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VEGETATION OF THE WOODS COUNTY, OKLAHOMA SAND DUNES

The University of Oklahoma

PH.D.

1980

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THE UNIVERSITY OF OKLAHOMA
GRADUATE COLLEGE

VEGETATION OF THE WOODS COUNTY, OKLAHOMA SAND DUNES

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

BY
ROSS TERELL BOWLIN SHERWOOD
Norman, Oklahoma

1980

VEGETATION OF THE WOODS COUNTY, OKLAHOMA SAND DUNES

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ACKNOWLEDGEMENTS

The author would like to thank the following people at the University of Oklahoma for their aid and assistance in preparing this dissertation. I would like to thank Dr. George Goodman for his assistance in identifying some of the species collected at the sand dunes and Dr. Forrest Johnson for the time he spent demonstrating and explaining the use of much of the apparatus used in mineral analysis. I would also like to thank other graduate students at the University of Oklahoma for their comments, suggestions, ideas, and aid which made preparation of the dissertation easier. I especially wish to thank the members of my committee, Dr. Estes, Dr. Boke, Dr. Schnell, Dr. Sonleitner, and most importantly, my major professor Dr. Risser for their help and assistance.

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VEGETATION OF THE WOODS COUNTY, OKLAHOMA SAND DUNES

PREFACE

In northwestern Oklahoma deposits of windblown sand occur on the north side of the major rivers. This sand is formed into a topographically complex series of low hills or dunes, and is frequently well vegetated. There is a paucity of information on the vegetation of inland sand dune areas in the United States, and most of the available information is more than 30 years old. There is no published literature on the vegetation of the sand dune areas in Oklahoma, and so in 1977 I began a study of the vegetation of the sand dunes in Woods county, Oklahoma. The study consisted of three sections: (1) an annotated list of the species present in Little Sahara State Park and a comparison of the flora of Little Sahara State Park with the floras of other sand dune areas in the central United States, (this part will hereafter be called SPECIES); (2) an investigation of the plant communities of the sand dunes and description and definition of these communities using mathematical techniques (PHYTOSOCIOLOGY); (3) an investigation of the mineral relationships of twelve species of plants from the sand dunes; in these species both intra- and inter-specific levels of mineral accumulation were examined in different phenological stages (MINERALS).

Each of the three sections is written in the form of a paper and prepared for submission to a specific journal. Section I was submitted to the Southwestern

Naturalist and is currently in press. Section II has been prepared for Ecology. Additional information considered pertinent to the dissertation is contained in an appendix, which will not be submitted for publication. Section III has been prepared for the Journal of Ecology.

Each section is independent of the others and has its own figures, tables, appendices, and literature citations. In each section the figures and tables for the main body of the paper are placed after the bibliography, followed by an appendix (if present), and then by figures and tables associated with the appendix.

VEGETATION OF THE WOODS COUNTY, OKLAHOMA SAND DUNES

BY: ROSS T. BOWLIN SHERWOOD

MAJOR PROFESSOR: PAUL G. RISSER, Ph.D.

The vegetation of the sand dunes in Woods County, Oklahoma was examined using three different approaches. First, an annotated checklist of the plant species was prepared. A total of 181 species of plants, encompassing 145 genera and 55 families were found. Two families, the Poaceae and Asteraceae together accounted for one-third of the species. Second, the plant communities of the dunes were analyzed using cluster analysis. Though the vegetation showed variation in time and space, no sharp divisions were found that would permit the division of the sand dune vegetation into discrete communities. Finally mineral analysis was done on 12 selected species of dune plants. The above and below ground parts of the plants were analyzed separately for seven different elements (N, P, K, Ca, Mg, Fe, Mn) at four different phenological stages (vegetative, flowering, senescening, dormant). Considerable intra- and inter-species partitioning of elements was found. General trends in seasonal mineral level fluctuations were well displayed with nitrogen and weakly displayed in phosphorus, but were not apparent in the other five elements.

THE PLANT SPECIES OF THE SAND DUNES

INTRODUCTION

In northwestern Oklahoma there are deposits of windblown sand on the north side of the major rivers. For the most part, this sand is stabilized into thickly vegetated sandhills or sand dunes, but there are areas where the sand is largely without vegetation and forms active dune complexes. Little is known about either the species composition or the community structure of the vegetation of these sand dunes, and so in 1977, a study was begun on the species present at Little Sahara State Park. This study is part of a larger project on the vegetation and vegetation-environment relationships on sand dunes in Woods County, Oklahoma. There have been no comprehensive studies made of these dunes and even the basic information about species occurrences and distributions is lacking. Therefore, the purpose of this paper is to describe the plant species present on the sand dunes in Woods County and to provide a brief description of the habitat and growth form of each species. In addition the flora of these sand dunes is compared with the floras of four other sand dune areas.

STUDY AREA

Little Sahara State Park is located in Woods County, Oklahoma, approximately 4.8 km (3 miles) south of the town of Waynoka (R16W T24N; SW S23 & NW S26). The Park is eminently suitable for research since its relatively small size, 146 ha (360 acres), makes comprehensive species collections possible in all of the typical sand dune environments. These dunes appear to be representative of the dunes throughout Woods County and northwestern Oklahoma. Typical dune environments range from active, nonvegetated sand areas, through semi-stable dunes to stable vegetated dunes. There are also areas, though only forming a small proportion of the Park, that have unique species combinations that occur in specialized habitats, e.g. wooded dune slacks, blowouts, and even a temporary pool (Fig. 1).

The climate of Little Sahara State Park is continental with hot summers and frequent summer droughts (Borchert, 1950). The average annual precipitation is 64 cm with most of the precipitation occurring between April and September. The average annual temperature is 15.7 C with extremes of -22 C and 42 C. The average last frost is May 13 and the first frost is October 29 for an average growing season of 199 days (Curry, 1970). Soils of the sand dunes arise from Quaternary sands drifted from the bed of the Cimarron River. All soils consist of deep fine sands; on the stabilized dunes (Trivoli fine sand, dune phase) there may be a slight

darkening of the upper 20-25 cm, while the active and semi-stable dunes (Dune sand) show no evidence of horizon formation (USDA, 1950). Slopes range from 0-50% and the dunes are topographically complex. For descriptive purposes the parts of a sand dune are defined as follows: dune tops are the level or gently undulating upper portions of the dunes; dune sides are the steeply sloping portions of dunes; and dune slacks are the flat or gently sloping areas between dunes (Fig. 2). Slacks may be surrounded on all sides by dunes, therefore water erosion is minimal or non-existent and this prevents surface drainage from slacks. Despite the absence of drainage canals from the slacks, there is not even temporary pooling of water because of the high infiltration rate. Permanent or semipermanent pools can occur only where the surface of the sand dips below the water table.

The dominant vegetation of the stable dunes consists of sandsage (Artemisia filifolia), aromatic sumac (Rhus aromatica), sandhill plum (Prunus angustifolia), ragwort (Senecio riddellii), yellow evening primrose (Calylophus serrulatus), scarlet pea (Indigofera miniata), little bluestem (Schizachyrium scoparium), sand dropseed (Sporobolus cryptandrus) and big sandreed (Calamovilfa gigantea).

RESULTS

A total of 55 families, 145 genera, and 181 species of vascular plants were encountered in the course of this study. All but two of the families, each represented by only one species, were angiosperms. In the following list nomenclature follows Correll and Johnston (1970) as possible, though other sources (Barkley, 1977; Gould 1975; Steyermark, 1963; Waterfall, 1972) were consulted to resolve nomenclatural ambiguities or as a source for common names. Families are arranged according to Correll and Johnston and after each family heading, the genera and species are listed alphabetically. For each entry, the genus, species, and authority are given, followed by common name or names, a brief description of the plant, a brief description of where the plant occurs on the dunes, and lastly, time of flowering.

EQUISETACEAE

Equisetum laevigatum A. Br. smooth horsetail - erect herbaceous perennial,
rare, in moist dune slacks under cottonwoods, only a few plants seen.
Spring.

CUPRESSACEAE

Juniperus virginiana L. red cedar - tree infrequently found on dune sides
and in slacks. Fall.

POACEAE

Andropogon hallii Hack. sand bluestem - erect, tall rhizomatous-perennial, common on tops and sides of stable dunes, present in dune slacks, also along roads and fences. Summer, Fall.

Aristida purpurea Nutt. purple three-awn - low tufted perennial, common in open areas on stable dune tops and sides, also occasionally in disturbed areas along roads, etc. Summer, Fall.

Bothriochloa saccharoides (Sw.) Rydb. silver beardgrass - tufted perennial, present only on shoulder of Hwy 281, abundant when encountered. Fall.

Bouteloua curtipendula (Michx.) Torr. sideoats grama - tufted bunching medium perennial, scattered and infrequent on stable dunes, also along Hwy. 281. Summer, Fall.

Bouteloua gracilis (H.B.K.) Griffiths. bluegrama - low tufted perennial, common in slacks of stable dunes, occasionally on dune sides. Summer, Fall.

Bouteloua hirsuta Lag. hairy grama - low tufted perennial grass, infrequent on stable dune tops, but numerous plants when present. Fall.

Bromus tectorum L. downy chess - spreading annual, in disturbed areas on stable dunes, especially slacks, also around picnic tables, in lawns and along Hwy 281 and park roads. Spring.

Bromus unioloides H.B.K. rescue grass - spreading annual, weedy around picnic tables. Spring.

Calamovilfa gigantea (Nutt.) Scribn. & Merr. big sandreed - tall slender rhizomatous perennial, abundant on all parts of semi-stabilized dunes, often forming pure stands, also in open sandy areas of stable dunes, especially on sides and tops. Summer, Fall.

Cenchrus incertus M. A. Curtis. sandbar - spreading perennial or annual,

abundant in slacks of stable dunes, also on sides and tops of stable dunes,
and abundant along Hwy 281 and park roads. Spring, Summer, Fall.

Chloris verticillata Nutt. windmill grass - densely tufted perennial, infrequent

on stable dunes, along Hwy 281 and park roads. Spring, Summer.

Cynodon dactylon (L.) Pers. Bermuda grass - low rhizomatous perennial,

planted for lawns near picnic tables, escapes along park roads. Summer,
Fall.

Elymus canadensis L. Canada wildrye - tall solitary annual, scattered and

widespread on stable dunes. Spring.

Eragrostis arylepis (Torr.) Torr. red lovegrass - loosely tufted perennial,

scattered and widespread in open areas of stable dunes. Spring, Summer,
Fall.

Eragrostis trichodes (Nutt.) Wood. sand lovegrass - tufted tall perennial

abundant and widespread on stable dunes, often under shrubs and trees.
Fall.

Hordeum pusillum Nutt. little barley - small annual, occasional weed in lawns.

Spring.

Leptoloma cognatum (Schult.) Chase. fall witchgrass - spreading perennial

rare on stable dune sides and tops in open areas. Summer, Fall.

Panicum hillmanii Chase. witchgrass - large, freely lower branching annual,

weedy and common along park roads and in waste places. Summer.

Panicum oligosanthos Schult. panic grass - spreading perennial, infrequent

in stable dune slacks. Summer, Fall.

Panicum virgatum L. switchgrass - large rhizomatous perennial, scattered on stable dunes, also near temporary pool and along Hwy 281. Fall.

Paspalum setaceum Michx. fringleaf paspalum - spreading perennial, common and widespread in open areas on stable dunes. Spring, Summer, Fall.

Poa arachnifera Torr. Texas bluegrass - tufted perennial, common in stable dune slacks, occasionally on stable dune sides or tops. Spring.

Redfielda flexuosa (Thurber) Vasey. blowout grass - tall perennial with long slender rhizomes, locally abundant on semi-stable dunes, frequently growing in pure stands or with Calamovilfa gigantea. Summer, Fall.

Schizachyrium scoparium (Michx.) Nash. little bluestem - tufted, flat stemmed perennial, abundant and widespread on all parts of stable dunes, the most common grass of the stable dunes. Fall.

Setaria geniculata (Lam.) Beauv. knotroot bristlegrass - spreading perennial, infrequent near temporary pool. Summer, Fall.

Setaria viridis (L.) Beauv. green foxtail - tufted annual, weedy in lawns and along park roads. Spring, Summer, Fall.

Sorghastrum avenaceum (Michx.) Nash. Indian grass - tall perennial, occasionally in stable dune slacks, also found around temporary pool. Fall.

Sorghum halepense (L.) Pers. Johnson grass - tall perennial from scaly rhizome, found only on shoulder of Hwy 281, abundant where present. Spring, Summer.

Sphenopholis obtusata (Michx.) Scribn. prairie wedgescale - upright slender perennial, rare, a few plants occur near temporary pool. Spring, Summer.

Sporobolus cryptandrus (Torr.) Gray. sand dropseed - tufted perennial, abundant and widespread on stable dunes. Spring, Summer, Fall.

Sporobolus giganteus Nash. giant dropseed - large tufted perennial, infrequent on tops and sides of stable dunes. Summer, Fall.

Triplasis purpurea (Walt.) Chapm. purple sandgrass - low tufted annual, common and widespread in open areas of stable dune. Fall.

Vulpia octoflora (Walt.) Rydh. six-weeks fescue - low early spring annual, abundant and widespread on stable dunes in early spring, but disappearing rapidly. Spring.

CYPERACEAE

Cyperus ovularis (Michx.) Torr. globe flatsedge - low tufted perennial sedge. common in stable dune slacks and occasionally elsewhere on stable dunes. Spring, Summer, Fall.

Cyperus schweinitzii Torr. Schweinitz flatsedge - perennial sedge common in stable dune slacks with C. ovularis and scattered elsewhere on stable dunes. Spring, Summer, Fall.

Fuirena simplex Vah. umbrellagrass - low growing perennial found only near temporary pool, fairly common there. Fall.

Scirpus americanus Pers. three-square bulrush - tall rhizomatous perennial, a few plants in temporary pool. Summer.

Scirpus validus Vahl. soft stem bulrush - tall rhizomatous perennial forming extensive colonies, abundant in and around temporary pool, found nowhere else. Summer.

COMMELINACEAE

Commelina erecta L. var. angustifolia (Michx.) Fern. erect dayflower - clambering perennial herb, common and widespread on stable dunes, often climbing over shrubs. Spring, Summer, Fall.

Tradescantia occidentalis (Britton) Smyth. prairie spiderwort - fleshy perennial herb, widespread and uncommon, but not rare on stabilized dunes. Spring, Summer.

LILIACEAE

Yucca angustifolia Pursh. soapweed yucca - stiff leaved perennial with large rhizomes, fairly common on stable dune tops and sides, especially in open areas, may be locally abundant. Spring.

SALICACEAE

Populus deltoides Marsh. eastern cottonwood - large tree found in small stands or scattered individuals in some dune slacks, conspicuous, but never very abundant. Spring.

Salix interior Rowlee. sandbar willow - multitrunked shrubs, a few individuals around temporary pool, nowhere else. Spring.

Salix nigra L. blackwillow - a few small trees around temporary pool, nowhere else. Spring.

ULMACEAE

Celtis laevigata Willd. sugarberry - infrequent tree in mesic wooded slacks. Spring.

Celtis reticulata Torr. netleaf hackberry - scattered and fairly common on stable dunes, trees, often small and shrublike. Spring.

Ulmus americana L. American elm - large tree occasionally found in wooded slacks and planted near picnic tables. Spring.

MORACEAE

Morus rubra L. red mulberry - infrequent tree of mesic wooded slacks. Spring.

URTICACEAE

Parietaria pennsylvanica Muhl. hammerwort - herbaceous annual, one population found under Bumelia lanuginosa on stable dune side. Summer.

POLYGONACEAE

Eriogonum annuum Nutt. annual eriogonum - erect annual, scattered and common on stable dunes, usually in open areas, also along park roads and Hwy 281. Summer, Fall.

CHENOPODIACEAE

Chenopodium album L. lamb's quarters - robust annual, infrequent lawn weed near picnic tables. Spring.

Chenopodium leptophyllum Wats. sandhill goosefoot - slender annual, scattered and infrequent on stable dunes, also along Hwy 281. Summer, Fall.

Cycloloma atriplicifolium (Spring.) Coult. tumble ringweed - usually sub-spherical annual, scattered in open, bare areas on stable dunes, in blowouts, and in disturbed areas. Summer, Fall.

Salsola kali L. tumbleweed, Russian thistle - robust sub-spherical annual, scattered and uncommon in open areas on stable dunes, common in disturbed areas, especially along park roads and Hwy 281. Summer, Fall.

AMARANTHACEAE

Amaranthus palmeri Wats. Palmer pigweed - robust annual, infrequent weed of disturbed areas, especially along park roads. Summer, Fall.

Froelichia gracilis (Hook.) Moq. slender snake cotton - spreading decumbent annual, common in open areas in stable dune slacks, occasionally elsewhere on stable dunes and also along park roads. Summer, Fall.

NYCTAGINACEAE

Mirabilis albida (Walt.) Heimerl. white four o'clock - tall erect glabrous perennial herb, scattered and widespread on stable dunes. Summer, Fall.

AIZOCEAE

Mollugo verticillata L. Indian chickweed - prostrate annual, abundant in stable dune slacks, infrequently elsewhere on stable dunes. Spring, Summer, Fall.

PORTULACACEAE

Portulaca mundula L.M. Johnst. chisme - low succulent annual, infrequent in stable dune slacks and along Hwy 281. Summer.

Portulaca cleraceae L. purslane - low glabrous succulent annual, fairly common in stable dune slacks and occasionally elsewhere. Summer, Fall.

CARYOPHYLLACEAE

Silene antirrhina L. sleepy catchfly - slender erect annual, infrequent in stable dune slacks. Spring, Summer.

RANUNCULACEAE

Delphinium virescens Nutt. var. macroceratilis (Rudg.) Cory. white larkspur - erect perennial herb, rare, one seen in lawn near park road. Spring.

PAPAVERACEAE

Argemone polyanthemos (Fedde) G. Ownbey. white prickly poppy - tall taprooted annual or biennial with yellow sap, rare but occasionally encountered on stable dunes. Summer.

BRASSICACEAE

Camelina microcarpa Andrz. falseflax - early spring annual, rare weed along Hwy 281. Spring.

Capsella bursa-pastoris L. shepherd's purse - early spring annual, infrequent weed in lawns. Spring.

Descurainia pinnata (Walt.) Britt. tansy mustard - early spring annual, wide-spread and common but not abundant on stable dunes. Spring.

Dithyrea wislizenii Engelm. var. palmeri Pays. spectacle pod - large taprooted biennial, common and widespread on stable dunes, especially in open areas. Wide variation in numbers of plants from year to year. Summer, Fall.

Draba reptans (Lam.) Fern. whitlow grass - small inconspicuous early spring annual, scattered and infrequent populations of many plants on stable dunes. Spring.

Lepidium densiflorum Schrad. peppergrass - early spring annual, widespread and common on stable dunes, especially in open areas. Spring.

Lesquerella gordonii (Gray) Wats. bladderpod - small spreading spring annual, in disturbed areas and along park roads. Spring.

Streptanthus hyacinthoides Hook. twist-flower - tall annual, infrequent small populations on stable dunes. Spring.

CAPPARIDACEAE

Polanisia jamesii (T. & G.) Iltis. cristatella - small, much branched annual, fairly common in blowouts, on semi-stable dunes, and in bare open areas on tops and sides of stable dunes. Summer, Fall.

SAXIFRAGACEAE

Ribes odoratum Wendl. buffalo current - erect shrub, occasionally in wooded slacks. Spring.

ROSACEAE

Prunus angustifolium Marsh. Chickasaw sandplum - much branched thicket forming shrub, often in large colonies, widespread and abundant on stable dunes. Spring.

Prunus gracilis Engelm. & Gray. Oklahoma plum - thicket forming shrub,
rare on stable dune tops but forming extensive thickets where present.
Spring.

FABACEAE

Amorpha fruticosa L. false indigo - erect shrub, rare in open woods of stable
slacks, but may be common where found. Spring.

Cassia fasciculata Michx. partridge pea - erect slender glabrate annual,
common and widespread on stable and semi-stable dunes, especially in open
areas, in disturbed areas, and along park roads and Hwy 281. Summer, Fall.

Dalea lanata Spreng. woolly dalea - prostrate perennial herb with long woody
roots, common on tops and sides of stable dunes in open areas, also
occasionally on semi-stable dunes. Summer, Fall.

Desmanthus illinoensis (Michx.) Mac M. prairie mimosa - erect perennial
herb usually with several stems, infrequent in disturbed areas and along
Hwy 281. Summer.

Indigofera miniata Ort. scarlet pea - decumbent or prostrate herbaceous
perennial from a large taproot, common and widespread in open areas
on stable dunes and on semistable dunes. Spring, Summer, Fall.

Lespedeza stuevei Nutt. tall bush clover - erect, leafy stemmed perennial
herb, rare populations of a few individuals on stable dunes. Summer.

Melilotus officinalis (L.) Lam. yellow sweet clover - annual or biennial herb,
tall and open bushy, weedy plant along park roads. Spring, Summer.

Petalostemon villosum Nutt. silky prairie clover - ascending herbaceous
perennial with a woody taproot, common and scattered over stable dunes in
open areas and on semi-stable dunes. Summer.

Psoralea digitata T. & G. palm-leaved scurfpea - erect single stemmed

herbaceous perennial, branching above, scattered and infrequent on stable dunes. Spring.

Psoralea lanceolata Prush. lemon scurfpea - bushy herbaceous perennial with

long creeping rhizomes, often forming extensive colonies, semi-stable dunes and blowouts. Spring, Summer.

Strophostyles leiosperma (T. & G.) Piper. slickseed wildbean - vinelike

herbaceous annual, rare on semi-stable dunes or open areas of stable dunes. Summer, Fall.

OXALIDACEAE

Oxalis corniculata L. creeping lady's sorrel - small herbaceous perennial with

creeping stems, rooting at the nodes, rare populations in stable dune slacks. Spring.

LINACEAE

Linum lewisii Pursh. blue flax - glabrous erect herbaceous perennial, one plant seen along Hwy 281. Spring.

Linum rigidum Pursh. var. berlandieri (Hook) T. & G. yellow flax - glabrous erect annual, infrequent on sides of stable dunes. Spring, Summer.

ZYGOPHYLLACEAE

Tribulus terrestris L. puncture-vine, goat head - prostrate annual weed of disturbed areas. Spring, Summer.

EUPHORBIACEAE

Acalypha ostryaefolia Ridd. hophornbean copperleaf - erect annual, infrequent weed in lawns. Summer.

Croton glandulosa L. croton - taprooted ascending annual, widespread and common on stable dunes, frequently growing under shrubs. Spring, Summer, Fall.

Croton texensis (Kl.) Muell. Arg. Texas croton - erect pubescent dioecious annual, widespread and fairly infrequent in open areas of stable dunes and along park roads. Summer, Fall.

Euphorbia carunculata Waterfall. sand dune euphorbia - prostrate glabrous annual, blowouts and semi-stable dunes on bare sand areas. Summer, Fall.

Euphorbia glyptosperma Engelm. ridgeseed euphorbia - prostrate glabrous annual, often forming mats, infrequent in slacks and roadsides, including cracks in pavements. Summer, Fall.

Euphorbia hexagona Nutt. six angle euphorbia - erect taprooted annual with pseudodichotomous branching, infrequent on stable dunes and along Hwy 281. Summer, Fall.

Euphorbia missurica Raf. Missouri spurge - glabrous ascending spreading annual, widespread and abundant on stable dunes and along Hwy 281. Spring, Summer, Fall.

Reverchonia arenaria Gray. reverchonia - erect ascending glabrous annual, infrequent and localized in blowouts and open areas of semi-stable dunes. Summer, Fall.

Stillingia sylvatica L. Queen's delight - multiple stemmed perennial herb, from large fleshy-woody roots, fairly common and widespread on tops and sides of stable dunes, especially in open areas. Spring.

ANACARDIACEAE

Rhus aromatica Ait. aromatic sumac - sprawling to upright shrub, often forming large thickets, abundant and widespread on stable dunes. Spring.

Rhus glabra L. smooth sumac - erect sparsely branched shrub, often forming thickets, infrequent on stable dunes. Spring.

Rhus toxicodendron L. poison ivy - small shrub or sprawling or climbing vine, occasionally in wooded slacks in understory or climbing trees. Spring.

SAPINDACEAE

Sapindus saponaria L. var. drummondii (H. & A.) L. Benson. soapberry - trees or large shrub as scattered individuals on stable dunes, sometimes forming pure stands or growing with Bumelia lanuginosa. Spring.

VITACEAE

Cissus incisa (Nutt.) Des Moul. ivy treebind - woody vine with succulent leaves, climbing in shrubs and small trees, one population with numerous plants on stable dune side. Spring, Summer.

Parthenocissus quinquefolia (L.) Planch. Virginia creeper - high climbing woody vine, infrequent in wooded slacks. Spring, Summer.

Vitis acerifolia Raf. Panhandle grape - much branched woody vines, seldom climbing, usually sprawling over low shrubs or on ground, often forming large mats, infrequent but conspicuous on stable and semi-stable dunes. Spring.

MALVACEAE

Callihroe involucrata (Torr.) Gray. var. involucrata. purple prairie poppymallow, winecup - herbaceous perennial with decumbent stems from enlarged root, stable dune slacks, in lawns, and along park roads and Hwy 281. Spring, Summer, Fall.

LOASACEAE

Mentzelia nuda (Pursch) T. & G. sandlily - erect herbaceous perennial from a large taproot, common in open on stable dunes and on semi-stable dunes. Summer, Fall.

CACTACEAE

Coryphantha vivipara (Nutt.) Britt. & Rose. spiny ball cactus - small depressed globose succulent perennial, infrequent but widespread on stable dunes.

Summer.

Opuntia macrorhiza Engelum. plains prickly pear - herbaceous spiny perennial with stem composed of flattened decumbent pads, fairly common on stable dunes. Summer.

ONAGRACEAE

Calylophus serrulatus (Nutt.) Raven. yellow evening primrose - low bushy erect semi-woody perennial, common and widespread on stable dune tops and sides, occasionally in stable dune slacks. Spring, Summer.

Gaura villosa Torr. woolly gaura - open ascending perennial from woody base, fairly common in open areas on tops and sides of stable dunes and along park roads. Spring, Summer.

Oenothera grandis (Britt.) Smyth. evening primrose - small erect or decumbent annual, occurring only along Hwy 281, but fairly common there. Spring.

Oenothera laciniata Hill. var. laciniata. cut leafed evening primrose - small erect annual, similar to O. grandis, common in stable dune slacks, less frequent elsewhere on stable dunes. Spring.

Oenothera pallida Lindl. evening primrose - much branched erect rhizomatous perennial, rare on tops and sides of stable dunes in open areas. Spring, Summer.

Oenothera rhombipetala T. & G. four point evening primrose - tall erect taprooted biennial, infrequent on stable dunes and along Hwy 281. Spring, Summer.

APIACEAE

Spermolepis echinata (DC.) scaleseed - low inconspicuous annual, rare, one population of about ten plants in stable dune slack. Spring.

CORNACEAE

Cornus drummondii C. A. Mey. rough leaved dogwood - erect shrub, forming nearly impenetrable thickets, rare thickets in low, stable dune slacks. Spring.

SAPOTACEAE

Bumelia lanuginosa (Michx.) Pers. var. oblongifolia (Nutt.) Clark. chittamwood - trees or shrubs, stands of trees in stable dune slacks, scattered shrubby trees on stable dunes. Summer.

LOGANACEAE

Cynoctonum mitreola (L.) Britt. miterwort - low decumbent or erect herb, found only in bottom of dry temporary pool. Summer, Fall.

APOCYNACEAE

Apocynum cannabinum L. Indian hemp - erect ascending open branched herbaceous perennial, infrequent and scattered over semi-stable dunes and in open areas of stable dunes, may be locally common. Spring, Summer.

ASCLEPIADACEAE

Asclepias arenaria Torr. sand milkweed - robust spreadings ascending herbaceous perennials, fairly common in open areas of stable dune tops and sides, occasionally on semi-stable dunes. Spring, Summer.

Asclepias engelmanniana Woods. green milkweed - tall, stout stemmed, herbaceous perennial, unbranched or nearly so, very rare in open areas on stable dunes. Summer.

Asclepias tuberosa L. butterfly weed - herbaceous multistemmed perennial from a woody rootstock, rare on tops and sides of stable dunes. Spring, Summer.

Asclepias viridis Walt. antelope-horn - low herbaceous ascending or decumbent perennial from a thick rootstalk, very rare on sides of stable dunes. Spring.

CONVOLVULACEAE

Cuscuta cuspidata Engelm. cup dodder - parasitic achlorophyllous vinelike annual, clambering over other vegetation, infrequent on stabilized dunes, parasitic on other plants. Summer, Fall.

Evolvulus nuttallianus R. & S. Nuttall evolvulus - low ascending erect-stemmed herbaceous perennial, very rare on stable dune tops, only one plant seen. Spring.

Ipomoea leptophylla Torr. bush morning glory - ascending coarse much branched perennial herb from a large fibrous taproot, infrequent in open areas on tops and sides of stable dunes. Spring.

POLEMONIACEAE

Ipomopsis longiflora (Torr.) V. Grant. white flowered ipomopsis - erect, much branched annual or biennial, fairly common and scattered over stable dunes, especially in open areas. Fall.

BORAGINACEAE

Cryptantha minima Rydb. cryptantha - tiny annual, common in stable dune slacks, also less frequent on tops of stable dunes. Spring.

Heliotropium convolvulaceum (Nutt.) Gray. wild heliotrop - annual with single erect or branching stem, blowouts and less frequently open areas on tops and sides of semi-stable dunes. Summer, Fall.

Lithospermum incisum Lehm. narrow leaved puccoon - erect, several stemmed herbaceous perennial, infrequent and widespread on stable dunes, especially in more open areas. Spring, Summer, Fall.

VERBENACEAE

Phyla incisum Small. Texas frog fruit - suffrutescent perennial with prostrate stems, often rooting at the nodes, occurring only around temporary pool. Fall.

LAMIACEAE

Lycopus americanus Muhl. American bugleweed - slender erect annual, occurring only in dry bottom of temporary pool. Summer, Fall.

Monarda punctata L. spotted beebalm - erect unbranched or sparsely branched annual, abundant and widespread on stable dunes, numbers may vary considerably from year to year. Spring.

SOLANACEAE

Chamaesaracha coniodes (Dun.) Britt. chamaesaracha - much branched herbaceous perennial with decumbent stems, rare as weed of disturbed areas around picnic tables and along park roads. Spring, Summer.

Physalis heterophylla Nees. clammy ground cherry - erect, branched or unbranched herbaceous perennial from a deeply buried rootstalk, scattered and fairly common in open areas of stable dunes, in stable dune slacks, may be locally abundant on semi-stable dunes. Spring, Summer.

Solanum americanum Mill. black nightshade - bushy erect annual, waste places and infrequently in stable dune slacks. Spring, Summer, Fall.

Solanum dimidiatum Raf. western horse-nettle - erect few branched or unbranched perennial with deep rootstocks, occasionally in stable dune slacks, rare on stable dune tops. Summer.

Solanum elaeagnifolium Cav. silver-leaf nightshade - erect perennial herb

with deep rootstocks, infrequent in low stable dune slacks. Summer, Fall.

SCROPHULARIACEAE

Castilleja purpurea (Nutt.) G. Don. yellow paintbrush - herbaceous perennial

with simple upright clustered stems, very rare waif on stable dune sides.

Spring.

Linaria canadensis (L.) Dum. var. texana (Scheele.) Penn. oldfield toad-flax

- slender erect unbranched annual, infrequent in stable dune slacks. Spring.

Penstemon buckleyi Penn. Buckley's penstemon - herbaceous erect perennial,

one to few unbranched stems, common to locally abundant on tops and

upper sides of stable dunes in open areas. Spring.

OROBANCHACEAE

Orobanche fasciculata Nutt. broomrape - low fleshy achlorophyllous parasite,

infrequent, but may be locally common on stable dune tops and sides.

Spring, Summer.

Orobanche ludoviciana Nutt. Louisiana broomrape - low fleshy achlorophyllous

parasite, infrequent to rare but widespread on stable dunes. Spring,

Summer.

PLANTAGINACEAE

Plantago patagonica Jacq. var. gnaphalioides (Nutt.) Gray. woolly plantain

- short erect woolly annual, widespread and abundant, especially in slacks of stable dunes. Spring.

Plantago rhodosperma Dene. red-seeded plantain - rosette forming annual

with slender taproot, rare in stable dune slacks. Spring.

RUBIACEAE

Lophanthus occidentalis L. buttonbush - shrubs, a few plants around

temporary pool. Summer.

CAPRIFOLIACEAE

Symphoricarpos orbiculatus Moench. coral berry - small shrubs, often forming thickets, infrequent in understory in wooded slacks. Spring.

CUCURBITACEAE

Cucurbita foetidissima H.B.K. buffalo gourd - herbaceous vinelike perennial with numerous spreading stems from a large rootstock, rare on stable dune sides and slacks, may be locally common. Spring, Summer.

CAMPANULACEAE

Triodanis holzingeri McVaugh. Venus' looking glass - slender erect annual, unbranched or with few branches, rare in stable dune slacks. Spring.

ASTERACEAE

Ambrosia psilostachya DC. western ragweed - erect herbaceous perennial, forming extensive colonies from runnerlike roots, abundant in stable dune slacks and less common elsewhere on stable dunes.

Aphanostephus skirrhobasis (DC.) Trel. lazy daisy - short erect annual, branched above, abundant and widespread on stable dunes, especially in slacks. Spring.

Artemisia filifolia Torr. sandsage - low grey bushy shrubs with numerous long slender branches, conspicuous, widespread and abundant on stable dunes. Fall.

Artemisia glauca Pabl. silky wormwood - erect herbaceous perennial, several simple or slightly branched stems from a woody base, widespread and common on stable dunes, especially on tops and sides. Fall.

Artemisia ludoviciana Nutt. var. ludoviciana. white sage - herbaceous perennial, frequently multi-stemmed from woody base, rare populations in dune slacks. Fall.

Baccharis salicina T. & G. willow baccharis - bushy erect shrub, infrequent in open woods and around temporary pool. Summer, Fall.

Cirsium undulatum (Nutt.) Spreng. wavyleaf thistle - erect, usually unbranched, sub-rhizomatous perennial, rare on stable dune sides and slacks. Spring, Summer.

Conyza canadensis L. Cronq. horse weed - erect annual, unbranched below and much branched above, rare weed along park roads. Fall.

Croptilon divaricatum (Nutt.) Raf. scratch-daisy - bushy annual, usually from a single stem, widespread and fairly common on stable dunes, especially in open areas. Summer, Fall.

Engelmannia pinnatifida Nutt. Engelmann daisy - erect few branched herbaceous perennial from a stout rootstalk, common along park roads and Hwy 281. Spring.

Erigeron bellidiastrum Nutt. western fleabane - bushy annual with a slender taproot, common on semi-stable dunes and in open areas of stable dunes. Spring, Summer, Fall.

Gaillardia pulchella Foug. Indian blanket - taprooted annual, usually branched, common and widespread on stable dunes, especially in slacks, also along park roads. Spring, Summer.

Gnaphalium obtusifolium L. cat foot - erect annual with ascending branches above, rare around temporary pool. Fall.

Grindelia squarrosa (Pursh) Dun. Curly-cup gumweed - bushy taprooted annual, scattered along Hwy 281. Summer, Fall.

Helianthus petiolaris Nutt. plains sunflower - tall coarse taprooted annual, common on semi-stable dunes, disturbed areas and along park roads.

Summer, Fall.

Heterotheca villosa (Pursh) Shinn. golden aster - low herbaceous perennial with numerous erect or ascending stems from a thick woody taproot, abundant on tops and sides of stable dunes in open areas, often forming large patches. Spring, Summer.

Hymenopappus scabiosaeus L' Her. old plainsman - tall erect biennial, single stemmed, branched above, infrequent on tops of stable dunes. Spring.

Kuhnia eupatorioides L. false boneset - herbaceous erect - ascending perennial from an obconical woody taproots, rare in stable dune slacks. Fall.

Liatris punctata Hook. blazing star - multistemmed herbaceous perennial with usually unbranched stems, rare on tops and sides of stable dunes. Fall.

Lygodesmia rostrata (Gray) Gray. annual skeleton weed - open erect annual, infrequent on semi-stable dunes. Fall.

Palafoxia texana DC. Texas palafoxia - low bushy annual, common on semi-stable dunes. Summer, Fall.

Pyrropappus grandiflorus (Nutt.) Nutt. tuber false dandelion - herbaceous, rosette forming perennial from buried tuberous roots, infrequent in small populations on stable dunes. Spring.

Senecio riddellii T. & G. Riddell's groundsel - herbaceous perennial from a woody taproot, freely branching from base and above, stems erect and ascending, widespread and common on semi-stable and stable dunes. Fall.

Solidago gynnospermoides Greene. narrow leaved goldenrod - herbaceous perennial with erect stems from a creeping rhizome, infrequent around temporary pool. Fall.

Solidago petiolaris Ait. downy goldenrod - herbaceous perennial with numerous erect stems from a rhizome, fairly common on tops and sides of semi-stable dunes and less common on tops and sides of stable dunes in open areas. Fall.

Thelesperma filifolium (Hook.) Gray. greenthread - tallish erect annual, somewhat bushy, rare on stable dune tops and along Hwy 281. Spring.

Thelesperma megapotamicum (Spreng.) O. Ktze. Rio Grande greenthread - herbaceous erect perennial from slender horizontal rhizomes, rare, small populations of a few individuals on the tops of stable dunes. Spring, Summer.

Tragopogon dubius Scop. goat's beard - low herbaceous bushy biennial from deep taproot, rare weed in lawns near picnic tables. Spring.

Vernonia baldwinii Torr. western ironweed - robust erect herbaceous perennial rare in stable dune slacks. Fall.

DISCUSSION

Two families, Poaceae and Asteraceae contribute more than one-third of all the species present and more than one-third of all the genera. The next largest family, Fabaceae, includes less than 7% of the genera and about 6% of the species. Only five families, the above three and the Brassicaceae and the Euphorbiaceae, contribute four or more genera to the flora of the sand dunes.

The vast majority of the genera present are represented by only one species, and less than 20% of the genera have more than one species at the dunes. Just three genera, Euphorbia, Oenothera, and Asclepias have four or more species present.

When the vegetation of the Little Sahara State Park is compared with the vegetation of other sand dune areas, the dunes at Little Sahara are vegetationally more like the dune areas to the southwest than those of the northwest. For the purposes of comparison, I have eliminated the weedy species that occur in artificially disturbed or artificially maintained areas, thus eliminating species such as Tribulus terrestris and Cynodon dactylon but retaining species that occur in areas of natural disturbance such as blowouts. Caution should be used when conclusions are drawn from floristic comparisons, since there may be considerable differences in the amount of time devoted to collection, season of collection, size of area surveyed, etc. Another problem may arise from bias introduced by use of different taxonomic works and by nomenclatural changes when collections from many years apart are compared.

Of the five sand dune areas considered, the vegetation occurring at Little Sahara is most similar to that of the Texas Panhandle (Rowell, 1967), which is not surprising considering the proximity of these two areas (Table 1). Also there are almost continuous areas of sandy soil connecting these two areas. By dividing the number of species lost from Little Sahara to the sand dune in the Texas Panhandle by the distance to these dune areas, about one species is lost for every 16 km. A similar comparison for the dune areas in Winkler and Ector Counties (Collins, 1966), Texas gives a loss rate of about one species for every 11 km. However the loss rate for Little Sahara species is much higher when Little Sahara is compared to the dune areas to the northwest, the dune areas in Weld County, Colorado (Ramaley, 1939) and the Nebraska sandhills (Pool, 1914). For Weld County, Colorado, the loss rate is about one species for each 5 km and for the Nebraska sandhills about one species for each 6 km. The rates of species loss with distance from Little Sahara are about 2-3 times higher for the sand dune areas to the northwest than the corresponding rates of species loss for the sand dune areas to the southwest. While many widespread species such as Psoralea lanceolata occur at all five dune areas, several species such as Reverchonnia arenaria and Calamovilfa gigantea reach their northern distributional limits near the Little Sahara areas, and do not extend as far as the sand dune areas farther northwest. Almost all of the species present at both the northwestern sand dunes areas and at Little Sahara ranges extend into the southwestern sand dune areas.

This study of Little Sahara State Park identified the species present at the sand dunes and briefly describes for each species its growth form, habitat and time of flowering. The flora of Little Sahara State Park was compared with the floras of four other sand dune areas and Little Sahara was found to be more similar to that of

dune areas to the southwest, even though these dune areas are farther geographically from Little Sahara than dune areas to the northwest.

LITERATURE CITED

- BARKLEY, T. M. (ed.) 1977. Atlas of the flora of the Great Plains. Iowa State University Press, Ames, Iowa. 600 pp.
- BORCHERT, J. R. 1950. The climate of the central North American grassland. *Ann. Assoc. Amer. Geogr.* 40:1-39.
- COLLINS, L. T. 1966. Vascular flora of the concho bluff ecotone. MS thesis (unpublished), Texas Technological College, Lubbock, Texas.
- CORRELL, D. S. and M. C. JOHNSTON. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Texas. 1881 pp.
- CURRY, B. R. 1970. Climate of Oklahoma. U. S. Government Printing Office, Washington, D.C. 17 pp.
- GOULD, F. W. 1975. Texas plants -- A checklist and ecological summary. Texas Agricultural Experiment Station MP-585, College Station, Texas. 121 pp.
- POOL, R. J. 1914. A study of the vegetation of the sandhills of Nebraska. *Minn. Botanical Studies*, 4(III):189-312.
- RAMALEY, F. 1939. Sand-hill vegetation of northeastern Colorado. *Ecol. Mongr.* 9:1-51.
- ROWELL, C. M. Jr. 1967. Vascular plants of the Texas panhandle and south plains. Ph.D. dissertation (unpublished) Oklahoma State University, Stillwater, Oklahoma. 207 pp.

STEYERMARK, J. A. 1963. Flora of Missouri. Iowa State University Press, Ames, Iowa. 1728 pp.

UNITED STATES DEPARTMENT OF AGRICULTURE. 1950. Soil Survey, Woods County, Oklahoma. Department of Agriculture, Washington, D.C. 107 pp.

WATERFALL, U. T. 1972. Keys to the flora of Oklahoma. published by author, Oklahoma State University, Stillwater, Oklahoma. 246 pp.

FIGURE 1. LITTLE SAHARA STATE PARK SHOWING VEGETATION DISTRIBUTION

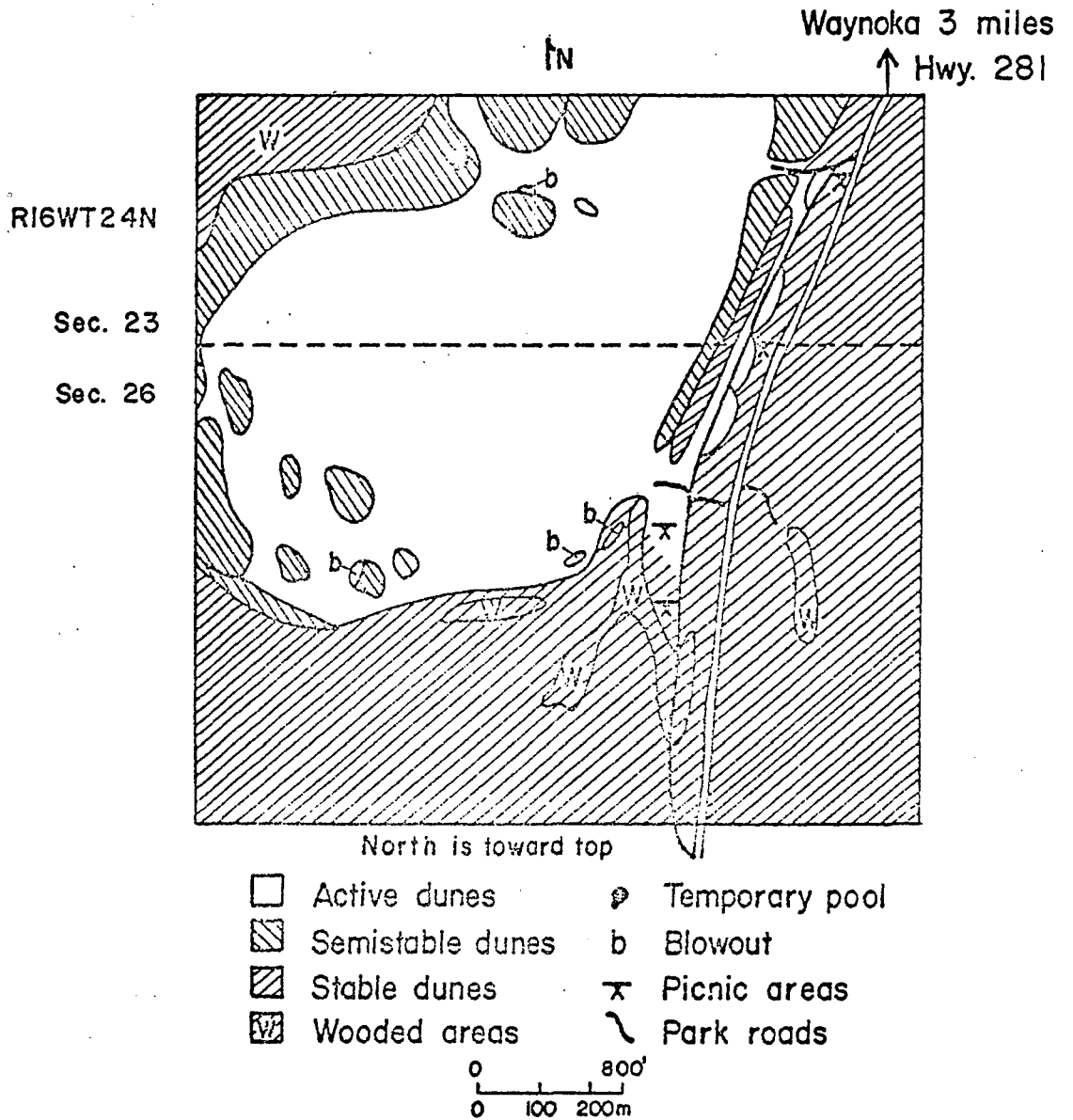


FIGURE 2. DIAGRAMMATIC REPRESENTATION OF THE PARTS OF A TYPICAL SAND DUNE

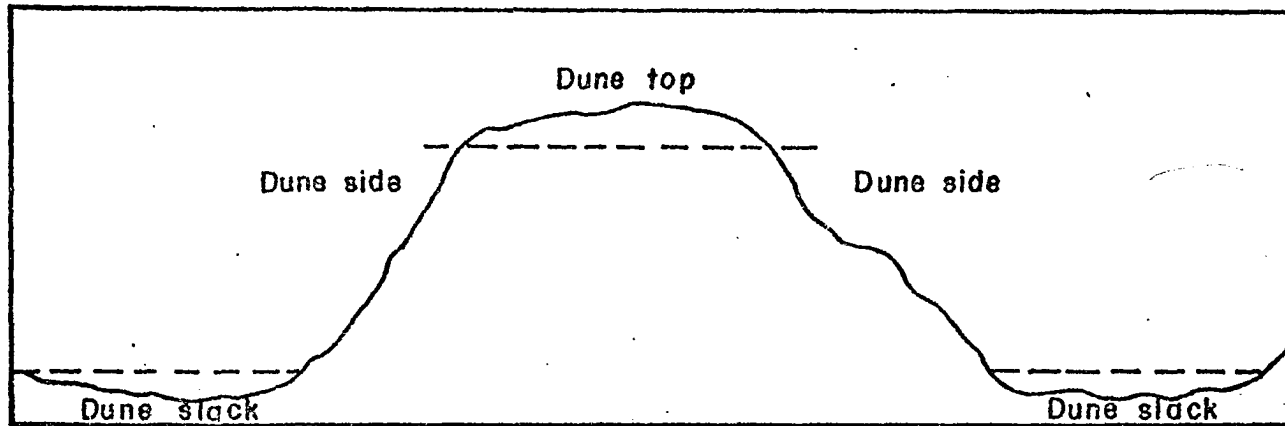


TABLE 1

A comparison of the species at Little Sahara State Park with four other sand dune areas.

AREA	LOCATION FROM LITTLE SAHARA AND SIZE	% OF AREA'S SPP. AT LITTLE SAHARA	% OF LITTLE SAHARA SPP. AT AREA
NE Texas Panhandle (Rowell, 1967)	150 km WSW 100+ sq km	70	94
Winkler & Ector Co., Texas (Collins, 1966)	700 km SW 1100 sq km	54	59
Weld Co., Colorado (Ramaley, 1939)	550 km NW "a few sq km"	32	28
Nebraska sandhills (Pool, 1914)	650 km NNW 47000 sq km	32	34

THE PLANT COMMUNITIES OF THE SAND DUNES
IN NORTHWESTERN OKLAHOMA

INTRODUCTION

In northwestern Oklahoma there are deposits of wind blown sand and some active sand dune complexes on the north sides of the major rivers. Not much is known about the vegetation of these dune areas. They have an assortment of plant communities, with areas of active non-vegetated sand dunes, semi-stable dunes with sparse vegetation of one or a few species, and areas of stable dunes that support comparatively dense diverse vegetation.

Little has been published on factors affecting the vegetation communities of non-coastal sand dune areas in recent years. Several studies dealing with coastal dunes in Europe found moisture, effects of other plants, and seed dispersal important factors in plant distribution (Ranwell, 1958; Pemadasa, et al., 1974; Pemadasa and Lovell, 1974; Morton, 1974a and b). On coastal dunes in the United States others have noted the importance of salt spray (Wells and Shunk, 1938; Oosting and Billings, 1942; Art, et al., 1974).

The study of the ecology of plant communities on non-coastal dunes in the United States began with Cowles' (1899) study on succession on the Lake Michigan sand dunes. Many workers after Cowles have described different successional

sequences for plant communities in sand dune areas. Pool (1914) described a number of successional and climax communities in the Nebraska Sandhills. Later, nonquantitative investigations of sand dunes in Colorado (Ramaley, 1939), the Nebraska Sandhills (Tolstead, 1942) and the western Texas Panhandle (Hefley and Sidwell, 1947) reported climax communities of these areas and the successional stages that led to them.

Many of these sand dune studies provide inferred successional sequences based on field observation, but except where pioneer species can be observed colonizing barren sand, the age of a stabilized sand area must be inferred from the vegetation present. Most of these studies are of insufficient duration to observe all the successional stages that occur on one initially barren area. With the exception of the Lake Michigan studies by Cowles (1899) and Olsen (1958), most early dune investigators had no way to assess the ages of plant communities or dunes. In some recent analyses carbon dating has been used (Yarranton and Morrison, 1974) or dunes were investigated that move at fairly steady rates in one direction (Chadwick and Dalke, 1965).

There are two other types of studies on dune areas in the Great Plains of North America. One consists of taxonomic lists of families, genera, and species with some information on their abundance and distribution (Collins, 1966; Rowell, 1967). The other contains quantitative assessments of the dune vegetation, as found in a study of the sand hills of Saskatchewan (Hulett et al., 1968) and one carried out in eastern Colorado (Daley, 1972).

Since quantitative information on the sand dune communities similar to those in northwestern Oklahoma is exceedingly sparse, and since there is no published information on the sand dune regions of Oklahoma, I began a study in 1977

of the plant communities at two sets of sand dunes in Woods County in northwestern Oklahoma.

The purposes of this study were: (1) collect data on the vegetation of the sand dunes and (2) describe the communities of the stable sand dunes by a quantitative and repeatable method.

THE RESEARCH SITES

The first of two sites investigated, and the most intensively studied site, was Little Sahara State Park, (T24N, R16W, SW Sec. 23 and NW Sec. 26) located 4.8 km south of Waynoka in Woods County, Oklahoma. The park is relatively small (146 ha) and though there is some light cattle grazing it is used primarily for recreation: picnicking, hiking, and off-road vehicles. The off-road vehicular activity is confined almost exclusively to the active nonvegetated dune areas.

The other dune site, also in Woods County, was a 65 ha area on the Eden Ranch (T26N, R17W, SE Sec. 17, SW Sec. 16 NW Sec. 21), 8 km ESE of Freedom and is in private ownership. The sampled dunes are subject to very light cattle grazing and cattle or their effects were never seen. This dune area consists mainly of unstable and semi-stable dunes with numerous active, unvegetated dunes and blowouts. Other than the cover being generally less at the Eden Ranch the two sites appeared quite similar. The Eden Ranch is about 26 km northwest of Little Sahara State Park and both sites are just north of the Cimarron River.

Both sites consist of dune complexes, with dunes up to 10 m high, and intervening low areas or slacks. These slacks frequently lack drainage channels, but due to the high infiltration rate of the sand soil, even after heavy rains, no pooling of water occurs.

The climate of both sites is continental with hot summers and frequent summer droughts (Borchert, 1950). The average annual precipitation at the Eden

Ranch is 64 cm and at Little Sahara State Park is 65 cm, with most occurring from April to September (Curry, 1970).

Both sites have the same two soil types: (1) Dune Sands -- unconsolidated Quaternary sand drifted from the bed of the Cimarron River, frequently showing the effects of wind erosion, and normally unvegetated or with sparse and patchy vegetation; (2) Trivoli Fine Sands, Dune Phase -- unconsolidated, wind drifted Quaternary sands, differing from Dune Sands in having a fairly heavy cover of vegetation and not subject to wind erosion unless the vegetational cover is disturbed (USDA Soil Survey, Woods Co., 1950).

While water erosion at the research sites is non-existent, wind erosion has resulted in the formation of a topographically complex environment. The general direction of dune movement is eastward and all long axes of the stabilized dunes are similarly oriented, though these may also occur as circular mounds without a major axis. If present, the long axis of a dune is serpentine because these dunes do not move as a unit but rather in a piecemeal, non-uniform manner.

During the study, 181 species of vascular plants, encompassing 145 genera and 55 families were found at the research site. An annotated checklist of the vascular plants of the Little Sahara research site can be found elsewhere (Sherwood and Risser, 1980).

Dominant and conspicuous vegetation observed on the stable sand dunes consists of sandsage (Artemisia filifolia*), aromatic sumac (Rhus aromatica), sandhill plum (Prunus angustifolia), Riddell groundsel (Senecio riddellii), yellow evening primrose (Calylophus serrulatus), little bluestem (Schizachyrium scoparium), sand lovegrass (Eragrostis trichoides), and sand dropseed (Sporobolus cryptandrus).

*Artemisia filifolia follows Carroll and Johnston (1970)

The semi-stable dunes often show quite variable species composition but several common species are Riddell grounset, scarlet pea (Indigofera miniata), Missouri spurge (Euphorbia missurica), sandlily (Mentzelia nuda), plains sunflower (Helianthus petiolaris), sand dropseed, purple sandgrass (Triplasis purpurea), and big sandreed (Calamovilfa gigantea). There are only three species that are the primary invaders on non-vegetated sand dunes, the two grasses, big sandreed and blowout grass, (Redfielda flexuosa) and the legume, lemon scurfpea (Psoralea lanceolata). These species grow alone in pure stands or grow together in all possible combinations. In addition to the differences in plant species caused by variations in topography and sand stability, there is also a temporal or seasonal differentiation, with some species like six-week fescue (Vulpia octoflora) and spotted beebalm (Monarda punctata) present only in the spring and absent in the fall. Others, such as northern croton (Croton glandulosus) and Texas palafoxia (Palafoxia texana) are present only in the fall.

METHODS

Since one of the purposes of this study was to find and quantitatively define plant communities on the stable dunes, selection of sampling areas was based upon physical characteristics, rather than on the species present or the "field appearance" of the communities. Topographic position and the amount of natural disturbance were used as the criteria in sample area selection. The stable dunes (i.e., dunes with no sand movement and densely vegetated) were divided into three parts for sampling purposes: dune tops - the level or gently undulating upper portions of the dunes; dune sides - the steeply sloping portions of the dunes; and dune slacks - the flat of gently sloping areas between dunes (Fig. 1). Transects were randomly placed along the long axis of dune tops, horizontally and vertically on dune sides, and in dune slacks (Fig. 1). Because the long axes of most dunes were oriented north-south, the dunes had extensive east and west facing sides, but the south facing and especially the north facing sides were almost nonexistent. Therefore only the east and west facing sides were sampled.

Most transects consisted of 32 contiguous, 1-m² quadrats. Depending on local topography, occasionally a transect deviated slightly from 32 quadrats. A total of 32 quadrats were used for three reasons: (1) this proved to be an adequate to sample the major species when tested statistically at the 5% level (Avery, 1975); (2) this length is divisible into subsets by two or powers of two and; (3) this length

would, on vertical dune sides, normally span the distance from the dune top to the slack. Quadrats of 1-m² were chosen because this size was not so large as to obscure transitions between communities and not so small that a single plant, such as a large sandsage, would appear in several adjacent quadrats. In each quadrat the species present and aerial cover of each were recorded, as well as the amount of bare ground. A total of 42 transects, (composed of 1276 quadrats) were taken, 30 from Little Sahara State Park and 12 from the Eden Ranch. Because rare species provide little or no useful information but can obscure results, species with both low cover values and infrequent occurrence were eliminated from the analyses. Of 107 species encountered in the sample quadrats, 62 were retained for subsequent analyses.

Two potential classification methods were considered, ordination and cluster analysis. Ordination techniques have been widely used in ecological analysis (Anderson, 1971; Gauch and Whittaker, 1972; Goff and Mitchell, 1975; Kessel and Whittaker, 1976; Gauch, et al., 1977). Ordination techniques have a significant shortcoming because the results of ordinations still must be divided into groups more or less subjectively, even with a technique such as principal component ordination (Noy-Meir and Austin, 1970).

The problem of selecting groups from ordination results can largely be overcome by the use of cluster analysis techniques. The technique employed in this study was an unweighted pair-group arithmetic average method using standardized species cover data (Sneath and Sokal, 1973). Results of this clustering method can be used to generate a phenogram showing relationships among the units being investigated. I employed Pearson product-moment correlation similarity matrices, hereafter called correlation matrices, since they give high similarities between the

operational units when the units show the same pattern of variation. However cluster analysis forms clusters regardless of whether or not clusters exist in the input data. This potential complication is not insurmountable since phenograms that result from cluster analysis can be evaluated for spurious clustering. A cophenetic matrix can be calculated from the phenogram, compared to the original data matrix, and a cophenetic correlation coefficient between the two matrices generated. The two matrices can be plotted against each other in a bivariate scatter diagram and the areas of high and low congruence can be ascertained; therefore the regions and amount of distortion present in the phenogram can be determined (Sneath and Sokal, 1973).

Care should be used in interpretation of phenograms so that they are not used to describe relationships that have resulted from distortion of the input matrix rather than actual relationships implicit in the input. In general the distortion in a phenogram increases from the branches to the trunk with the portions nearest the trunk being in the region of greatest distortion. To aid in the interpretation of phenograms used in this study, a dashed line has been placed across the phenogram to indicate the center of the region where the distortion, as determined from comparison of the cophenetic correlation matrix with the original data matrix, is increasing rapidly. The reader should keep in mind that the line is merely centered on a region where distortion increases rapidly. Normally small shifts of the line to the right or left have little effect on the interpretation of a phenogram.

To reduce the size of some phenograms and aid in the illustration of the results, selected portions of some phenograms were eliminated. This was done in such a manner so the reduced phenograms accurately represent the entire phenogram from whence they were derived. Phenograms thus reduced will be designated as "partial phenograms" in the figures.

RESULTS

Percent cover of 62 species and bare ground were analyzed. These same three species had the highest frequency and cover values, though the order was not the same for frequency and cover (Sherwood, 1980). The species with the highest percent relative cover (RC) and percent relative frequency (RF) were: sandsage (RC=19.5%, RF=6.8%), little bluestem (9.6%, 7.0%), and sand dropseed (7.8%, 7.5%).

ANALYSIS OF SINGLE TRANSECTS

Results from single transect analysis will be presented first, then results from analyses that incorporate more than one transect. Since placement of sample transects was determined by topographic position and not vegetation, transects from the different positions were analyzed to determine if there were distinguishable communities within these topographic regions. The results of these analyses were as expected: when single transects either from dune tops, horizontally on dune sides, or those in slacks were clustered by quadrats, no discrete, nondistorted clusters were found. This was true for samples taken in the spring and fall, and for both research sites. The major clusters that occur in these phenograms were highly distorted and the cophenetic correlation coefficients were relatively low (less than 0.7). A horizontal transect (Little Sahara, Fall, 1977) from the west side of a dune is used as a representative example (Fig. 2). This phenogram has no major distinct clusters and a low cophenetic correlation coefficient (0.676). These results indicate that

there are not distinct or discrete communities in this transect. Another result from the phenogram (Fig. 2) is that the quadrats of the transect, which were numbered sequentially during sampling, frequently do not initially pair with adjacent quadrats. Some initial pairings (e.g. quadrats 2 and 20, 10 and 25) are of spatially separated rather than adjacent quadrats. Apparently there is not a gradient along the transect but rather the vegetation is fairly uniform. The observed groupings to the right of the distortion line in Fig. 2 are most likely caused by the heterogeneity of the vegetation within one sampling areas and are not indicative of different communities. All the other types of transects mentioned previously gave results similar to those described above and presented in Fig. 2.

The only type of single transects not mentioned thus far are those which were placed vertically on dune sides (transects running from dune tops to slacks). When the quadrats from a vertically placed transect on a dune side were analyzed, they usually formed two major nondistorted clusters. The phenogram that resulted from a vertical transect (Little Sahara, Spring, 1977) illustrated in Fig. 3 is typical. This transect was from the west side of a dune, and the quadrats in this transect were numbered sequentially from the dune top to the dune slack. The two major clusters in this phenogram (Fig. 3), called the upper cluster and the lower cluster, are respectively composed of quadrats 1-19, except 18 (from the upper part of the dune side) and quadrats 20-32 and 18 (from the lower part of the dune side). Quadrats 17-19 appear to be in a transition zone, quadrats 17 and 19 are the last two to join the upper cluster, though 18 is not the last to join the lower cluster. Within the upper cluster there is little pattern to the arrangements of the quadrats except for the aforementioned 17 and 19. The lower cluster does have some internal arrangement of quadrats. The two major subclusters are composed of quadrats 20-25 and of 26-32 plus 18. The two subgroupings of the lower cluster are composed

of quadrats that formed linear sequences in the original transect (with the exception of quadrat 18).

The cophenetic correlation coefficient for this phenogram (Fig. 3) was 0.838, higher than the cophenetic correlation coefficients obtained from the phenograms for transects placed on dune tops, horizontally on dune sides, and in slacks. The amount of distortion in this phenogram was not as high as in the Fig. 2 phenogram, the highest distortion shown in the Fig. 3 phenogram occurred when the two major clusters were joined. Because distortion was highest in joining the two major clusters that divided the transect (and the corresponding dune side) into an upper and a lower portion, these two regions are considered discrete. Similar results were obtained when quadrats from other vertically placed transects were clustered, namely there would form a cluster of quadrats from the upper slope and a cluster of quadrats from the lower slope. In most cases these clusters would exhibit arrangement of quadrats like that in the lower cluster of Fig. 3, that is, there would be groups of quadrats within the cluster that formed linear sequences in the original transect. In all single vertical transect phenograms the amount of distortion was lower and the cophenetic correlation coefficients were higher (greater than 0.8) than in the other types of single transect phenograms.

At this point in the analyses the results from single transects were similar to what had been reported in the literature and what was suggested by field reconnaissance. That is, the top and the base of a dune are different.

ANALYSIS OF COMBINED TRANSECTS

As the next step in the analysis, quadrats from more than one transect were combined and clustered. When transects from two different dune slacks were clustered, no distinct major clusters were formed (Fig. 4). The cophenetic

correlation coefficient (0.706) was low and the distortion near the trunk portion of the phenogram was high. Quadrats from both slacks were intermingled and often grouped together at high levels of similarity. While there were groupings involved quadrats from only one of the slacks, there was sufficient association of quadrats from the two slacks to conclude that the slacks were not different. Similar results were obtained when other combinations of dune slack transects were clustered. Likewise, when transects from different dune tops were clustered, the resultant phenograms consisted of intermingled quadrats from different dune tops. Different dune tops do not appear to be different from each other.

To investigate if dune tops are distinct from slacks, transects from dune tops and dune slacks were combined and clustered, giving clearcut results (Fig. 5). This phenogram shows division into two well defined major groups with little distortion. The cophenetic correlation coefficient is 0.928. All quadrats from the dune top were in one of the major subclusters and all of the quadrats from the dune slack were in the other major subcluster. Results very similar to these were obtained from clustering other combinations of dune tops and dune slack transects.

All results so far indicate that there are two distinct types of vegetation on the dunes, a dune top vegetation type and a dune slack vegetation type. To investigate the relationships and boundaries of these types further, quadrats from more than one vertical transect on a dune side were clustered. The results from these clusterings were not as expected. The two distinct major clusters found when single vertical transects were analyzed disappeared and instead, numerous small and poorly separated clusters formed. Typical results were obtained when vertical transects from the east and west facing sides of a dune were clustered and no distinct clusters were formed (Fig. 6).

Quadrats from the east facing dune side are found intermingled with those from the west facing dune side. East and west facing side quadrats seldom formed an initial pair, but usually were clustered together in small groups. This result indicates that the two different exposures did not support different vegetation types. In the entire phenogram there were eight subclusters to the branch side of the region of high distortion, the four in Fig. 6 are representative of these. The cophenetic correlation coefficient (0.662) was lower than the cophenetic correlation coefficients for the single vertical transect phenograms (ca. 0.8). The disappearance of the two distinct clusters was probably due to the increased number of quadrats in the analysis which increases the total amount of information about the dune sides. The increase number of quadrats in the analyses suggests that the rather definite result obtained from single vertical transect analyses may have been due to the small sample size. This is evidence against the existence of two distinct vegetation types on the dunes, since there are not two distortion-free major clusters in these combined phenograms as there were in the single vertical transect phenograms (Fig. 3). Even if the two major clusters in the phenograms generated from combined vertical transects are examined, ignoring the distortion, they are not composed of quadrats from the upper and lower portions of the dune sides, but rather a scattering of quadrats from all parts of the dune side transects.

The analyses were then carried one step further, and large combinations were made by joining transects from dune tops, dune slacks, and vertically dune sides. The large phenograms that resulted from clustering such combinations of transects did not show two non-distorted major groups. When quadrats on a dune top, a dune slack, and a vertical side were combined, the resultant phenogram had high distortion when the major subclusters are joined (Fig. 7). Also there was an intermingling of quadrats from the dune top with those from the vertical side and an

intermingling of quadrats from the vertical side with those from the slack. Quadrats from the dune top are never joined with those from the slack, these come together only in the final union of the two major clusters. The distinctness of the dune top quadrats from the slack quadrats is still observable in this phenogram, but the addition of an intermediate region (the dune side, spanning the distance between top and slack) obscures the non-distorted distinctness between tops and slacks.

The apparent distinctness found earlier between dune tops and slacks is probably an artifact of the sampling method employed. The high distortion in the phenogram (Fig. 7) is probably a result of trying to divide a continuously changing region (dune tops to dune slacks) into discrete units or clusters. When sampling areas are disjunct, as when tops are compared to slacks, discrete clusters can be formed without high distortion. When the sampling areas are continuous and contain large numbers of quadrats, as when tops, sides, and slacks are combined, no discrete or nondistorted major groups are formed.

I also expected that comparisons of the same area at different times would give distinct clusters. When the same area (such as a slack) was sampled in the spring and fall, two distinct clusters were formed, one containing all the quadrats from the spring sample and the other containing all the quadrats from the fall sample (Sherwood, 1980).

All the analyses performed thus far have been concerned with quadrats. Investigation of individual species response by cluster analysis generally gave non-interpretable results. When species were clustered, the resultant phenograms were not good representations of the data, they had high distortion and low cophenetic correlation coefficients (Sherwood, 1980).

CONCLUSIONS

The intention of this study was to find and describe distinct plant communities on the stable sand dunes in northwestern Oklahoma. The communities were to be identified and defined by use of repeatable mathematical techniques. In the results from single transect analyses, there appeared to be two different vegetation types or communities on the stable dunes, one occurring in dune slacks and on the lower slopes of the dunes and the other occurring on the dune tops and the upper slopes, with a relative narrow transition zone between them. When larger samples containing quadrats from all regions were clustered, the clear division between dune tops and slacks disappeared, and no definite demarcation between these two areas remained. The rather definite results from single transect analyses seems to be partly an artifact of small sample size. Discrete boundaries cannot be drawn to delineate proposed dune tops and slack communities.

The stable sand dunes are vegetated by a single community that is composed of casual associations of species that co-exist in time and are in near proximity. With a sufficient distance, either spatially or temporally, comparison of the disjunct areas will show them to be distinct and clearly separable. When the regions that connect areas are included, the distinctiveness disappears and only a single variable region remains. The northwestern Oklahoma sand dunes are as complex vegetationally as they are topographically, and cannot be divided mathematically into distinct communities.

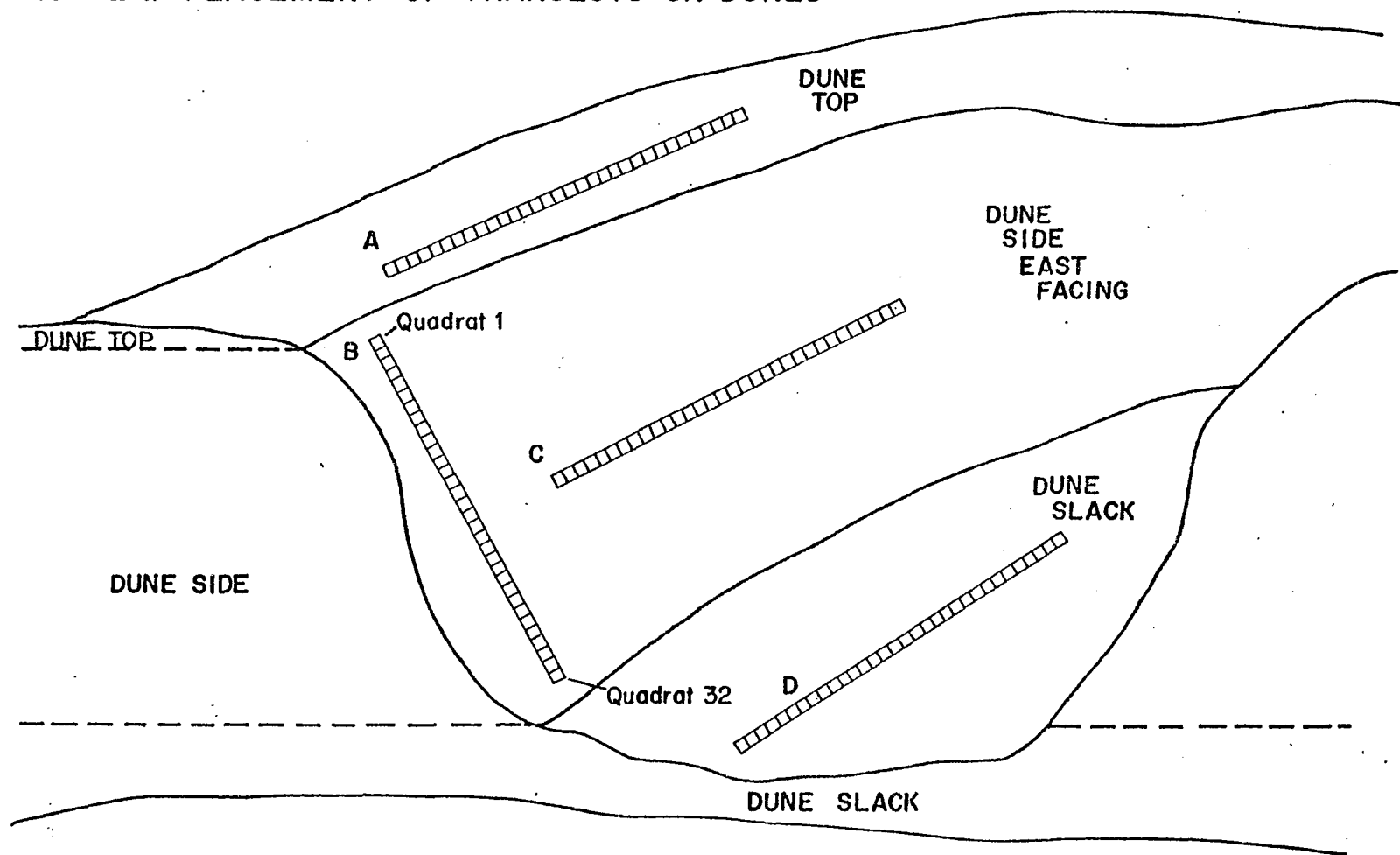
LITERATURE CITED

- ANDERSON, A. J. B. 1971. Ordination methods in ecology. *J. Ecol.* 59: 713-726.
- ART, H. W., F. H. BORMANN, and G. M. WOODWELL. 1974. Barrier Island forest ecosystem: role of meteorological nutrient inputs. *Science* 184: 60-62.
- AVERY, T. E. 1975. Natural resources measurement. McGraw-Hill, St. Louis, MO.
- BORCHERT, J. R. 1950. The climate of the central North American grassland. *Ann. Amer. Geogr.* 40: 1-39.
- CHADWICK, H. W. and P. D. DALKE. 1965. Plant succession on dune sands in Fremont county, Idaho. *Ecology* 46: 750-780.
- COLLINS, L. T. 1966. Vascular flora of the Concho Bluff ecozone. M.S. thesis (unpublished). Texas Technological College, Lubbock, Texas.
- CORRELL, D. S. and M. C. JOHNSTON. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner, Texas.
- 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; 361-399.
- CURRY, B. R. 1970. Climate of Oklahoma. U.S. Government Printing Office, Washington, D.C.
- DALEY, R. H. 1972. The native and sage vegetation of Western Colorado. M.S. thesis (unpublished). Colorado State University, Ft. Collins, Colorado.
- GAUCH, H. C. and R. H. WHITTAKER. 1972. Comparison of ordination techniques. *Ecology* 53: 858-875.

- _____, _____, and T. R. WENTWORTH. 1977. A comparative study of reciprocal averaging and other ordination techniques. *J. Ecol.* 63: 157-174.
- GOFF, F. G. and R. MITCHELL. 1975. A comparison of species ordination results from plot and stand data. *Vegetatio* 31: 15-22.
- HEFLEY, H. M. and R. SIDWELL. 1947. Geological and ecological observations of some high plains dunes. *Amer. J. Science* 243: 361-376.
- HULETT, G. K., R. T. COUPLAND, and R. L. DIX. 1966. The vegetation of dune sand areas within the grassland region of Saskatchewan. *Canad. J. Bot.* 44: 1307-1331.
- _____, C. D. SLOAN, and G. W. TOMANEK. 1968. The vegetation of remnant grasslands in the loessial regions of northwestern Kansas and southwestern Nebraska. *Southwest. Nat.* 13: 377-391.
- KESSEL, S. R. and R. H. WHITTAKER. 1976. Comparison of three ordination techniques. *Vegetation.* 32: 21-29.
- MORTON, A. J. 1974a. Ecological studies of a fixed dune grassland at Newborough Warren, Anglesey. I. The structure of the grassland. *J. Ecol.* 62: 253-260.
- _____. 1974b. Ecological studies of a fixed dune grassland at Newborough Warren, Anglesey. II. Causal factors of the grassland structure. *J. Ecol.* 62: 261-278.
- NOY-MEIR, I. and M. P. AUSTIN. 1970. Principal components ordination and simulated vegetational data. *Ecology.* 51: 551-552.
- OLSEN, J. S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. *Bot. Gaz.* 119: 125-170.
- OOSTING, H. J. and W. D. BILLINGS. 1942. Factors affecting vegetational zonation on coastal dunes. *Ecology.* 23: 131-142.

- PEMEDASA, M. A., P. GREIG-SMITH, and P. H. LOVELL. 1974. A quantitative description of the distribution of annuals in the dune system at Aberffraw, Anglesey. *J. Ecol.* 62: 379-402.
- _____, and P. H. LOVELL. 1974. Factors affecting the distribution of some annuals in the dune system at Aberffraw, Anglesey. *J. Ecol.* 62: 403-416.
- POOL, R. J. 1914. A study of the vegetation of the sandhills of Nebraska. *Minn. Bot. Studies*, part III. 4: 189-312.
- RAMALEY, F. 1939. Sand-hill vegetation of northeastern Colorado. *Ecol. Mongr.* 9: 1-51.
- ROWELL, C. M. 1967. Vascular plants of the Texas Panhandle and south plains. Ph.D. dissertation (unpublished). Oklahoma State University.
- SHERWOOD, R. T. B. 1980. Vegetation of the Woods County, Oklahoma sand dunes. Ph.D. dissertation (unpublished). University of Oklahoma.
- SHERWOOD, R. T. B. and P. G. RISSER. 1980. Annotated checklist of the vascular plants of Little Sahara State Park, Oklahoma. *Southwest. Nat.* in press.
- SNEATH, P. H. A. and R. R. SOKAL. 1973. *Numerical Taxonomy*. W. H. Freeman and Co., San Francisco, Calif.
- TOLSTEAD, W. L. 1942. Vegetation of the northern part of Cherry County, Nebraska. *Ecol. Mongr.* 12: 255-292.
- UNITED STATES DEPARTMENT OF AGRICULTURE. 1950. *Soil Survey, Woods County, Oklahoma*. Washington, D.C.
- WELLS, B. W. and I. V. SHUNK. 1938. Salt spray: an important factor in coastal ecology. *Bull. Torrey Bot. Club.* 65: 486-492.
- YARRANTON, G. A. and R. G. MORRISON. 1974. Spatial dynamics of a primary succession: nucleation. *J. Ecol.* 62: 417-428.

FIGURE 1. PLACEMENT OF TRANSECTS ON DUNES



A - DUNE TOP TRANSECT

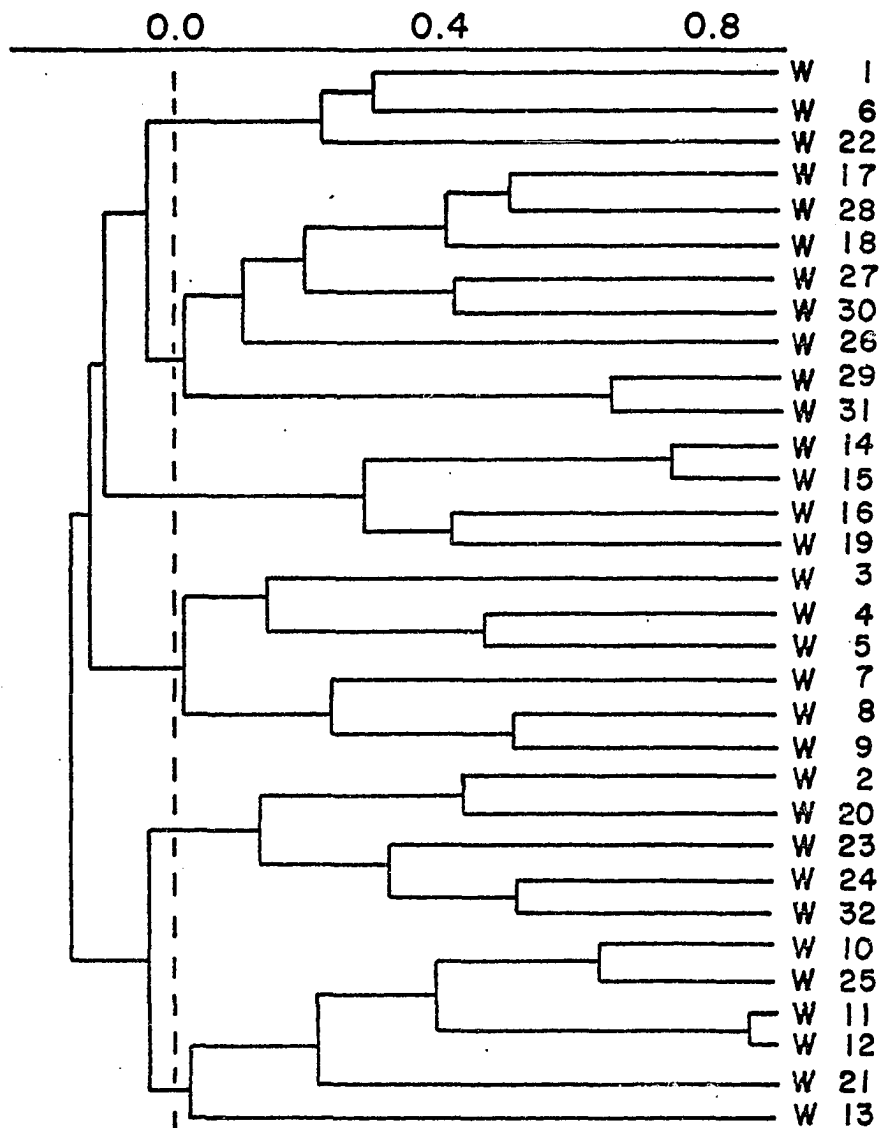
B - DUNE VERTICAL SIDE TRANSECT

C - DUNE HORIZONTAL SIDE TRANSECT

D - DUNE SLACK TRANSECT

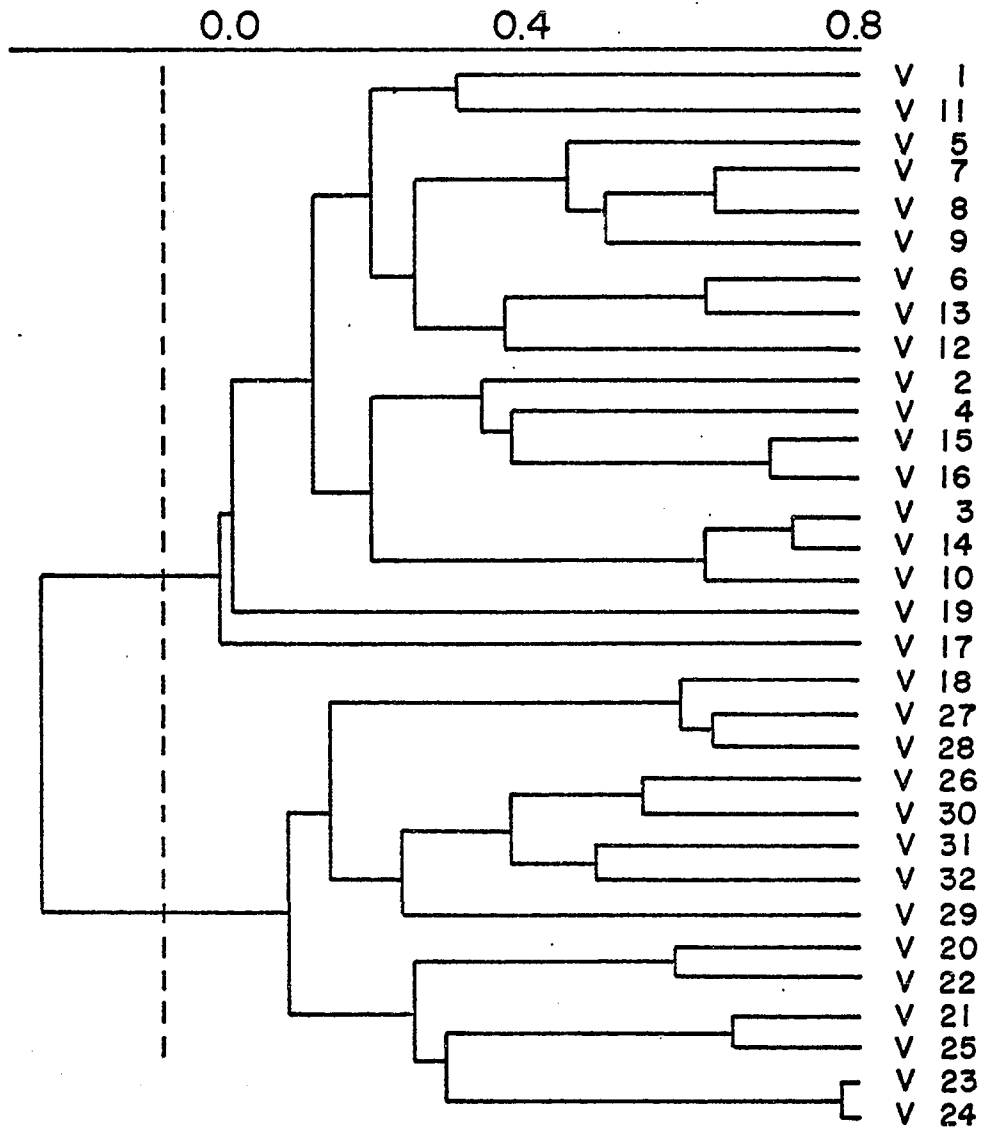
ALL TRANSECTS ARE COMPOSED OF 32 CONTIGUOUS 1 METER² QUADRATS

Figure 2. WEST FACING HORIZONTAL TRANSECT



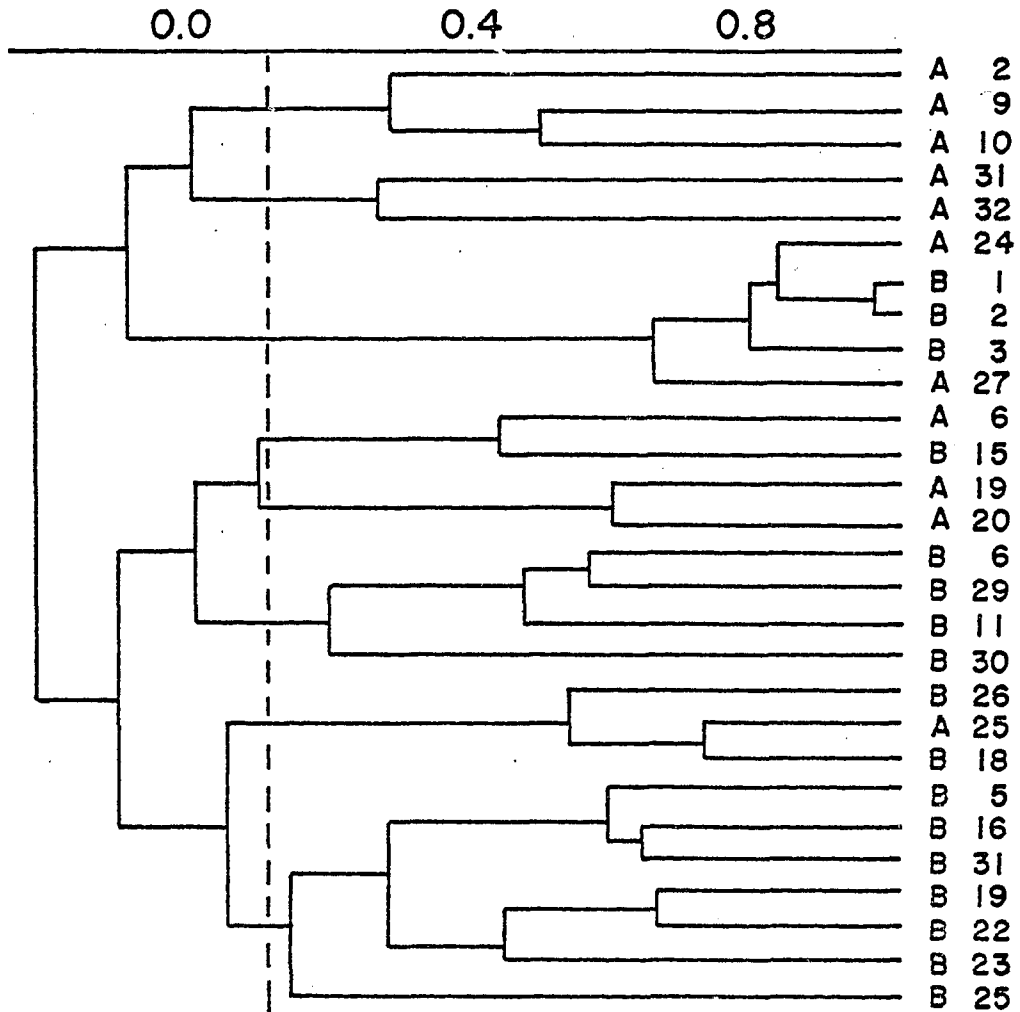
W(i) (i)TH QUADRAT FROM THE TRANSECT
 COPENETIC CORRELATION COEFFICIENT = .676

Figure 3. WEST FACING VERTICAL TRANSECT



V(i) (i)TH QUADRANT FROM TRANSECT
 V 1 AT TOP OF DUNE, V 32 AT BASE OF DUNE
 CORHENETIC CORRELATION COEFFICIENT = .838

FIGURE 4. TWO DUNE SLACKS COMBINED



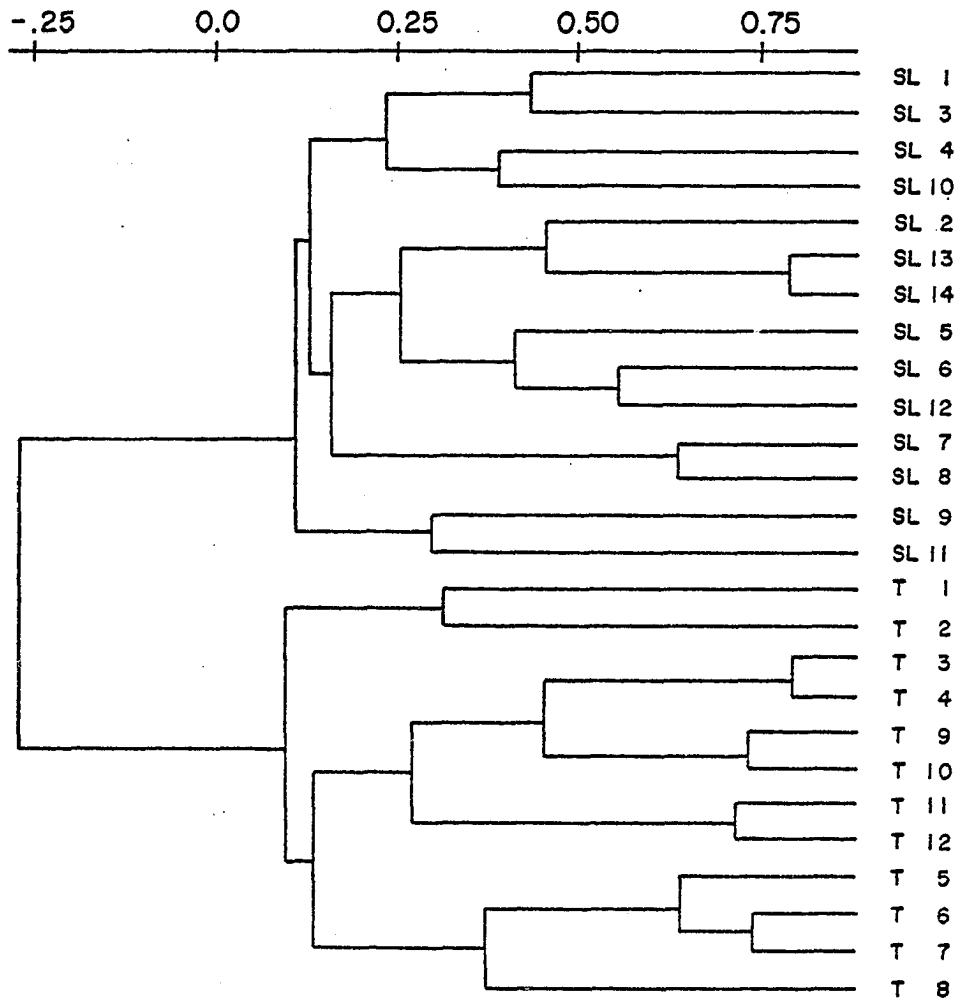
PARTIAL PHENOGRAM

A(i) QUADRAT (i) FROM SLACK A

B(j) QUADRAT (j) FROM SLACK B

COPHENETIC CORRELATION COEFFICIENT = .706

FIGURE 5. DUNE TOP AND DUNE SLACK COMBINED



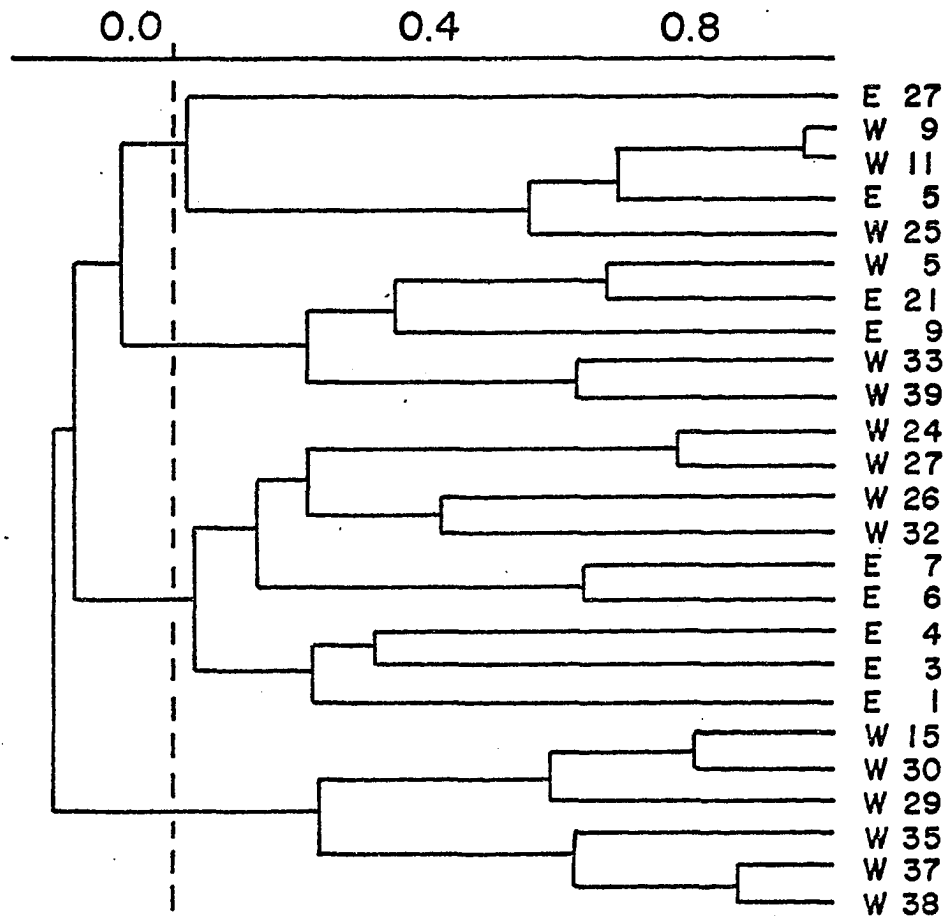
PARTIAL PHENOGRAM

T(i) (i)TH QUADRAT FROM A DUNE TOP TRANSECT

SL(j) (j)TH QUADRAT FROM A DUNE SLACK TRANSECT

COPHENETIC CORRELATION COEFFICIENT = .928

FIGURE 6. EAST AND WEST FACING VERTICAL
TRANSECTS COMBINED



PARTIAL PHENOGRAM

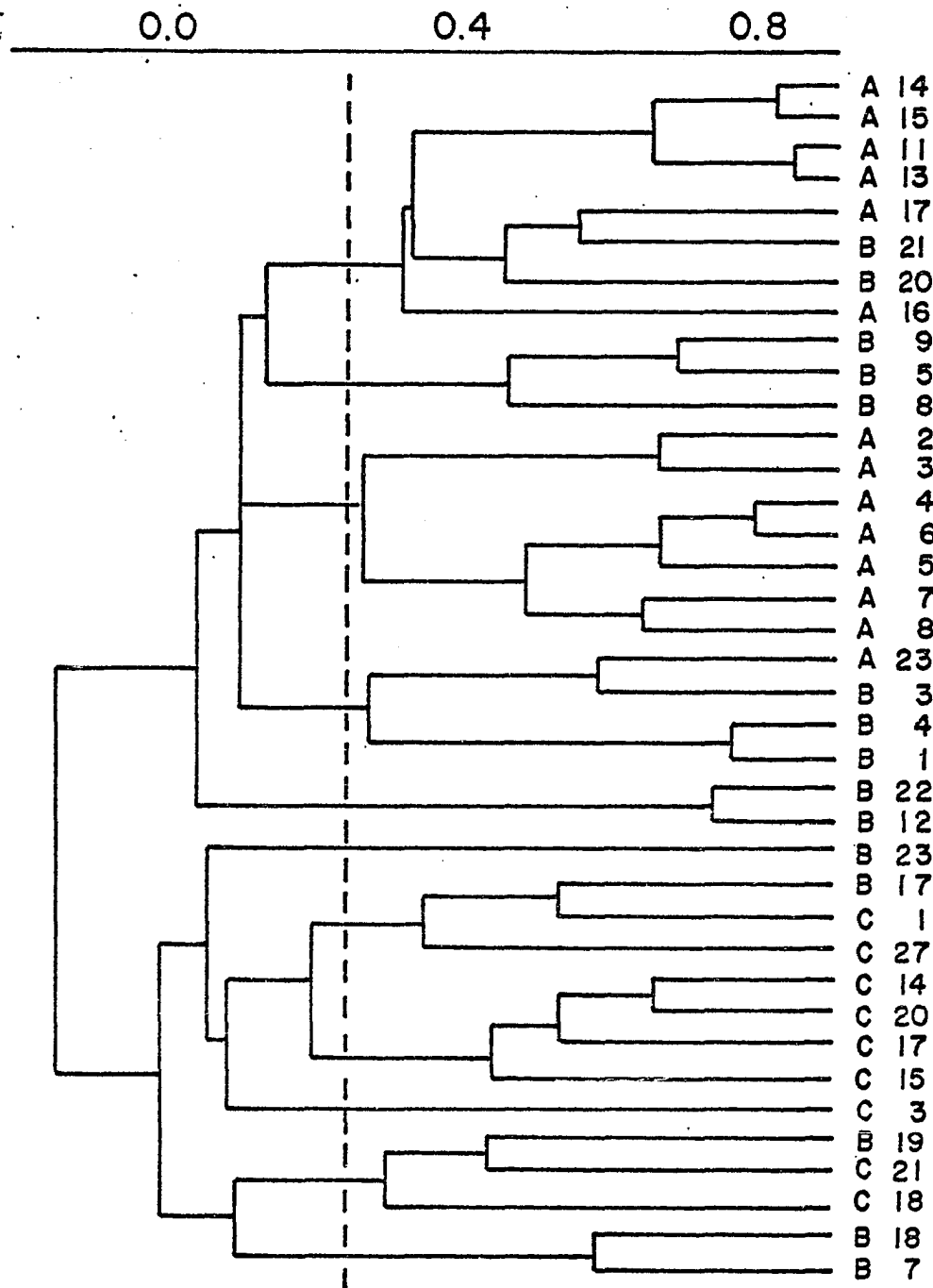
QUADRATS NUMBERED FROM THE DUNE TOP TO THE DUNE
SLACK

W(i) (i)TH QUADRAT FROM THE WEST FACING TRANSECT

E(j) (j)TH QUADRAT FROM THE EAST FACING TRANSECT

COPHENETIC CORRELATION COEFFICIENT = .662

FIGURE 7. TOP, VERTICAL, SIDE AND SLACK TRANSECTS
COMBINED



PARTIAL PHENOGRAM

A(i) (i)TH QUADRANT FROM DUNE TOP TRANSECT

B(j) (j)TH QUADRANT FROM DUNE VERTICAL SIDE TRANSECT;
QUADRANT I AT UPPER END

C(k) (k)TH QUADRANT FROM DUNE SLACK TRANSECT

COPHENETIC CORRELATION COEFFICIENT = .770

APPENDIX i

SPECIES COVER VALUES AND OCCURRENCES

SPECIES	TOTAL COVER M ²	TOTAL OCCURRENCES
<u>Artemisia filifolia</u>	146.711	725
<u>Schizachyrium scoparius</u>	72.155	743
<u>Sporobolus cryptandrus</u>	58.885	799
<u>Rhus aromatica</u>	55.898	350
<u>Indigofera miniata</u>	33.132	229
<u>Prunus angustifolia</u>	30.981	249
<u>Plantago patagonica</u>	22.885	141
<u>Ambrosia psilostachya</u>	22.190	304
<u>Eragrostis trichoides</u>	21.855	210
<u>Croton glandulosa</u>	20.546	360
<u>Paspalum setaceum</u>	17.176	337
<u>Calamovilfa gigantea</u>	17.008	663
<u>Helianthus petiolaris</u>	16.414	304
<u>Heterotheca villosa</u>	14.122	128
<u>Senecio riddellii</u>	13.147	148
<u>Psoralea lanceolata</u>	13.315	68
<u>Monarda punctata</u>	12.235	254
<u>Vulpia octoflora</u>	10.413	138
<u>Triplasis purpurea</u>	10.143	199
<u>Calylophus serrulatus</u>	8.315	244
<u>Aphanostephus skirrhobasis</u>	6.636	202
<u>Palafoxia texana</u>	6.413	150

<u>Celtis reticulata</u>	6.391	50
<u>Erigeron bellidiastrum</u>	6.348	199
<u>Yucca angustifolium</u>	5.870	42
<u>Mollugo verticillata</u>	5.747	68
<u>Andropogon hallii</u>	4.896	92
<u>Euphorbia missurica</u>	4.874	187
<u>Stillingia sylvatica</u>	4.327	72
<u>Ipomopsis longiflora</u>	4.057	52
<u>Cyperus</u> spp.	4.038	209
<u>Eriogonum annuum</u>	3.928	362
<u>Solidago petiolaris</u>	3.585	42
<u>Portulaca oleracea</u>	3.421	23
<u>Redfielda flexuosa</u>	3.136	31
<u>Croptilon divaricatum</u>	3.115	137
<u>Mentzelia nuda</u>	2.880	172
<u>Cenchrus incertus</u>	2.861	64
<u>Lepidium densiflorum</u>	2.832	101
<u>Commelina erecta</u>	2.677	167
<u>Bouteloua gracilis</u>	2.305	23
<u>Physalis heterophylla</u>	2.163	59
<u>Prunus gracilis</u>	2.100	7
<u>Froelichia gracilis</u>	1.696	20
<u>Penstemon buckleyi</u>	1.695	56
<u>Euphorbia carunculata</u>	1.546	27
<u>Sapindus saponaria</u>	1.476	34
<u>Opuntia humifusa</u>	1.471	29

<u>Dithyrea wislizenii</u>	1.443	117
<u>Solanum dimidiatum</u>	1.407	22
<u>Euphorbia glyptosperma</u>	1.400	38
<u>Gaura villosa</u>	1.361	36
<u>Dalea lantana</u>	1.306	49
<u>Ipomoea leptophylla</u>	1.300	26
<u>Portulaca mundula</u>	1.180	23
<u>Cryptantha minima</u>	1.150	25
<u>Chloris verticillata</u>	1.135	49
<u>Aristida purpurea</u>	.997	40
<u>Artemisia glauca</u>	.991	26
<u>Poa arachnifera</u>	.880	21
<u>Oenothera laciniata</u>	.855	39
<u>Bromus tectorum</u>	.795	22
<u>Elymus canadensis</u>	.775	38
<u>Apocynum cannabinum</u>	.743	69
<u>Bumelia lanuginosa</u>	.710	6
<u>Reverchonia arenaria</u>	.690	25
<u>Petalostemon villosum</u>	.642	15
<u>Croton texensis</u>	.631	35
<u>Psoralea digitata</u>	.605	9
<u>Polanisia jamesii</u>	.558	53
<u>Salsoli kali</u>	.537	31
<u>Rhus glabra</u>	.530	6
<u>Lithospermum incisum</u>	.525	39

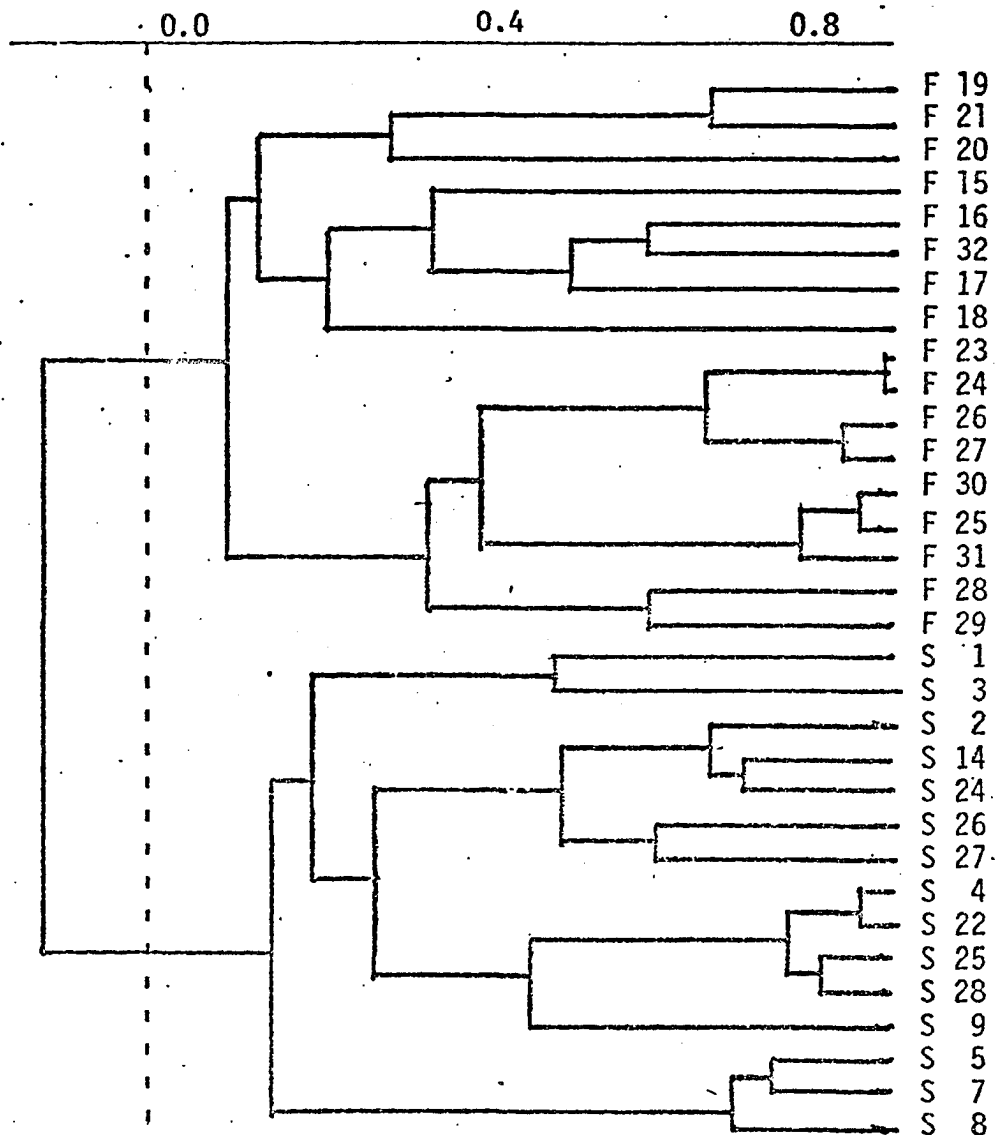
<u>Strophostyles leiosperma</u>	.426	11
<u>Mirabilis albida</u>	.422	41
<u>Asclepias arenaria</u>	.420	25
<u>Bromus unioloides</u>	.410	2
<u>Tradescantia occidentalis</u>	.285	33
<u>Triodanuis holzingeri</u>	.280	3
<u>Artemisia ludoviciana</u>	.230	6
<u>Cycloloma atripicifolium</u>	.228	24
<u>Cassia fasciculata</u>	.203	23
<u>Heliotropium convolvulaceum</u>	.193	16
<u>Linaria canadensis</u>	.187	29
<u>Pyrropappus grandiflorus</u>	.170	6
<u>Linum ridigum</u>	.095	8
<u>Lygodesmia rostrata</u>	.081	8
<u>Gaillardia pulchella</u>	.080	10
<u>Euphorbia hexagona</u>	.075	4
<u>Coryphantha vivipara</u>	.075	7
<u>Eragrostis oxylepis</u>	.070	3
<u>Vitis acerfolia</u>	.060	3
<u>Chenopodium leptophyllum</u>	.059	13
<u>Plantago rhodosperma</u>	.045	4
<u>Sorghastrum avenaceum</u>	.040	1
<u>Leptoloma cognatum</u>	.020	1
<u>Cirsium undulatum</u>	.020	3
<u>Symphoricarpus orbitulatus</u>	.015	2

<u>Solanum elaeagnifolium</u>	.015	2
<u>Orobanche ludoviciana</u>	.010	1
<u>Panicum oligosanthos</u>	.010	1
<u>Solanum americanum</u>	.010	1
<u>Oenothera rhombipetala</u>	.010	1
<u>Conyza canadensis</u>	.010	2
<u>Amaranthus palmeri</u>	.001	1

APPENDIX ii
TEMPORAL ANALYSIS

The sand dunes were sampled during two different times of year, with about a three month period in between. When quadrats from the spring sampling were clustered with those from the fall, the quadrats divided into distinct clusters. Figure 8 is an example of a phenogram from a dune slack that was sampled twice, once in the spring and once in the fall. In the phenogram (Fig. 8) quadrats separated into the spring sampling and the fall sampling. The cophenetic correlation coefficient for the phenogram in Fig. 8 was .790 and major distortion occurred only when the two major clusters, representing the two sampling times, were joined. As might be expected when quadrats from dune slacks are clustered, there is no noticeable pattern of the quadrats within the two major clusters in the phenogram. Other comparisons of spring and fall samples from the same parts of dunes gave results similar to those in Fig. 8, with the two major subclusters based on time of sampling. This is true when several transects from the spring and fall are combined and the quadrats clustered. Increasing the number of quadrats clustered does not result in loss of distinctiveness between the two sample times.

Figure 8 PARTIAL PHENOGRAM



FALL VS. SPRING, DUNE SLACK TRANSECTS, SAME AREA

COPHENETIC CORRELATION COEFFICIENT = .790

F (i) iTH QUADRAT FROM FALL SAMPLE

S (j) jTH QUADRAT FROM SPRING SAMPLE

MINERAL RELATIONS OF SELECTED SAND DUNE PLANT SPECIES

INTRODUCTION

In northwestern Oklahoma belts of wind-deposited sand occur on the north side of the major rivers. This sand is formed into a topographically complex series of low hills or dunes which are frequently well-vegetated. Because the soil of the dune areas is almost exclusively fine sand, water runoff and erosion are minimal. Precipitation infiltrates rapidly and much of the water percolates beyond the root zone.

The combination of a high infiltration rate with almost no clay or organic matter in the soil should result in low levels of many essential plant nutrients in the dune habitat. High rainfall and concomitant leaching of nutrients in tropical sandy soils has led to very low nutrient levels in these soils with the preponderance of the nutrients occurring in the vegetation (Stark, 1970; Westman, 1978; Stark and Jordan, 1978; Vitousek and Reiners, 1975). In tropical areas, differential selection of nutrients by different species has been found (Ernst, 1975; Westman, 1978). Woody species in the northeast United States also show differential selection and accumulation of various elements. Woodwell et al. (1975) concluded that plant species were apparent specialists in their use of nutrient elements. In Wisconsin, little bluestem was found to be an invader on low phosphorus soils as a result of a lower phosphorus requirement than existing vegetation (Wuenschel and Gerloff, 1971). In Oklahoma

however, Rice et al. (1960) found that little bluestem was apparently unable to invade abandoned fields because nitrogen and phosphorus levels were too low in these fields. Gerloff et al. (1966) found that different species of plants from similar habitat conditions exhibit considerable variation in mineral content levels. For example, some potassium accumulating species demonstrated dry weight concentrations of greater than 7% potassium whereas the average for other species from the same site was approximately 2%. Similarly the range of manganese levels in plants growing in a manganese rich bog was from 149-1061 ppm.

Seasonal trends in the nutrient levels of plant materials have been shown in several studies, though below ground parts have not been studied as well as above ground materials (Guna and Mitchell, 1966; Hart et al., 1932; Marrs, 1978). The little work on mineral retention in sand dune areas in the temperate zone has been mostly from coastal sand dunes. Coastal dune environments are very different from those of inland dunes, primarily as a result of factors such as salt spray (though other conditions such as high leaching rates may be similar).

At the onset of this study I anticipated that the soil of the Oklahoma sand dunes would have low levels of minerals present in the ecosystem because the same factors of high leaching and low retention. Some studies on sand dune soils have found nitrogen, phosphorus, potassium, and calcium to have deficient levels for most plant growth (Pool, 1914; Burzlaff, 1962; Eck, et al., 1968). Other studies on mineral nutrition in sand dune plants have shown that nitrogen and phosphorus appear especially limiting, and other elements are less limiting. In experimental studies, addition of these other elements had little effect on plant growth, but addition of nitrogen and phosphorus had a major effect on growth (Pemadasa and Lovell, 1974).

I hypothesize that different species from the Oklahoma sand dunes would accumulate minerals in different amounts. In addition, there should be within plant fluctuations in nutrient levels throughout the year. To test these two hypotheses about mineral levels, I began a study of the vegetation of two sets of sand dunes that occur north of the Cimarron River in Woods County, Oklahoma.

THE RESEARCH SITES

Two sites were used in this study, the first was Little Sahara State Park, located approximately 4.8 km south of Waynoka (R16W T24N, SW S23 NW S26). The park is relatively small, 146 ha, and is used primarily for recreation such as picnicking, some hiking, and considerable activities involving off-road vehicles; also there is some light cattle grazing. Vehicular activity is confined almost exclusively to the active, non-vegetated dunes and there is no disturbance to the stable vegetated dunes at the south end of the park. Some of the semi-stable dunes show minor impact from off-road vehicles but areas of disturbance are easily avoided when sampling.

The other dune site was approximately 65 ha on the privately owned Eden ranch (T26N R17W; SE S17, SW S16, NW S21), located about 8 km east-southeast of Freedom. These dunes are subject to very light cattle grazing but the effects of the cattle are seldom observed. This dune area consists mainly of unstable or semi-stable dunes with numerous active dunes and blow-outs; areas of stabilized, heavily vegetated dunes are less frequent.

The two areas chosen represent mature, relatively undisturbed plant communities on the sand dunes of northwestern Oklahoma. The total vegetation cover and the number of species are somewhat less at the Eden ranch than at Little Sahara State Park but otherwise the two areas are very similar. Both sites consist

of dune complexes, with dunes up to 10 m high between the dunes are dune slacks. The Eden ranch site is 26 km northwest of the Little Sahara State Park Site and both sites are just north of the Cimarron River.

The climate is continental with hot summers and frequent summer drought (Borchert, 1950). Average annual precipitation is about 64 cm at both sites, with most occurring between April and September. The average annual temperature at both sites is 15.7 C with extremes normally ranging from -18 C to above 40 C. The average last frost date in the spring occurs in mid-May and the first fall frost is late in October (Curry, 1970).

Both research sites have the same two soil types: Dune Sands -- unconsolidated Quaternary sand drifted from the bed of the Cimarron River, frequently showing the effects of wind erosion, and either unvegetated or with sparse and patchy vegetation; and Trivoli Fine Sands, Dune Phase -- unconsolidated wind drifted Quaternary sands, differing from Dune Sands in having a fairly heavy cover of vegetation (USDA, 1950).

The dominant vegetation of the stable dunes consists of sandsage (Artemisia filifolia)*, aromatic sumac (Rhus aromatica), sandhill plum (Prunus angustifolia), Riddell groundsel (Senecio riddellii), yellow evening primrose (Calylophus serrulatus), scarlet pea (Indigofera miniata), little bluestem (Schizachyrium scoparium), sand dropseed (Sporobolus cryptandrus), and big sandreed (Calamovilfa gigantea).

During the study a total of 55 families, 145 genera, and 181 species of vascular plants were found on the study sites. All but two families, each represented by a single species, were angiosperms (Sherwood and Risser, 1980).

*Nomenclature follows Correll and Johnston (1970).

METHODS

Twelve species were selected for detailed analysis and seven additional species were examined less intensively. The species and reasons for their selection are listed below (abundance values are based on plant canopy cover).

Artemisia filifolia, sandsage -- This is the most abundant species on the sand dunes, and a member of the Asteraceae, the family with the second greatest number of species at the sand dunes.

Calamovilfa gigantea, big sandreed -- This is the first or one of the first invader species on semi-stable dunes, restricted to deep sands and often occurring in pure stands or with Psoralea lanceolata. It is one of the three species analyzed that belongs to the Poaceae, the family with the most species at the sand dunes.

Calylophus serrulatus, yellow evening primrose -- This is a common species on the sand dunes, also common off the dunes on other soil types. It is a member of the Onagraceae, the family with the sixth largest number of species at the sand dunes.

Dithyrea wislizenii, spectacle pod -- This is a robust winter annual, restricted to deep sand soils and is common on the sand dunes. It is a member of the Brassicaceae, the family with the fifth largest number of species at the sand dunes.

Indigofera miniata, scarlet pea -- This is the fifth most common species on the sand dunes and the most common member of the Fabaceae, the family with the third largest number of species at the sand dunes.

Penstemon buckleyi, Buckley's beardtongue -- This species is restricted to deep sand, and is fairly common at the sand dunes.

Psoralea lanceolata, lemon scurfpea -- This species is the first member of the Fabaceae to colonize semi-stable dunes. It occurs in pure stands or frequently with Calamovilfa gigantea.

Rhus aromatica, aromatic sumac -- This is the second most abundant shrub and the fourth most abundant species occurring at the sand dunes, also widespread in non-dune soils.

Schizachyrium scoparium, little bluestem -- This is the most abundant of the 33 species of grass found on the sand dunes, and the second most abundant species at the dunes; widespread and abundant both on and off the dunes.

Senecio riddellii, Riddell's groundsel -- This is the species most uniformly distributed over the sand dunes, a non-woody member of the Asteraceae, and restricted to deep sand soils.

Sporobolus cryptandrus, sand dropseed -- This is the third most abundant species at the sand dunes, the second most abundant member of the Poaceae, and as common name implies, a species of sandy soils, though it is not restricted to deep sand soils.

Stillingia sylvatica, Queen's delight -- This is a common species at the sand dunes, and though not restricted to deep sand soils, much more abundant there than in non-dune areas; a member of the Euphorbiaceae, the family with the fourth most number of species on the dunes.

The total cover for the 12 species was 57% of the total cover for all species at the sand dunes and their frequency was 48% of the total frequency for all species.

Seven other species were briefly examined as part of the initial survey of the dune vegetation. These seven species were analyzed only once or twice and are:

Dalea lanata, Erigeron bellidiastrum, Gaura villosa, Helianthus petiolaris, Heterotheca villosa, Monarda punctata, and Yucca angustifolia.

The 12 species were sampled four times a year. Because investigation of fluctuations in mineral levels between phenological stages was a major concern of this project, the sample periods for each species were chosen on the basis of phenological state rather than on a calendar date. The four phenological stages used were: (1) vegetative or pre-flower, when the plant is actively growing; (2) flowering, when the plant has open flowers present; (3) senescing, when the plant is no longer growing and is beginning to go dormant or die (this stage is marked by loss of chlorophyll and abscission of annual parts and; (4) dormancy, when growth has ceased (the winter condition for perennial plants).

Dithyrea wislizenii dies after senescing so it has no dormant state and this phenological stage is absent in the analysis. Rhus aromatica flowers before leafing and so the pre-flower vegetative state is absent. The species Calamovilfa gigantea, Indigofera miniata, Penstemon buckleyi, Psoralea lanceolata, Schizachyrium scoparium, Senecio riddellii, Sporobolus cryptandrus, and Stillingia sylvatica are all herbaceous perennials. Therefore only the below ground portions of these species were analyzed during the winter or dormant stage.

Because one intent of this study was to determine if there were within plant fluctuations of minerals, plant material was separated and analyzed in two parts, above ground portions and below ground portions. Normally four replicates were analyzed for each combination of species, phenological stage, and plant portion, though in a few cases five replicates were analyzed.

The samples were analyzed for seven elements: nitrogen, phosphorus, potassium, calcium, magnesium, iron, and manganese. Plant material for mineral

analysis was collected from the research sites and brought to the laboratory, where it was cleaned of foreign material and separated into above and below ground portions. This material was then dried for 48 hr at 70 C, weighed, and finely ground. Well mixed subsamples of the material were used for the determination of mineral levels. Potassiums, calcium, magnesium, manganese, and iron were determined by wet ashing with a 10% perchloric - 60% nitric acid solution. The resultant solution was analyzed on a model 303 Perkin-Elmer Atomic Absorption Spectrophotometer, using the procedure given in the analytical manual (Perkin-Elmer Corp., 1966). Phosphorus was determined by the method of Fiske and Subbarow (1925) with modifications (Forrest Johnson, personal comm.) and nitrogen was determined by use of the kjeldahl method as modified by Rice (1964).

To compare the species and determine if mineral levels in a species were high or low, a grand mean from all species for each element was computed and the actual values for each species at each stage were divided by this grand average. Separate grand means were computed for the above and below ground parts, and for the whole plant. A value of 1.0 for an element in a particular species means that in this plant this element was present at the grand mean level. Comparison of different means was done using analysis of variance and the Student Newman-Keuls tests. For all tests a 5% significance level was chosen. Analysis techniques were employed to examine interspecific trends in mineral levels. I employed an unweighted pair-group method of cluster analysis using arithmetic averages (UPGMA; Sneath and Sokal, 1973). Both Pearson product-moment correlation (hereafter called correlation) and Euclidean distance (hereafter called distance) matrices were analyzed. In phenograms resulting from cluster analyses, distortion increases from the branch side to the trunk side. By calculation of a cophenetic

matrix (an exact representation of the phenogram) and comparing this to the original input matrix, a cophenetic correlation coefficient can be calculated. The two matrices can be plotted against each other to form a bivariate scatter diagram, and the regions of high and low distortion in a phenogram can be found. A dashed line has been drawn, where necessary, to indicate the region of the phenogram where distortion is increasing rapidly. The placement of this line is based on the bivariate scatter diagrams.

RESULTS AND DISCUSSION

The dune soils contained about 0.0009% nitrogen and 0.0011% phosphorus, considerably less than the 1% levels found in nearby, non-dune soils. Other elements investigated in this study, while present in low levels in dune soils, were not as relatively low when compared to nearby non-dune soils as were nitrogen and phosphorus.

There is little published data useful in making comparisons of mineral levels in sand dune species with other mineral analyses on the same species, either on sand dunes or elsewhere. Some early work in Oklahoma gave results on Schizachyrium scoparium (as Andropogon scoparius) and Calamovilfa gigantea, but from only the above ground parts and only for three elements: nitrogen, phosphorus, and calcium (Daniel, 1931). Harper, et al (1933) evaluated a large number of Oklahoma species for mineral levels, once again analyzing only above ground parts for nitrogen, phosphorus, and calcium. The only species in common with the present study were Schizachyrium scoparium and Helianthus petiolaris. Daniel (1934) analyzed 23 grasses and 10 legumes from 52 Oklahoma counties, though none of the legumes he examined were in the present study. A study of fire on Schizachyrium scoparium in Missouri gave results for calcium and phosphorus in the above ground portions of this grass (Smith and Young, 1959). The most comprehensive study of minerals in Oklahoma plant species had only one sample, collected in June, of Sporobolus cryptandrus a species that also occurred at the dunes (Harper and Reed,

1964). In June Sporobolus cryptandrus is most likely to be in the vegetative stage. The site where the Sporobolus cryptandrus was sampled was a clay loam soil, quite different from the fine sand soils of the dune areas. In a study of Wisconsin plant species (Gerloff, et al., 1964) results were given for all seven elements included in my study. The only plant common to the Wisconsin study and this study was Monarda punctata, a species only briefly examined in my study. Difficulties might arise even in making this comparison because the environment of Wisconsin is quite different from that of Oklahoma. A summary of other research and my comparable results is found in Table 1. The most useful interpretation of species mineral levels results when the species of my study are compared with each other.

Few well defined general trends are found in total mineral levels within species through different phenological stages. However there is a tendency for the grasses and the woody shrubs to have lower average values than the herbaceous dicots. This may be due to the woody tissue in shrubs and a previously reported tendency for grasses to be lower in minerals than herbaceous dicots (Harner and Harper, 1973).

When individual elements are examined, nitrogen and phosphorus show the most consistent seasonal trends among species, other elements display almost no consistent interspecific trends. In most species nitrogen in the above ground portions tends to steadily decline from the vegetative to the dormant stage. In three species nitrogen shows little yearly fluctuations (Fig. 1). In seven of the species the below ground portions were lower in nitrogen during vegetative or flowering stages than in the senescent or dormant stages, the other five either had no significant variations among the stages or individualistic patterns of variation. In many species nitrogen appeared to be translocated from the below to the above ground portions early in the year. With the onset of growth nitrogen levels decline

in the below ground portions while simultaneously rising in the above ground portions (Fig. 1). Later in the year there is a general tendency for nitrogen levels to decline in the above ground portions during senescence, at this same time nitrogen levels are generally rising in the below ground portions (Sherwood, 1980).

Phosphorus in the above ground portions was higher during the vegetative and flowering stages and dropped to lower levels either during the senescent or dormant stage (Fig. 1). With only two exceptions, phosphorus did not show a corresponding rise in the below ground portions of these species. This may be partly due to the high variability in phosphorus levels between different individuals within a species. This resulted in high variance for phosphorus values and may have obscured phosphorus trends in the species. The most noteworthy exception to the general nitrogen and phosphorus trends was Dithyrea wislizenii. Dithyrea wislizenii has high levels of minerals during the vegetative, when it is a rosette with a well developed taproot, and the levels of these minerals drop in both above and below ground portions when it flowers. Dithyrea wislizenii flowers by bolting and shows a large increase in biomass at this time, and after flowering it dies.

The other five elements investigated (potassium, calcium, magnesium, iron, and manganese) showed widely divergent behavior between species with respect to seasonal trends. No general or consistent seasonal trends for these five elements could be drawn from the analyses. A complete and detailed listing of the intra-species mineral levels in each of the 12 species is found elsewhere (Sherwood, 1980).

When intra-species mineral levels are examined for evidence of partitioning, all species were significantly high or low in one or more elements when compared to the grand average for all plants (Table 2). Most species show evidence

of accumulation of some elements and lack of accumulation of others. Variation from the grand averages is best developed in Schizachyrium scoparium which has significant high or low levels of every element studied.

In addition to partitioning between species, some species showed partitioning of elements in the above and below ground portions. This is shown in Psoralea lanceolata which had intra-plant partitioning for three elements: phosphorus, potassium, and manganese. Manganese in Psoralea lanceolata was significantly higher than average in the above ground portions and significantly lower than average in the below ground portions. Potassium and phosphorus were both significantly lower than average in the above ground portions but average in the below ground portions. Intra-plant partitioning was shown to a lesser extent for some other species and some other elements. For example iron was accumulated in the above ground portion of Artemisia filifolia and in the below ground portion of Penstemon buckleyi, but not in the opposite portions of either plant. The only element that never showed significant partitioning between the above and below ground portions was nitrogen. While nitrogen levels would vary between above and below ground at different stages, there was no significant trends in any of the species (Table 2).

When the above and below ground results were compared, for all species and all phenological stages combined, no significant differences were found between the above and below ground parts for any element. This may be due to the high variation between species for individual elements.

Because inter-specific relationships are difficult to observe in the data (Table 2), further analysis was undertaken to clarify similarities and differences among the 12 species. One apparent trend was the similarity of response of the

three grasses. The three grasses, Calamovilfa gigantea, Schizachyrium scoparium, and Sporobolus cryptandrus are all significantly lower than the grand average for five elements. These five elements, considered plant macro-nutrients, are: nitrogen; phosphorus; calcium; potassium; and magnesium. Typically the three grasses significantly higher than the grand average in the two micronutrient elements: iron and manganese.

To investigate further species relationships, the mineral data were used to calculate two types of species similarity matrices, and these matrices were clustered. The phenogram that resulted from clustering a correlation matrix between species yielded several clusters that are of interest (Fig. 2). This method produces clusters that are based on similar mineral trends between species, but is little affected by absolute differences in mineral levels. Examination of the species correlation phenogram (Fig. 2) reveals that there are four general groups of clusters. The grasses Schizachyrium scoparium and Calamovilfa gigantea form a tight pair-group and Sporobolus cryptandrus joins this group at a lower level so that the three grasses form a distinct cluster. The subshrub Calylophus serrulatus then joins this cluster and the resulting group of four species is well separated from the remaining species. The two fall flowering composites, the shrub Artemisia filifolia and the herbaceous Senecio riddellii form a loose pair-group which is joined by Indigofera miniata. Psoralea lanceolata, the semi-stable open dune legume and Rhus aromatica, the stable, heavily vegetated dune shrub form a pair-group which is joined by Stillingia sylvatica. This cluster of three species joins with the previous cluster of three species, but the distortion is high at the level where they join, so this grouping, as other groupings made at lower levels, is not as informative as to the actual correlation of the species included in the clusters. The final pair-group is

Dithyrea wislizenii with Penstemon buckleyi, a loose pairing of the two species which flower mainly in the spring and then senescence early in the growing season. To summarize the correlation phenogram (Fig. 2), there are four general clusters: a grass cluster plus Calylophus serrulatus; a fall flowering composite cluster plus Indigofera miniata; a mixture of species with no obvious morphological, taxonomic, or phenological affinities among the members; and fourth a spring flowering and early senescing group.

When the results from clustering the distance similarity matrix are examined (Fig. 3), the results are quite different from those obtained in clustering the correlation matrix. In distance phenographing, species with low mineral levels are more likely to be clustered with other species that also have low levels rather than with species having high levels. The effect of similar trends is not eliminated, but similar trends between species may have less effect than in the case of clustering a correlation matrix.

The first grouping in the distance phenogram (Fig. 3) is similar to that from the correlation phenogram. The grasses Schizachyrium scoparium and Calamovilfa gigantea pair initially and are joined by Sporobolus cryptandrus to form a fairly tight cluster. This cluster is next joined by Calylophus serrulatus and the resultant cluster of four species is distinct from the remaining species. This cluster of four species joins the other clusters at a sufficiently high level that the distortion at this level prevents an accurate assessment of the actual relationships among these groups.

The second cluster is a mixture of five species, with the tightest pair-group the Psoralea lanceolata - Rhus aromatica pair, two species that had similar results

in the correlation phenogram. This two species group is joined next by Penstemon buckleyi, then by Artemisia filifolia and finally loosely joined by Stillingia sylvatica. I have no ready explanation for this grouping, which is quite different from the results obtained in the previous phenogram. The three remaining species join as three one species clusters. These species join in a part of the phenogram that suffers from high distortion, but the levels of joining provide some useful information about species relationships despite the distortion.

Senecio riddellii joins with the cluster of five species, and perhaps the dashed line could be placed on the trunk side of this junction rather than on the branch side as depicted in the phenogram. This cluster of six species then joins with the cluster containing the three grasses and Calylophus serrulatus, and only then does Indigofera miniata join this 10 species cluster. Because there is a single species, Indigofera miniata, joining with a cluster of 10 species, much of the distortion results from Indigofera miniata being at a different distance from each of the 10 species in the large cluster, but in the phenogram (Fig. 3) it joins at a single average distance of 0.8 units from the 10 species cluster. Because it can join only at one level, rather than 10, this is where the distortion occurs. Perhaps despite this high distortion, inferences about the relationship of Indigofera miniata to the 10 species can be drawn. Indigofera miniata is farther from the cluster of 10 species due to its having extremely high nitrogen content.

The twelfth and remaining species, Dithyrea wislizenii joins the other species at a greater distance than Indigofera miniata. Dithyrea wislizenii was the only annual species analyzed and it contained very high levels of most elements in the vegetative stage. These declined rapidly throughout the growing season

and dropped to low levels by senescence for most elements. The total change in levels throughout the growing season was much greater for Dithyrea wislizenii than for the other eleven species (Sherwood, 1980). As noted earlier, Dithyrea wislizenii failed to show the same seasonal trends with respect to nitrogen and phosphorus as the other species.

The phenograms that resulted from clustering the correlation matrix and from clustering the distance matrix, though giving different results, produced two consistent groups. The first group was composed of the three grasses plus Calylophus serrulatus. The grasses are all warm season plants and all three grasses tend to be lower than average in nitrogen, phosphorus, potassium, calcium, and magnesium and higher than average in iron and manganese. In addition, the genus Calylophus is thought by some to be a warm season genus (like the grasses) in contrast to most other genera in the Onagraceae (Dr. James Estes, personal comm.). Parallel adaptation of Calylophus and the grasses may be why they are clustered together despite differences in external appearance and taxonomic classification.

The second group that was consistent in both phenograms was the Psoralea lanceolata - Rhus aromatica pair. This is an unexpected pair, Psoralea lanceolata is a herbaceous legume that occupies open, semi-stable dunes and is one of the first species to invade non-vegetated dunes. It does not occur on the stabilized, heavily vegetated dunes and apparently required open, low diversity habitat. Rhus aromatica occurs almost entirely on stabilized, heavily vegetated dunes and normally grows with many other species. It apparently requires a stable substrate, which is frequently rich in other species. This habitat is very unlike that preferred by Psoralea lanceolata. Both of these species show complex internal mineral

relationships, and examination of the raw mineral data by phenological stage or plant portion does not suggest any apparent reason for this close relationship produced by cluster analysis. When principal component analysis was performed, and the results ordinated, this same pair resulted. This suggests that this odd pair is not a result of the method of analysis but that there is a similarity in the patterns of nutrient content in these two species.

An alternate way to examine mineral relations is to examine the relationships of the different elements. As with the species, different elements were compared by cluster analysis on a correlation matrix between elements. A distance matrix was not clustered because the different elements were already known to be present at consistently different levels (Sherwood, 1980).

The phenogram for elements had two major groupings and some minor groupings (Fig. 4). This phenogram has a very high cophenetic correlation coefficient (0.967) and thus accurately portrays the relationships between the seven elements with very little distortion. Phosphorus and potassium form the most similar pair and then this pair-group is joined by nitrogen. Calcium and magnesium form a pair and then join with the nitrogen, phosphorus, and potassium group. This five element group is quite distinct from the remaining two elements, iron and manganese. These two elements form a very loose pair-group. They are more similar to each other than they are to the other elements, but are not very similar to each other. The two major groupings, the nitrogen, phosphorus, potassium, calcium, and magnesium group, and the iron and manganese group, correspond to plant macronutrients and micronutrients respectively.

Interpretation of mineral response from the phenogram are different from those reported by Parker and Truog (1920). They found nitrogen and calcium levels to be highly correlated, and potassium, phosphorus, and magnesium showed little

correlation to nitrogen. Their work was on crop plants and they did not sample through different phenological stages. The plants they investigated were all domesticated annual species, while all species in my study were wild plants, and all but one species were perennials.

CONCLUSIONS

The patterns of elements in plants of the sand dunes shows a complex and variable set of relationships. Intraspecific trends for specific elements were most clearly seen with nitrogen and phosphorus, the two elements with the lowest levels in the dune soils as compared to non-dune soils. In the above ground portions there is a tendency for nitrogen and phosphorus levels to be high early in the year when the plants are in a vegetative stage and actively growing and to decline as the plants flower, senescence, and become dormant. Nitrogen levels generally declined in the below ground portions from the senescent and dormant stages to the vegetative stage, with a corresponding rise in the above ground portion. Phosphorus had less clearly developed trends, this was probably due to the high variability of phosphorus levels within species, which may have obscured trends. The other five elements, potassium, calcium, magnesium, and especially iron and manganese showed little consistent behavior through the phenological stages.

All species exhibit significant accumulation or non-accumulation of one or more elements, so there is strong interspecific partitioning of nutrients. Many species displayed above and below ground partitioning of one or more of six of the elements, the only element to never show overall above and below ground partitioning was nitrogen.

When the different species were compared to find similar behavior with respect to mineral levels, there were two consistent groups regardless of the type of analysis used. One group consisted of Calypogeomys serrulatus and the three grasses.

This may be due to similar life history phenomena, namely all four are warm season plants. The other group that showed similar behavior was the perplexing pair, Rhus aromatica and Psoralea lanceolata.

When the elements were compared, they formed two major groups, corresponding to macronutrients and micronutrients. The macronutrients group was further divided into two subgroups, a nitrogen phosphorus, and potassium subgroup and a subgroup consisting of calcium and magnesium.

The patterns of elements in the sand dunes were found to be more complex than originally anticipated. Element levels are highly variable both between and within plants. Within plant variations include both variations between plant portions and between phenological stages. In very few cases could specific patterns be found that were consistent. This study has analyzed some of the complexity, but more work remains before a total understanding of mineral relationships of dune plants will be obtained.

LITERATURE CITED

- BORCHERT, J. R. 1950. The climate of the central North American grassland. *Annals. Assoc. Am. Geographers.* 40: 1-39.
- BURZLAFF, D. F. 1962. A soil and vegetative inventory and analysis of three Nebraska sand hill range sites. *Univ. Nebr. Agr. Exp. Sta. Res. Bull.* 206.
- CORRELL, D. S. and M. C. JOHNSTON. 1970. Manual of the vascular plants of Texas. Texas Research Foundation. Renner, Texas.
- CURRY, B. R. 1970. Climate of Oklahoma. U.S. Government Printing Office, Washington, D.C.
- DANIEL, H. A. 1931. A study of certain factors which affect the calcium, phosphorus, and nitrogen content of prairie grass. *Proc. Okla. Acad. Sci.* 12: 42-45.
- _____. 1934. The calcium, phosphorus, and nitrogen content of grasses and legumes and the relation of these elements in the plant. *J. Am. Soc. Agron.* 26: 496-503.
- ECK, H. V., R. F. DUDLEY, R. H. FORD, and C. W. GANTT, Jr. 1968. Sand dune stabilization along streams in the southern great plains. *J. Soil and Water Cons.* 23: 131-134.
- ERNST, W. 1975. Variation in the mineral content of leaves of trees in miombo woodland in south central Africa. *J. Ecol.* 63: 801-807.

- FISKE, C. H. and Y. SUBBARROW. 1925. Method for the determination of phosphorus. *J. Biol. Chem.* 66: 375-400.
- GERLOFF, G. C., D. C. MOORE, and J. T. CURTIS. 1964. Mineral content of native plants of Wisconsin. *Univ. Agr. Exp. Res. Report 14*. Madison, Wisconsin.
- _____, _____, and _____. 1966. Selective absorption of mineral elements by native plants of Wisconsin. *Plant and Soil.* 25: 393-405.
- GUHA, M. M. and R. L. MITCHELL. 1966. The trace and major element composition of the leaves of some deciduous trees. *Plant and Soil.* 24: 90-112.
- HARNER, R. F. and K. T. HARPER. 1973. Mineral composition of grassland species of the eastern great basin in relation to stand productivity. *Canad. J. Bot.* 51: 2037-2046.
- HARPER, H. S., H. A. DANIEL, and H. F. MURPHY. 1933. The total nitrogen, phosphorus, and calcium content of common weeds and native grasses in Oklahoma. *Proc. Ok. Acad. Sci.* 14: 36-44.
- HARPER, H. S. and L. W. REED. 1964. Effects of chemical composition of soil on micro nutrients and other elements in Oklahoma forage plants. *Ok. Agr. Exp. St. Processed Ser. P-486*. Stillwater, Oklahoma.
- HART, G. H., H. R. GILBERT, and H. GOSS. 1932. Seasonal changes in the chemical composition of range forage and their relation to nutrition of animals. *Univ. of Calif. Ag. Exp. St. Bull.* 543.
- MARRS, R. H. 1978. Seasonal changes and multivariate studies of the mineral element status of several members of the Ericaceae. *J. Eco.* 66: 523-545.

- PARKER, F. W. and E. TRUOG. 1920. The relation between calcium and the nitrogen content of plants and the function of calcium. *Soil Science*. 10: 49-56.
- PEMADASA, M. A. and P. H. LOVELL. 1974. The mineral nutrition of some dune annuals. *J. Ecol.* 62: 647-657.
- PERKIN-ELMER CORP. 1966. Analytical methods for atomic absorption spectrophotometry. Perkin-Elmer Corp., Norwalk, Connecticut.
- POOL, R. J. 1914. A study of the vegetation of the sand hills of Nebraska. *Minn. Bot. Studies, Part III.* 4: 189-312.
- RICE, E. L. 1964. Physiological ecology laboratory procedures. Univ. Okla. Bookstore, Norman, Oklahoma.
- RICE, E. L., W. T. PENFOUND, and L. M. ROHRBAUGH. 1960. Seed dispersal and mineral nutrition in succession in abandoned fields in central Oklahoma. *Ecology* 41: 224-228.
- SHERWOOD, R. T. B. 1980. Vegetation of the Woods County, Oklahoma sand dunes. Ph.D. dissertation. University of Oklahoma. Norman, Oklahoma.
- SHERWOOD, R. T. B. and P. G. RISSER. 1980. An annotated checklist of the vascular plants of Little Sahara State Park, Oklahoma. *Southwest. Nat.*, in press.
- SMITH, E. F. and V. A. YOUNG. 1959. The effects of burning on the chemical composition of little bluestem. *J. Range Manag.* 12: 139-140.
- SNEATH, P. H. A. and R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman and Company, San Francisco, California.
- STARK, N. M. 1970. The nutrient content of plants and soils from Brazil and Suriman. *Biotropica* 2: 56-60.
- _____ and C. F. JORDAN. 1978. Nutrient retention by the root mat of an Amazonian rain forest. *Ecology* 59: 434-437.

- UNITED STATES DEPARTMENT OF AGRICULTURE. 1950. Soil Survey, Woods County, Oklahoma. Washington, D.C.
- VITOUSEK, P. M. and W. A. REINERS. 1975. Ecosystem succession and nutrient retention: a hypothesis. *Bioscience* 25: 376-381.
- WESTMAN, W. E. 1978. Inputs and cycling of mineral nutrients in a coastal subtropical eucalypt forest. *J. Ecol.* 66: 513-531.
- WOODWELL, G. M., R. H. WHITTAKER, and R. A. HOUGHTON. 1975. Nutrient concentration in plants in the Brookhaven oak-pine forest. *Ecology* 56: 318-332.
- WUENSCHER, M. L. and G. C. GERLOFF. 1971. Growth of Andropogon scoparius (little bluestem) in phosphorus deficient soils. *New Phytol.* 70: 1035-1042.

Table 1

A comparison of mineral analysis results

SOURCE	SPECIES	N %	P %	Ca %	K %	Mg %	Fe ppm	Mn ppm
Daniel 1931 (OK)	<u>Schizachyrium scoparius</u>	.84	.083	.32				
Daniel 1934 (OK)	" "	.614	.072	.269				
Smith and Young 1959 (MO)	" "unburned " "burned		.098 .109	.39 .22				
Sherwood 1979 (OK)	" "veg.	1.09	.093	.478				
Sherwood 1979 (OK)	" "flower	1.22	.057	.301				
Daniel 1931 (OK)	<u>Calamovilfa gigantea</u>	.544	.141	.167				
Daniel 1934 (OK)	" "	.58	.178	.17				
Sherwood 1980 (OK)	" "veg.	.76	.088	.176				
Sherwood 1980 (OK)	" "flower	.62	.055	.105				
Harner et al. 1933 (OK)	<u>Helianthus petiolaris</u>	1.8	.19	1.79				
Sherwood 1979 (OK)	" "	1.3	.13	5.86				
Gerloff et al. 1964 (WI)	<u>Monarda punctata</u>	1.3	.24	1.22	1.9	.41	199	305
Sherwood 1980 (OK)	" "	1.7	.18	1.45	2.1	.20	517	92
Harper and Reed 1964 (OK)	<u>Sporobolus cryptandrus</u>	1.23	.12	2.17	.61	.39	437	14
Sherwood 1980 (OK)	" "veg.	1.26	.14	.42	.96	.20	124	26
Sherwood 1980 (OK)	" "flower	1.24	.13	.36	.87	.27	211	34

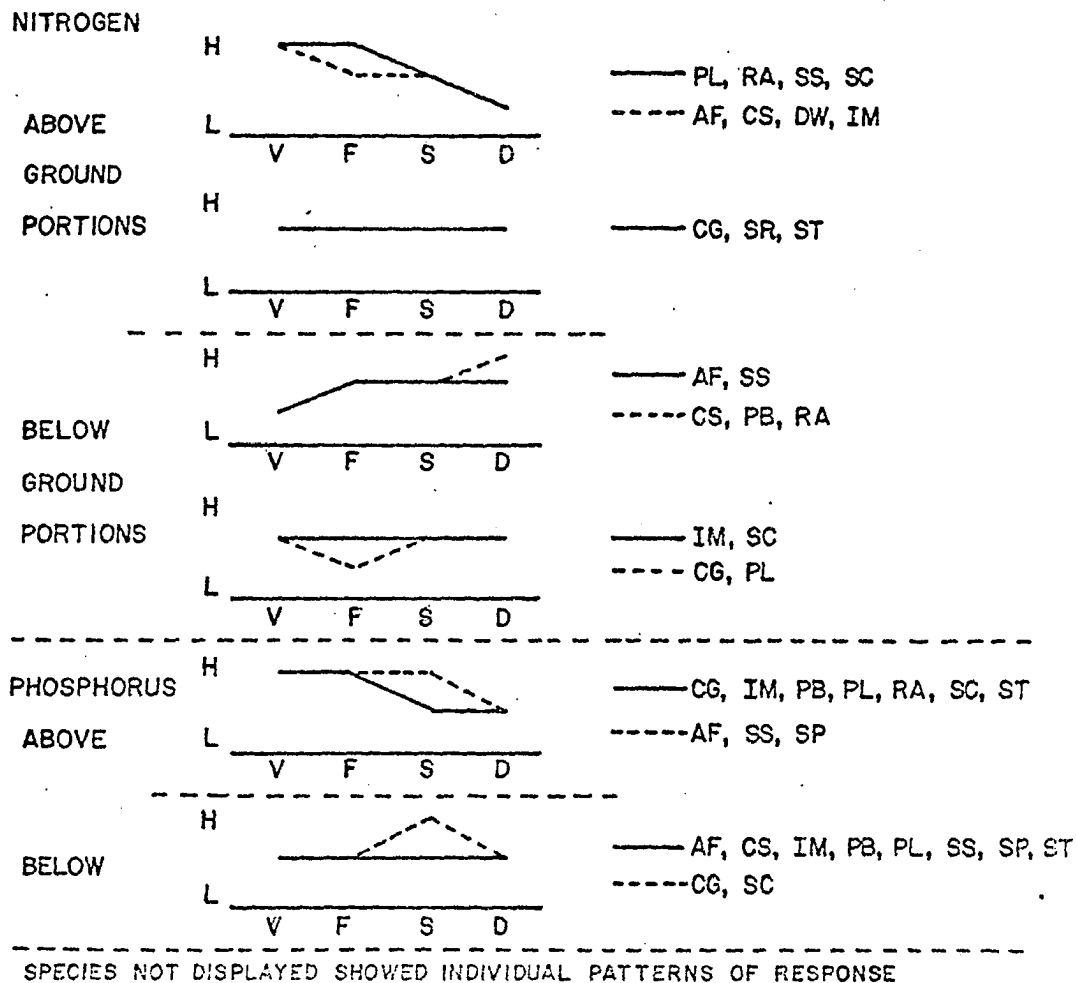
Table 2

Significant Deviations From Average Value
For Comparable Portion Of All Dune Plants

SPECIES	N %	P %	K %	Ca %	Mg %	Fe %	Mn %
<u>Schizachyrium scoparius</u>	64	53	40	27	33	148	146
<u>Calamovilfa gigantea</u>	58	57(A)	50	16	56		169
<u>Sporobolus cryptandrus</u>			54	26		139	150(B)
<u>Artemisia filifolia</u>	61	50	55		145(B)	150(A)	
<u>Rhus aromatica</u>	51	56			49		
<u>Calylophus serrulatus</u>			55	166(B)	61	155	185
<u>Indigofera miniata</u>	180	164(B)					43(B)
<u>Psoralea lanceolata</u>		57(A)	56(A)				140(A)/51(B)
<u>Penstemon buckleyi</u>			171(B)		59(A)	166(B)	
<u>Dithyrea wislizenii</u>		182	194		61	160	56
<u>Senecio riddellii</u>					146(B)		164(A)
<u>Stillingia sylvatica</u>				146(B) /54(A)ns			

(A) - above ground portions of the plant
(B) - below ground portions of the plant
ns - non-significant

FIGURE 1. INTERSPECIFIC PATTERNS IN NITROGEN AND PHOSPHORUS



H - HIGH AVERAGE MINERAL LEVELS

L - LOW AVERAGE MINERAL LEVELS

AF *Artemisia filifolia*

PL *Psoralea lanceolata*

CG *Calamovilfa gigantea*

RA *Rhus aromatica*

CS *Calylophus serrulatus*

SS *Schizachyrium scoparius*

DW *Dithyrea wislizenii*

SR *Senecio riddellii*

IM *Indigofera miniata*

SC *Sporobolus cryptandrus*

PB *Penstemon buckleyi*

ST *Stillingia sylvatica*

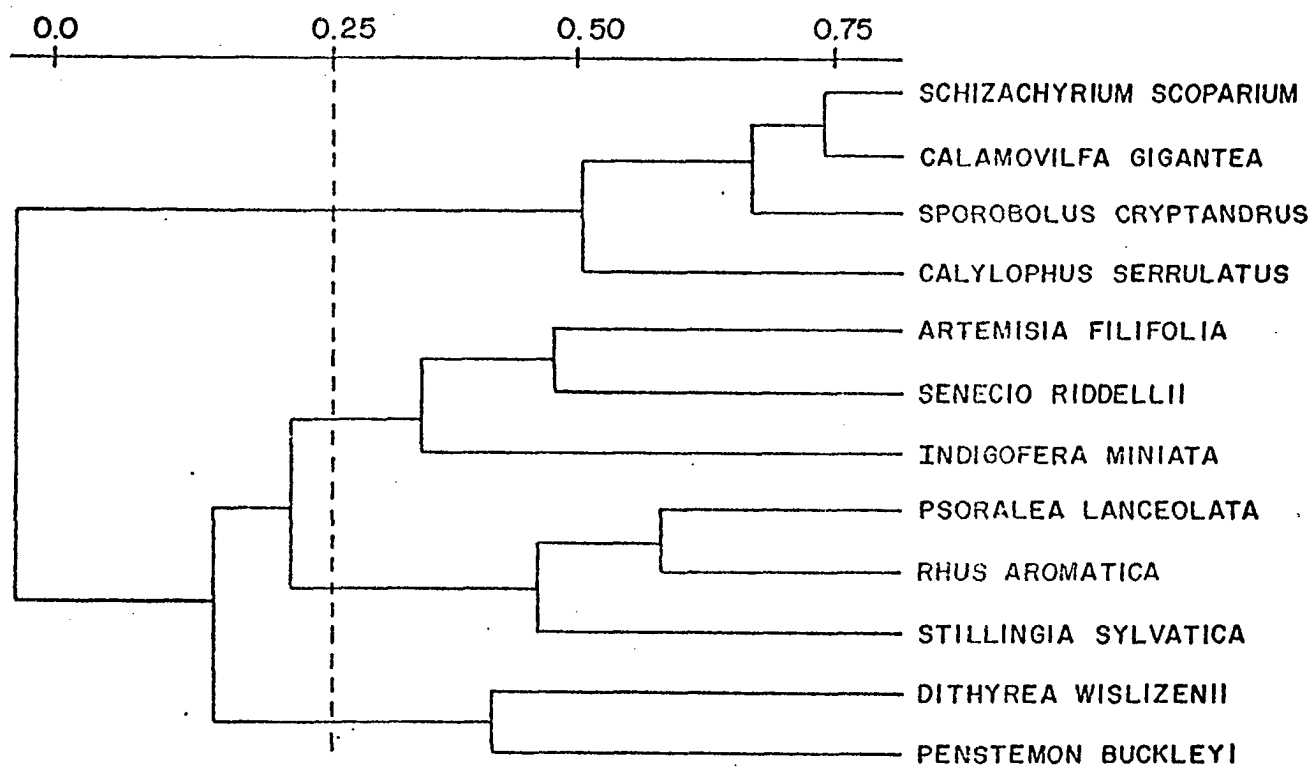
V - VEGETATIVE

S - SCENSCENT

F - FLOWERING

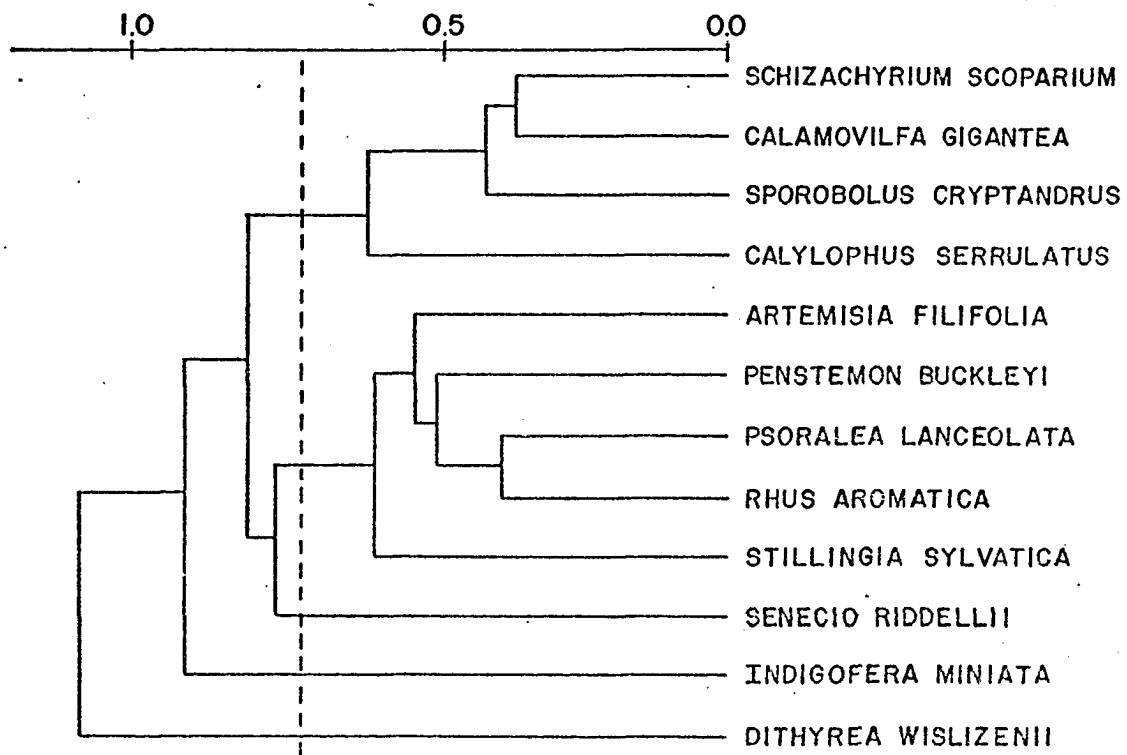
D - DORMANT

FIGURE 2. SPECIES PHENOGRAM FROM CORRELATION MATRIX



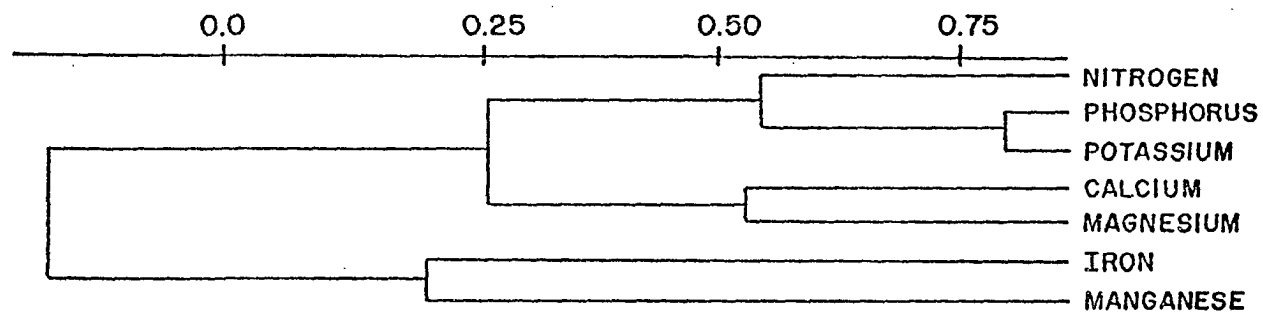
COPHENETIC CORRELATION COEFFICIENT = .845

FIGURE 3. SPECIES PHENOGRAM FROM DISTANCE MATRIX



COPHENETIC CORRELATION COEFFICIENT = .885

FIGURE 4. PHENOGRAM FROM CORRELATION MATRIX OF ELEMENT SIMILARITIES



COPHENETIC CORRELATION COEFFICIENT = .967

APPENDIX

Species Mineral Values

SPECIES	STAGE	% NITROGEN		PHOSPHORUS		POTASSIUM PPM.	
		ABOVE	BELOW	ABOVE	BELOW	ABOVE	BELOW
1 <u>Artemisia filifolia</u>	veg.	1.15	.62	747	377	9137	3021
	fl.	.95	.77	575	503	6647	3033
	scn.	.84	.91	523	552	4963	3291
	dor.	.65	.87	286	562	5155	5529
2 <u>Calamovilfa gigantea</u>	veg.	1.00	.75	1366	424	7772	3637
	fl.	.82	.58	850	351	5472	3222
	scn.	.82	.90	527	731	3555	3365
	dor.		.68		442		3843
3 <u>Calylophus serrulatus</u>	veg.	1.72	.70	1439	352	7555	4314
	fl.	1.22	.88	891	410	5850	3766
	scn.	1.46	.94	1937	1103	6290	4201
	dor.	1.05	1.23	636	531	5106	3465
4 <u>Dithyrea wislizenii</u>	veg.	2.83	1.62	2690	2878	24861	20952
	fl.	1.68	.91	1516	1872	14500	18928
	scn.	1.38	.72	1048	969	9540	18928
5 <u>Indigofera miniata</u>	veg.	2.68	2.39	1502	840	11710	4543
	fl.	2.42	2.68	1260	1244	10400	6110
	scn.	2.19	1.77	995	910	7800	5350
	dor.		2.75		1100		6530
6 <u>Penstemon buckleyi</u>	veg.	1.76	.72	1160	490	12050	10600
	fl.	1.30	.74	1660	710	13750	10100
	scn.	.65	.76	320	500	6400	8000
	dor.		1.21		540		9900
7 <u>Psoralea lanceolata</u>	veg.	2.44	1.02	1250	475	8800	4450
	fl.	1.34	1.37	920	680	7900	6230
	scn.	.93	1.20	320	490	4600	4080
	dor.		1.27		520		4680
8 <u>Rhus aromatica</u>	fl.	1.22	.56	1230	650	12380	4340
	scn.	.64	.55	570	380	7300	4550
	dor.	.68	.65	380	380	10750	3800
9 <u>Schizachyrium scoparius</u>	veg.	1.09	.62	930	500	7160	2980
	fl.	1.22	.75	575	300	3970	2790
	scn.	.80	.88	670	450	4520	2590
	dor.		.83		430		1850
10 <u>Senecio riddellii</u>	veg.	1.98	1.06	1300	670	20890	12270
	fl.	1.55	1.01	1430	570	13350	7510
	sev.	1.43	.74	1000	640	12490	5890
	dor.		.82		570		7460

STAGE	CALCIUM PPM		MAGNESIUM PPM		IRON PPM		MANGANESE PPM		
	ABOVE	BELOW	ABOVE	BELOW	ABOVE	BELOW	ABOVE	BELOW	
1	veg.	16220	13220	3750	2500	209	150	26	25
	fl.	16330	10450	1960	3100	170	120	24	17
	scn.	13700	10660	3960	2790	172	116	26	37
	dor.	4390	4740	920	1080	173	190	26	24
2	veg.	2300	2000	2050	950	77	160	58	59
	fl.	1480	1110	1360	920	51	153	51	60
	scn.	3360	2880	2050	1160	123	173	51	52
	dor.		1700		580		159		117
3	veg.	8450	12660	2010	950	128	105	47	62
	fl.	12870	14510	1600	1000	138	307	49	67
	scn.	15250	16060	1610	1170	303	400	48	67
	dor.	10000	19250	1490	1490	233	266	88	126
4	veg.	38340	6870	2560	1350	226	221	45	23
	fl.	20800	4090	1960	910	178	122	17	10
	scn.	13760	5580	1080	800	402	252	17	11
5	veg.	27000	6500	4600	1770	106	120	34	20
	fl.	25270	6750	4130	1860	76	90	30	19
	scn.	25790	3440	2430	1120	184	130	37	11
	dor.		4480		1860		120		22
6	veg.	15050	8700	2140	1800	95	305	40	42
	fl.	13900	9040	2180	1670	173	341	35	38
	scn.	9000	8300	1260	1500	107	214	15	24
	dor.		9600		2100		311		39
7	veg.	15800	13800	2230	1900	176	174	40	20
	fl.	10140	18890	1270	2640	82	182	21	41
	scn.	24600	14490	2020	2560	104	207	49	19
	dor.		13660		2530		172		31
8	fl.	11360	11120	1230	700	106	95	26	22
	scn.	14730	15220	1370	930	133	145	39	25
	dor.	16170	17200	1400	1090	105	153	37	39
9	veg.	4780	3750	1320	720	315	417	50	69
	fl.	3000	3000	900	480	194	236	31	55
	scn.	3320	2740	830	520	209	170	36	70
	dor.		3300		540		195		102
10	veg.	10800	4570	1990	920	118	123	44	37
	fl.	25320	11720	5100	3720	94	154	53	49
	scn.	20320	9070	4200	3550	75	103	54	42
	dor.		4810		1260		145		42

SPECIES	STAGE	% NITROGEN		PHOSPHORUS		POTASSIUM PPM.	
		ABOVE	BELOW	ABOVE	BELOW	ABOVE	BELOW
11 <u>Sporobolus cryptandrus</u>	veg.	1.26	.91	1350	610	9600	3400
	fl.	1.24	1.00	1310	520	8700	3380
	scn.	.73	.99	700	750	4750	2640
	dor.		1.13		433		3020
12 <u>Stillingia sylvatica</u>	veg.	2.09	1.45	1700	400	12330	3360
	fl.	1.61	.75	1260	530	9500	3500
	scn.	1.94	1.86	610	680	4460	4830
	dor.		.87		580		3550

STAGE	CALCIUM PPM		MAGNESIUM PPM		IRON PPM		MANGANESE PPM		
	ABOVE	BELOW	ABOVE	BELOW	ABOVE	BELOW	ABOVE	BELOW	
11	veg.	4210	3220	1990	1650	124	190	26	63
	fl.	3620	3180	2690	2400	212	327	34	78
	scn.	2720	2370	1780	1760	187	234	26	45
	dor.		3960		1080		217		75
12	veg.	7180	25080	2640	2180	136	191	30	43
	fl.	7290	29170	2800	2200	63	95	24	32
	scn.	15650	17410	2730	2220	52	108	34	43
	dor.		21610		3220		112		66