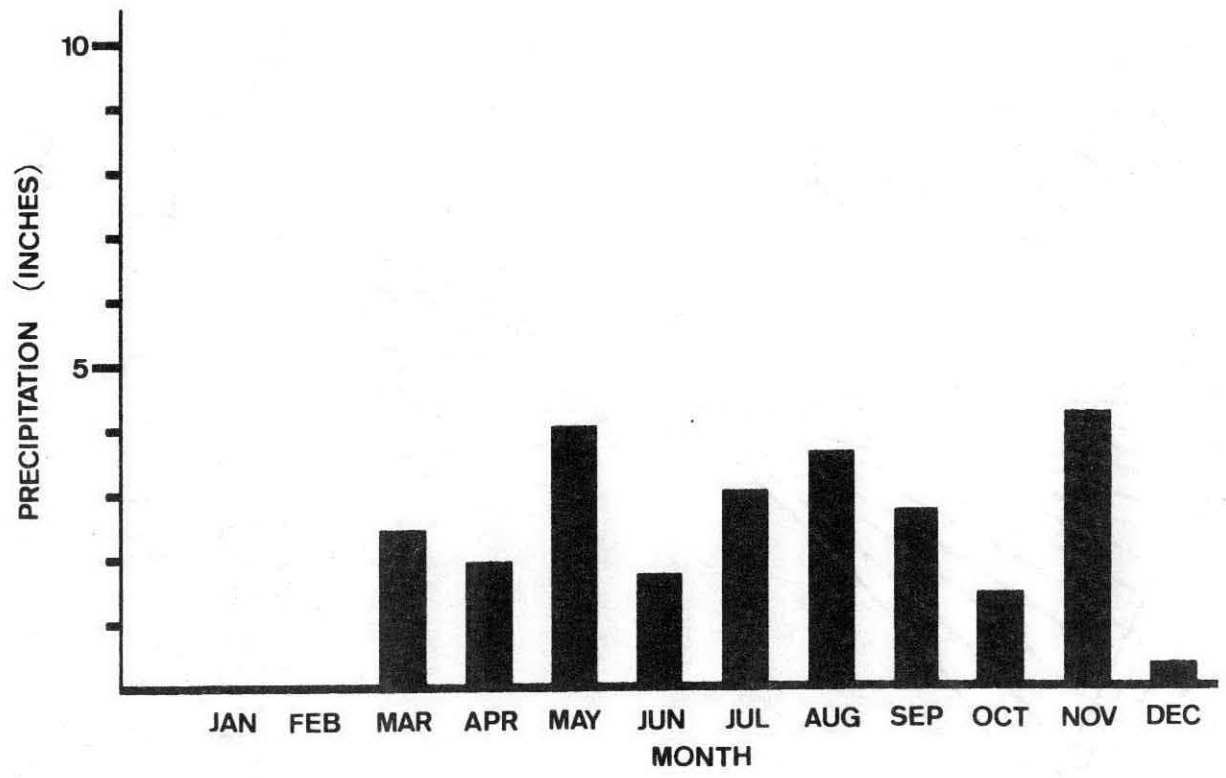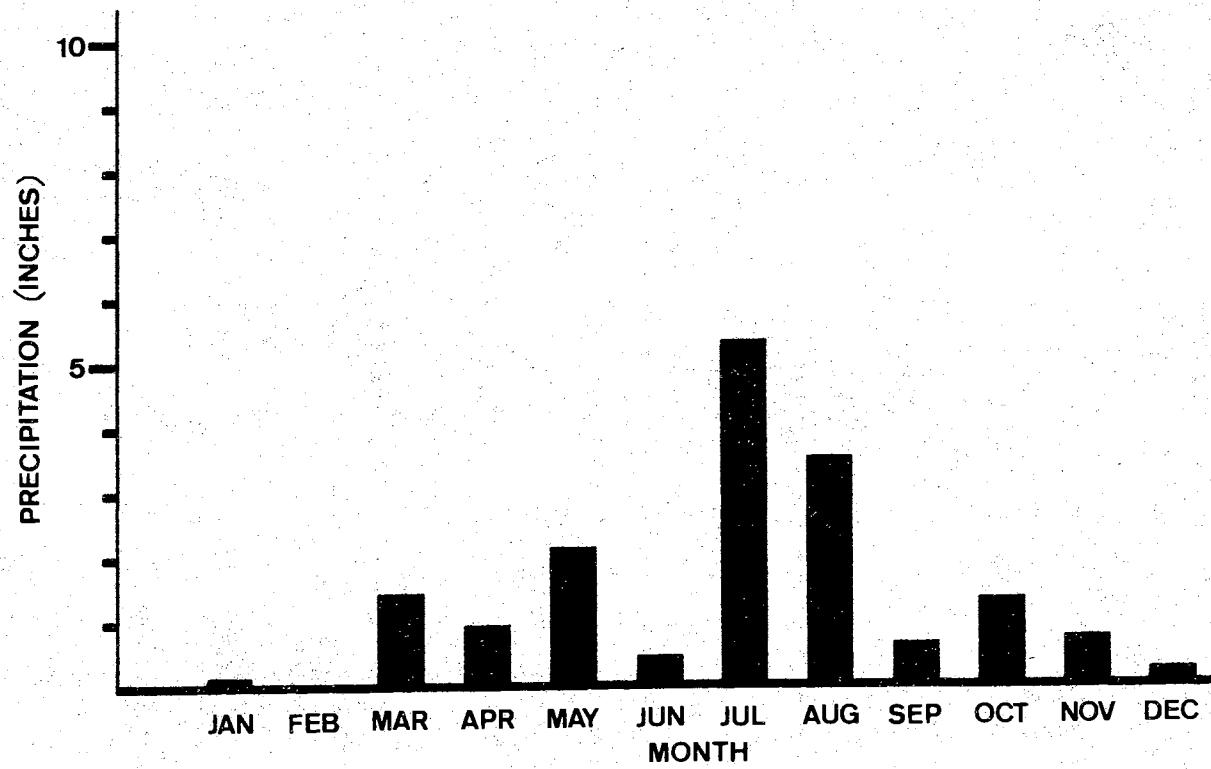
Figure 60.   1981 Monthly Precipitation at Range (Site 9)
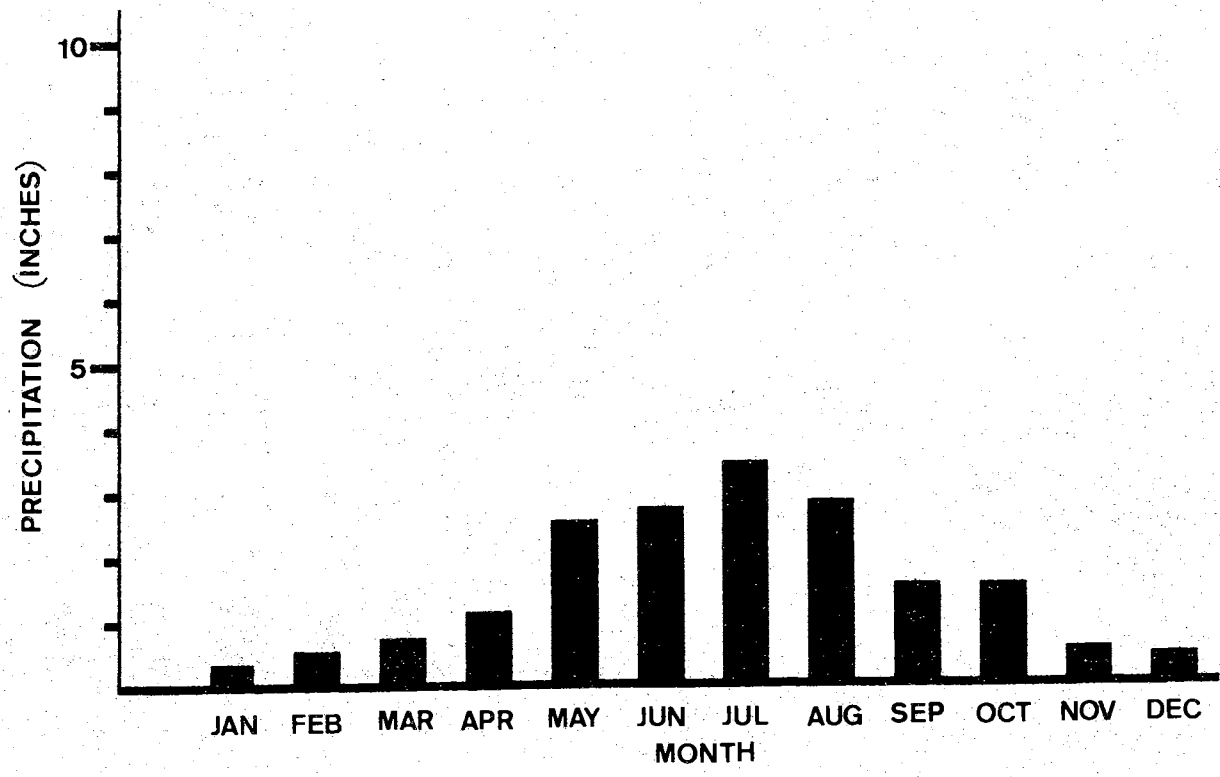
Figure 61. Monthly Normal Precipitation at Goodwell (Site 9)
(20 year average not available from Range)

APPENDIX D


LIST OF IDENTIFIED SPECIES

APPENDIX D

LIST OF IDENTIFIED SPECIES

AMHY – *Amaranthus hybridus* L. – annual

AMPS – *Ambrosia psilostachya* DC. – perennial

AMTR – *Ambrosia trifida* L. – annual

ANHA – *Andropogon hallii* Hack. – perennial

APSK – *Aphanostephus skirrhobasis* (DC.) Trel. – annual

ARFI – *Artemisia filifolia* Torr. – perennial

ARPU – *Aristida purpurea* Nutt. – perennial

ARLU – *Artemisia ludoviciana* Nutt. – perennial

BIBI – *Bidens bipinnata* L. – annual

BLVS – *Scleranthus annuus*? was not collected flowering – annual

BOCU – *Bouteloua curtipendula* (Michx.) Torr. – perennial

BOGR – *Bouteloua gracilis* (Willd. ex H. B. K.) Lag. ex Griffiths – perennial

BOHI – *Bouteloua hirsuta* Lag. – perennial

BRTE – *Bromus techtorum* L. – annual

BRUN – *Bromus unioloides* HBK. – annual

BULA – *Bumelia lanuginosa* (Michx.) Pers. – perennial

CAFA – *Cassia fasciculata* Michx. – annual

CAGI – *Calamovilfa gigantea* (Nutt.) Scribn. and Merr. – perennial

CATO – *Carya tomentosa* (Poir.) Nutt. – perennial

CECA – *Cercis canadensis* L. – perennial

CESC - <u>Celastrus</u> <u>scandens</u> L. - perennial

CHAL - <u>Chenopodium</u> <u>album</u> L. - annual

CHCO - <u>Chamaesaracha</u> <u>coniodes</u> (Moric.) Britt. - perennial

CHHY - <u>Chenopodium</u> <u>hybridum</u> L. - annual

CHLE - <u>Chenopodium</u> <u>leptophyllum</u> Nutt. - annual

CHPR - <u>Chaerophyllum</u> <u>procumbens</u> (L.) Crantz - annual

CHVI - <u>Chrysopis</u> <u>villosa</u> (Pursh) Nutt. - perennial

CHVE - <u>Chloris</u> <u>verticillata</u> Nutt. - perennial

CLTS - <u>Celtis</u> <u>laevigata</u> Willd, <u>C.</u> <u>occidentalis</u> Pursh, and
<u>C.</u> <u>reticulata</u> Torr. - perennial

COAU - <u>Corydalis</u> <u>aurea</u> Willd. - annusl-biennial

CODR - <u>Cornus</u> <u>drummondii</u> Meyer - perennial

COMM - <u>Commelina</u> <u>erecta</u> L. - perennial

CRGL - <u>Croton</u> <u>glandulosus</u> L. - annual

CRJA - <u>Cristatella</u> <u>jamesii</u> T. & G. - annual

CRTX - <u>Croton</u> <u>texensis</u> (Klotzsch) Muell. Arg. - annuaL

CYAT - <u>Cycloloma</u> <u>atriplicifolium</u> (Spreng.) Coult. - annual

DEPI - <u>Descurainia</u> <u>pinnata</u> (Walt.) Britt. - annual-biennial

DIWI - <u>Dithyrea</u> <u>wislizenii</u> Engelm. - biennial

ELCA - <u>Elymus</u> <u>canadensis</u> L. - perennial

ELVI - <u>Elymus</u> <u>virginicus</u> L. - perennial

ERAN - <u>Eriogonum</u> <u>annum</u> Nutt. - annual

ERBE - <u>Erigeron</u> <u>bellidiastrum</u> Nutt. - annual

EROX - <u>Eragrostis</u> <u>oxylepis</u> (Torr.) Torr.

ERRE - <u>Erysimum</u> <u>repandum</u> L. - annual

ERTR - <u>Eragrostis</u> <u>trichodes</u> (Nutt.) Nash - perennial

EUMI - <u>Euphorbia</u> <u>missurica</u> Raf. - annual

FEOC - <u>Festuca</u> <u>octoflora</u> Walt. - annual

FRGR - <u>Froelichia gracilis</u> (Hook.) Moq. - annual

GAAP - <u>Galium aparine</u> L. - annual

GAPU - <u>Gaillardia pulchella</u> Foug. - annual

GILO - <u>Gilia longiflora</u> (Torr.) Don - annual

GACO - <u>Garu coccinea</u> Pursh - perennial

GAPI - <u>Galium pilosum</u> Ait. - perennial

GECA - <u>Geum canadense</u> Jacq. - annual

GLTR - <u>Gleditsia triacanthos</u> L. - perennial

GYDI - <u>Gymnocladus dioica</u> (L.) K. Koch - perennial

HEPE - <u>Helianthus petiolaris</u> Nutt. - annual

JUNI - <u>Juglans nigra</u> L. - perennial

JUVI - <u>Juniperus virginiana</u> L. - perennial

LAAM - <u>Lamium amplexicaule</u> L. - annual

LARE - <u>Lappula redowskii</u> (Hornem.) Greene - annual

LECO - <u>Leptoloma cognatum</u> (Schultes) Chase - perennial

LEDE - <u>Lepidium densiflorum</u> Schrad. - annual

MEST - <u>Mentzelia stricta</u> (Osterhout) Stevens ex Jeffs &
       <u>Little</u> - perennial

MIAL - <u>Mirabilis albida</u> (Walt.) Heimerl - annual

MORU - <u>Morus rubra</u> L. - perennial

MOPU - <u>Monarda punctata</u> L. - perennial

MSDG - <u>Cyperus schweinitzii</u> Torr. - perennial

MUSQ - <u>Munroa squarrosa</u> (Nuttall) Torrey - annual

OELA - <u>Oenothera lanciniata</u> Hill - annual

OEHE - <u>Oenothera heterophylla</u> Spach - biennial

OESE - <u>Oenothera serrulata</u> Nutt. - perennial

OPMA - <u>Opuntia macrorhiza</u> Engelm. - perennial

OXST - <u>Oxalis stricta</u> L. - perennial

PACA - _Panicum capillare_ L. - annual

PAOL - _Panicum oligosanthes_ Schult. - perennial

PAPE - _Parietaria pensylvanica_ Muhl. - annual

PAQU - _Parthenocissus quinquefolia_ (L.) Planch. - perennial

PASP - _Paspalum setacium_ Michx. - perennial

PATE - _Palafoxia texana_ DC. - annual

PAVI - _Panicum virgatum_ L. - perennial

PEBU - _Penstemon buckleyii_ Pennell - perennial

PEVI - _Petalostemon villosum_ Nuttall - perennial

PHAM - _Phytolacca americana_ L. - perennial

PHLE - _Phryma leptostachya_ L. - perennial

PHYS - _Physalis virginiana_ Miller, and others

PLPU - _Plantago purshii_ R. & S. - annual

PODO - _Polanisia dodecandra_ L.

POOL - _Portulaca oleracea_ L. - annual

PRAN - _Prunus angustifolia_ Marsh. - perennial

PSDI - _Psoralea digitata_ - perennial

PYSC - _Pyrrhopappus scaposus_ DC. - perennial

QUMA - _Quercus macrocarpa_ Michx. - perennial

QUMR - _Quercus marilandica_ Muenchh. - perennial

QUMU - _Quercus muehlenbergii_ Englem. - perennial

QUST - _Quercus stellata_ Wang. - perennial

QUVE - _Quercus velutina_ Lam. - perennial

REAR - _Reverchonia arenaria_ Gray - annual

REFL - _Redfieldia flexuosa_ (Thurber) Vasey - perennial

RHAR - _Rhus aromatica_ Ait. - perennial

SACA - _Sanicula canadensis_ L. - perennial

SADR - <u>Sapindus</u> <u>drummondii</u> H. and A. - perennial

SAKA - <u>Salsola</u> <u>kali</u> L. - annual

SCSC - <u>Schizachyrium</u> <u>scoparium</u> (Michx.) Nash
       (<u>Andropogon</u> <u>scoparius</u> Michx.) - perennial

SEDG - <u>Cyperus</u> spp., possibly 4 species

SELO - <u>Senecio</u> <u>longilobus</u> Bentham

SERI - <u>Senecio</u> <u>riddillii</u> T. & G. - perennial

SELU - <u>Setaria</u> <u>lutescens</u> (Wiegel) F. T. Hubb - annual

SMBO - <u>Smilax</u> <u>bona-nox</u> L. - perennial

SMTA - <u>Smilax</u> <u>tamnoides</u> L. - perennial

SONU - <u>Sorghastrum</u> <u>nutans</u> (L.) Nash - perennial

SPCR - <u>Sporobolus</u> <u>cryptandrus</u> (Torr.) Gray - perennial

SPGI - <u>Sporobolus</u> <u>giganteus</u> Nash - perennial

STSY - <u>Stillingia</u> <u>sylvatica</u> L. - perennial

SYOB - <u>Symphoricarpos</u> <u>orbiculatus</u> Moench - perennial

TRPU - <u>Triplasis</u> <u>purpurea</u> (Walt.) Chapm. -annual

ULAM - <u>Ulmus</u> <u>americana</u> L. - perennial

ULRU - <u>Ulmus</u> <u>rubra</u> Muhl. - perennial

UNLA - <u>Uniola</u> <u>latifolia</u> Michx. - perennial

VEBA - <u>Vernonia</u> <u>baldwinii</u> Torr. - perennial

VEUR - <u>Verbena</u> <u>urticifolia</u> L. - annual

VIAC - <u>Vitis</u> <u>acerifolia</u> Raf. - perennial

VIRA - <u>Viola</u> <u>rafinesquii</u> Greene - annual

YUGL - <u>Yucca</u> <u>glauca</u> Nutt. - perennial

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# VITA

## Steven Dean Thompson

## Candidate for the Degree of

## Master of Science

Thesis:  CLIMATIC AND PHYSIOGRAPHIC INFLUENCES ON SAND HILL
        VEGETATION

Major Field:  Botany

Biographical:

    Personal Data:  Born in Liberal, Kansas, March 23,
        1955, the son of Mr. and Mrs. D. D. Thompson.

    Education:  Graduated from Forgan High School, Forgan,
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    Professional Experience:  Graduate teaching assistant,
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