THESIS

THE NATIVE SAND SAGE VEGETATION OF EASTERN COLORADO

Submitted by

Richard Halbert Daley

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY RICHARD HALBERT DALEY ENTITLED THE NATIVE SAND SAGE VEGETATION OF EASTERN COLORADO BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

Committee on Graduate Work

A. T. Grigar

William Berg

J. L. Dix
Adviser

R. Shard

R. Shard
Head of Department

ABSTRACT

THE NATIVE SAND SAGE VEGETATION OF EASTERN COLORADO

The native sand sage (Artemisia filifolia Torr.) vegetation in eastern Colorado has only received brief mention in the literature, and has never before been quantitatively studied. Consequently, this study was undertaken to provide a quantitative phytosociological description of the native sand sage vegetation. In addition, the vegetational-environmental complex was examined, and the relationship of this vegetation with other examples of sand vegetation in the North American grassland is suggested. This study is of timely importance because the land-use practices in eastern Colorado will likely destroy the last remnants of the native sand sage vegetation within a few years.

Colorado's sand sage vegetation appears to be a climax edaphic variant of the mixed-grass prairie. Furthermore, based upon species composition differences between northeastern and southeastern Colorado stands, the possibility of a tension zone between the northern and the southern Plains through central Colorado is suggested.

In addition to Artemisia filifolia, the most important species are Sporobolus cryptandrus, Bouteloua gracilis, and Helianthus petiolaris. Changes in species composition within each area are primarily a

function of changes in slope and exposure. Significant differences in species importances between the northern and the southern stands are noted. *Stipa comata* and *Calamovilfa longifolia*, which are quite common in the northern stands, do not occur in quadrats in the south. These differences are accounted for by differences in substrate stability and climate.

Substrate stability differences are hypothesized to account for the growth-form differences between the two Colorado study areas, which are similar, and the "stabilized dunes" of Saskatchewan and the sand sage vegetation of Nebraska, which are similar.

Richard Halbert Daley
Botany Department
Colorado State University
Fort Collins, Colorado 80521
July, 1972

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Finally, the warmest thanks of all to you, Joanne, for the encouragement, the love, and the understanding you have given me.

> The grass is rich and matted, you cannot see the soil. It holds the rain and the mist, and they seep into the ground, feeding the streams in every kloof. It is well tended, and not too many fires burn it, laying bare the soil. Stand unshod upon it, for the

ground is holy, being even as it came from the Creator. Keep it, guard it, care for it, for it keeps men, guards men, cares for men. Destroy it and man is destroyed.

Alan Patton, Cry the Beloved Country

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CHAPTER I

INTRODUCTION

The diversity of vegetational types on the Colorado High Plains is primarily a function of topography and parent material. Sand deposits, for example, are widespread and support vegetation distinct from that of the surrounding areas with finer soils.

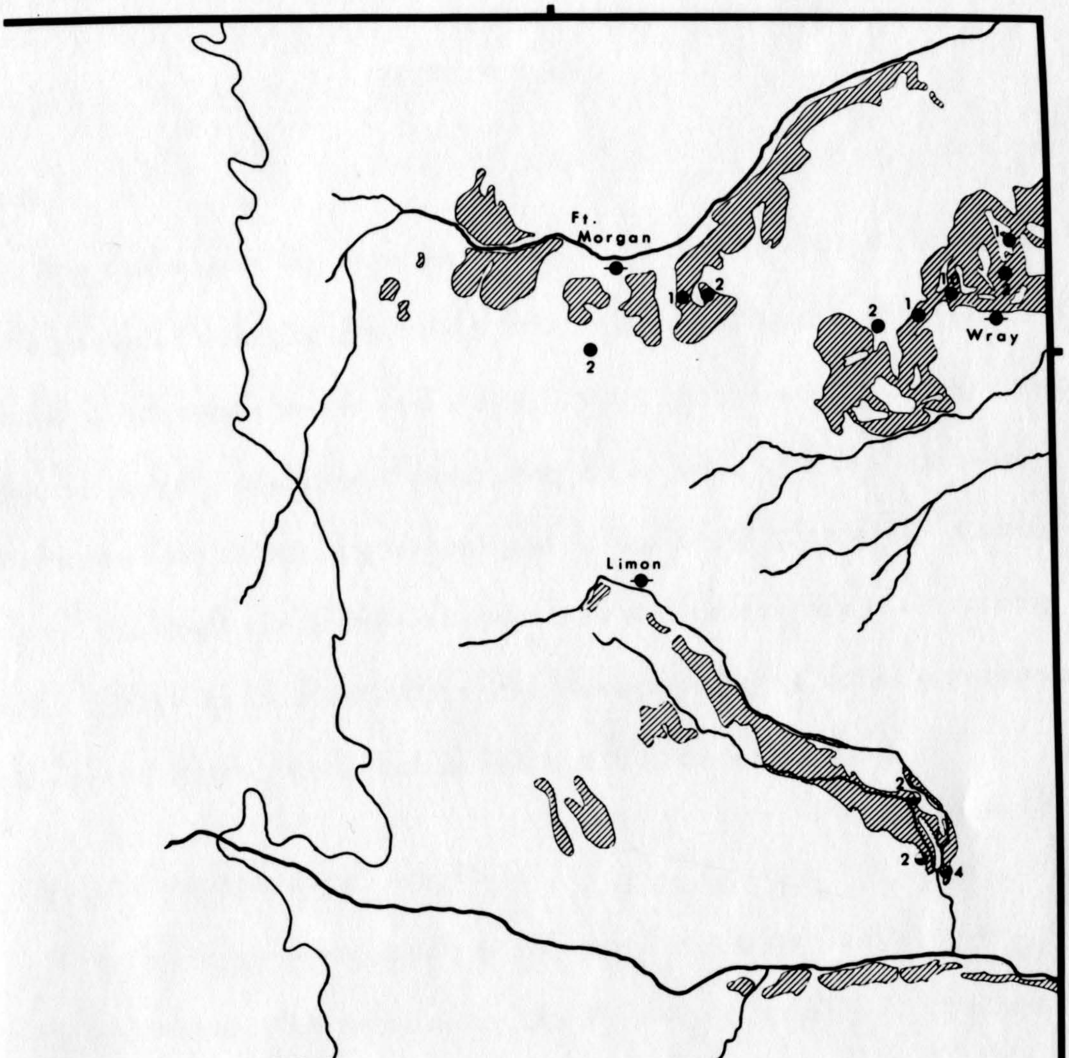
Sand communities are scattered throughout the Great Plains, especially on the extensive Ogallala Formation (Hill and Tompkin 1953, Smith 1965, and Thornbury 1965). Consequently, an investigation of sand vegetation in eastern Colorado provides an opportunity to gain insight not only into the vegetation of Colorado, but also into that of the Great Plains. After extensive field observations, it became obvious that most of the native sand vegetation in eastern Colorado has been destroyed, and that the sand sage (*Artemisia filifolia* Torr.) vegetational type is the most widespread type remaining. Consequently, it was selected for study.

The objectives of this study are to describe, using quantitative phytosociological techniques, the sand sage vegetation in eastern Colorado and to characterize its vegetational-environmental relationships. Furthermore, an interpretation of the relationship of this vegetation with other sand communities in the North American grassland, particularly with those of Nebraska, will be presented.

I travelled Colorado's eastern plains extensively from June through September, 1971, and located two major areas of sand sage vegetation (Fig. 1). The first is in the northeastern quarter of Colorado, which was previously discussed by Ramaley (1939), while the second area is located in the southeastern quarter of the State. The two areas are approximately 160 kilometers (100 miles) apart, and the stands in each area are widely distributed.

The current land-use practices in eastern Colorado tend towards the utilization of "marginal" land for beef production or irrigation agriculture, and these activities threaten to destroy this vegetational type within the very near future. My hope is that this study will provide a permanent description of the sand sage vegetation before its impending destruction.

Figure 1. Geographical location of stands in eastern Colorado showing location of northern and southern stands, separated through east-central Colorado. Northern stands are indicated by solid colored dots (total = 21); southern stands are indicated by half-colored dots (total = 10). Numerals adjacent to each dot indicate the number of stands at that location. Shaded area is location of the Colorado sand sage vegetation after Morris and Dix (1971).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CHAPTER II

STUDY AREA

Climate

The climate of the eastern Colorado plains is semi-arid and subject to periodic drought (Borchert 1950, 1971). There are significant climatic differences in the two study areas. In the south, the growing season is longer, the annual precipitation is less, and the potential evaporation rate is much greater than in the north (Table 4). Consequently, the southern stands are warmer and drier than the northern stands. There is also indication that drought may be more common and more severe in the south than in the north (Borchert 1971).

Geology, Geomorphology, and Soils

The entire northern study area is underlain by Cretaceous, marine-deposited, Pierre shale. The Pliocene Ogallala Formation, the most extensive non-marine pre-Pleistocene deposit in the United States (Thornbury 1965) overlays the shale. Above the Ogallala, the Kansan-aged Grand Island Formation, a fluviatile sand and gravel, was deposited, but in many areas it has been completely eroded away. In the floodplains, the surficial deposits are "valley fill," probably deposited in Pleistocene and Recent time. Strong northwesterly winds appear to have blown early Pleistocene valley fill from the river beds.

The comparatively heavy sand materials were deposited nearby to form the Sand Hills Formation north of the Republican River, while the comparatively lighter loess was carried farther southeastward to form the Peorian loess south of the Republican River (Hill and Tompkin 1953).

The only geological information available for the southern study area is from Scott's (1968) U.S. Geological Survey map (Trimble 1972) which shows extensive sand deposits of upper-Wisconsin age along the Arkansas River and its tributaries. Dunes in this area are lower in relief than those in the north, where they commonly reach 10 meters in height. This indicates to me either that the southern sand deposits are older and more eroded, or that they are younger and still building. Undoubtedly, along the stream courses, sand continues to blow and accumulate in places, but the area is probably more stable than the sand deposits in the north where the dunes continue to migrate southeastward (Hill and Tompkin 1953 and Trimble 1972). One further geomorphic dissimilarity between the areas is a general orientation of the northern sand deposits in a northwest-southeast direction (Hill and Tompkin 1953), whereas no orientation is illustrated on Scott's map (1968) for the southern area nor could I discern one in the field.

Soils are weakly developed on the sand in northern Colorado (Ramaley 1939, Hill and Tompkin 1953, and Brubacher et al. 1971). The only exception is in the valleys between the dunes where soil formation may be significant. This pattern, which is typical of sand areas (Olson 1958a), also appears true for southern Colorado.

CHAPTER III

METHODS

Stand selection is of critical importance in the study of vegetation and is often the most important single decision made by the ecologist (Ashby 1935). It is crucial, therefore, that objective stand criteria be established prior to field sampling. The following criteria were constructed in order to insure that native vegetation was being investigated and to aid in the interpretation of environmental parameters. A potential stand had to be:

(1) dominated by native species, and sand sage had to be present;

(2) free from sustained domestic stock grazing and from cultivation; and

(3) visually homogeneous with respect to slope position, exposure, and species composition.

I was able to visit several areas of sand sage vegetation in eastern Colorado which had been free from grazing or cultivation for 25-35 years, according to local residents. These areas differ greatly in composition from the areas sampled; common species included *Bromus tectorum*, *Festuca octoflora*, *Hordeum jubatum*, *Oenothera serrulata*, *Plantago purshii*, and *Yucca glauca*. Based on these observations, I felt that I could separate areas which had been disturbed by either grazing or cultivation for many years, and only areas free from such disturbance were selected for study.

Quantitative data were obtained by use of frequency measurements, which combine both density and pattern into one measure (Greig-Smith 1964). Frequency yields a large amount of information about many species in a minimum amount of time (Goodall 1970) and has been successfully used as a measure of grassland and shrubland vegetation in many parts of North America (Larson and Whitman 1942, Curtis 1955, Dix 1959, 1960, Dix and Butler 1960, and Hyder et al. 1963).

A 0.25 m^2, square, quadrat was used and sampling was conducted in a regular pattern. The stands were all small enough, with areas of approximately 25 square meters, that it was reasonable to sample one quadrat, then measure one-half meter, and sample the next quadrat. Thus approximately one-quarter of all 31 stands was sampled. The number of quadrats per stand varied from 15 to 35, but most stands had about 25.

To obtain an objective measure of the precision (i.e., repeatibility) of the method, I sampled one stand five times and compared the results. The seven most important species were the same in all replicates. In a few cases, relative ranks were changed, but even then the frequency differences were less than 10 per cent. Furthermore, in no case did a species with a frequency greater than 8 per cent in any replicate fail to occur in all other replicates. I interpreted this to mean that my sampling method gave repeatible results, and that it was relatively sensitive to minor elements in the vegetation.

Site characteristics were noted for each stand. Exposure was recorded as "N," "NE," "E," "SE," "S," "SW," "W," or "NW" - facing, and slope position was recorded as "top of slope," "upper slope," "mid-slope," "lower slope," "bottom," or "level." During later analysis some of the categories were combined (e.g., "top of slope" and "upper slope") since some categories proved to be represented by only a few stands. Any disturbance from small mammals or stray stock was also noted.

Surface soil samples were collected and analyzed by the Bouyoucos hydrometer method (Day 1965) for sand, silt, and clay fractions. Field capacity was determined on representative samples according to the "field capacity determination test for disturbed soils" as used by the Colorado State University Agronomy Department. A one inch diameter plexiglass cylinder is filled with a known weight of soil, usually about 200 g., a known volume of distilled water, 5 or 10 mls., is introduced to the surface, and the cylinder is covered with a plastic sheet to prevent evaporation. After 48 hours, the dry soil is removed from the cylinder and weighed. The weight of the wet soil is found by subtraction of the dry soil weight from the original weight.

Finally, a percentage is obtained by dividing the volume of water by the weight of the wet soil and multiplying by 100. This percentage is an estimate of the field capacity.

Plant nomenclature follows Harrington (1964), and common names follow Weaver and Albertson (1965). Two species of *Carex* could not be separated with certainty in vegetative condition (*C. heliophila* and *C. eleocharis*) and are here considered together. Voucher plants are deposited in the herbarium at Colorado State University.

CHAPTER IV

LITERATURE REVIEW

Dune Formation and Origin

Extensive inland sand deposits are limited to arid and semi-arid regions where streams fluctuate greatly in volume resulting in large expanses of stream beds periodically exposed to wind action (Thornbury 1969). In some areas, sand deposits result from weathering of the underlying bedrock with subsequent wind removal of the loess leaving the sand behind as "lag" (Thornbury 1969). In North America, large sand deposits are located in all parts of the arid and semi-arid West (Lobeck 1939 and Whitfield and Perrin 1939).

The largest sand area is located in north-central Nebraska, the Sandhills, encompassing about 20, 000 square miles and formed in two major periods of massive dune building; the first occurred in early Wisconsin and the second in late Pleistocene and Recent time (Smith 1965). These dunes are vegetated and not currently subject to widespread erosion. The sand deposits in Saskatchewan are another example of extensive deposits in the North American grassland, but unlike the Colorado or the Nebraska sand deposits, they are derived from glacial alluvium and lacustrine sediments which have been subsequently modified by wind action (Mitchell _et al._ 1944).

Factors Affecting Plant Growth on Sand Deposits

Cowles (1899) emphasized that wind is the single most important factor affecting dune vegetation. It effects plant adaptations, as well as the species composition of the vegetation. It acts directly by increasing transpiration, for example, but most importantly, it acts indirectly as a vector of substrate movement; hence the plants must be able to survive periods of root exposure and stem burial.

Substrate instability, as exemplified by the successional patterns which have been shown to correlate well with stability, is of great import to dune communities (Cowles 1899, Pool 1914, Tolstead 1942, Ramaley 1939, Salisbury 1952, and Olson 1958a, b). Stability is influenced by many factors, including slope, climate, especially wind velocity and season of maximum winds, but principally by the vegetation itself. Thus a "reciprocating" effect occurs, with the vegetation both influencing and being influenced by substrate stability.

The course texture of sandy soils provides not only a highly unstable surface, but also permits high rates of water infiltration. Since surficial sand deposits are normally associated with arid or semi-arid regions, infiltration is an important factor for plant growth. The more water that penetrates the surface, the less which can be lost directly to surface evaporation or to surface run-off. Furthermore, the sand particles do not hold water tenaciously, and, therefore, most of the water which reaches the soil surface penetrates and is made available to the plants. This is the best explanation for the higher productivities of sandy soils compared to finer soils in arid and semi-arid regions and, at least partially, accounts for the differences in floras between such areas (Taylor 1960 and Tomanek 1963).

Despite the fact that sandy soils have relatively high moisture availability, other environmental factors are often deleterious to plant growth (Olson 1958a). Soil organic matter is low (Pool 1914), and consequently so are nutrient levels. In particular, nitrogen is frequently deficient in sandy soils (Pool 1914, Olson 1958a, and Eck et al. 1968). Some workers have also detected deficiencies in other elements, phosphorus, potassium, calcium, and sulfur (Burzlaff 1962 and Eck et al. 1968). Surface temperatures are extreme, usually warmer in summer and colder in winter than adjacent hardlands (Pool 1914).

All of the above factors help account for the differences between sand vegetation and vegetation from similar climatic regions but with differing edaphic conditions.

Vegetational Comparisons

Central to the problem of the Colorado sand sage vegetation is an understanding of its relationship with other examples of sand vegetation (see Introduction). It is appropriate, therefore, to review some of the techniques which have been utilized in the past to describe vegetational affinities between similar, but disjunct examples of vegetation.

Different methods of comparison will provide different types of information, and therefore one must first examine the type of question under consideration. Ecologists attempt to establish floristic or ecological relationships, but frequently fail to distinguish the two.

If the question is phytogeographical in nature, the simplest method is to compare the floras at the specific, generic, or familial levels. This method, however, may lead to erroneous conclusions concerning the ecological relationship, (i.e., similarities in controlling factors) between two areas since populations may differ widely in their ecological tolerances (McMillan 1959, Whittaker 1954, and McIntosh 1970), and floristically dissimilar areas may be similar ecologically.

Spatially separated areas have been compared and related on non-floristic bases for many years (Specht 1969 and Mooney and Dunn 1970). Raunkiaer (1934) developed one of the most successful systems of comparing regions based on morphological adaptations. Life-form systems of classification have shown that vegetational types with similar physiognomies frequently develop in environmentally similar regions. However, they are of much less value when used to make comparisons within one vegetational type. Hence, several workers have attempted to develop growth-form systems which are more sensitive to variations within one vegetational type, and, consequently, are more restrictive in their applications (Gimingham 1951, Knight 1965, and Knight and Loucks 1969).

The use of life-form or growth-form systems rests upon the premise that the characteristics used in the classification are of adaptive value (cf. DuRietz 1931). Whittaker and Woodwell (1972) assert that such characteristics represent the best integrator of a species' niche. Even without making such a bold assertion, the physiognomy of the vegetation has often been used as an indicator of the ecological situation (Gimingham 1951, Arnold 1955, Roux and Warren 1963, Specht 1969, Chandapillai 1970, Mooney and Dunn 1970, Mooney et al. 1970, 1972, and Whittaker and Woodwell 1972). Thus area can be compared on their growth-forms, and, where a similarity exists, it may be reasonable to hypothesize certain ecological factors as being similarly important.

Studies on Sand Vegetation

Cowles' (1899) study of the Lake Michigan sand dunes was the first detailed study of any North American dunes. Since then, many more investigations have been conducted which have been motivated by one of two different types of questions. Beginning with Cowles, plant ecologists have investigated dune vegetation for its intrinsic interest (Pound and Clements 1900, Pool 1914, Ramaley 1939, Tolstead 1942, Olson 1958a, b, Curtis 1959, Wohlrad et al. 1963, Chadwick and Dalke 1965, Watts and Wright 1966, Hulett et al. 1966, Nicholson and Hulett 1969, and Quinn and Ward 1969). A second type of interest has spawned many other studies, an interest in reclamation, stabilization of shifting dunes or alteration of the native vegetation to improve the forage value (Lamson-Scribner 1898, Whitfield and Perrin 1939, Smith et al. 1947, Whitfield and Brown 1948, Allred 1949, McIlvain and Savage 1949, Burzlaff 1962, 1971, Everson et al. 1966, Quinn and Hervey 1970, and Sims et al. 1971). However, very little study, whether motivated by basic ecological interests or by reclamation desires, has concentrated on sand sage vegetation. Pound and Clements (1900) were the first to describe the sand sage vegetational type and termed it the "*Artemisia filifolia* society" occurring in southwestern Nebraska. Their account is neither complete nor quantitative, but it does list some of the associated species. Pool (1914), again working in Nebraska, mentions the sand sage vegetation, but with even less detail than given by Pound and Clements. Weaver and Albertson (1956) also mention the sand sage vegetation of Nebraska, but with hardly any more detail than Pool.

Passing notes are made on the sand sage vegetation of western Texas and western Oklahoma by range managers interested in sagebrush eradication to improve range condition (Allred 1949 and McIlvain and Savage 1949). McIlvain and Savage (1949) describe the vegetation this way:

> The vegetation consists of an upper story of shrubs averaging about three feet in height but ranging from one to six feet. The plants of sand sagebrush are uniformly spaced and foliage cover usually occupies about one third of the ground area. Skunkbrush (*Rhus trilobata* Nutt.) and sand plum (*Prunus angustifolia*) usually occur as scattered plants throughout the sand areas.

> Shinnery oak (Quercus harvardi Rydb.) is confined to the Miles series of loamy fine sand where it often makes up more than 75 per cent of the foliage density. Dominant grasses in the understory are blue grama (Bouteloua gracilis (H. B. K.) Lag.) and sand dropseed (Sporobolus cryptandrus (Torr.) A. Gray). Sufficient grasses occur between and within the shrubs to provide a good basis for rapid natural recovery when the shrubs are killed [by 2, 4-D spraying].

This is the complete description of the vegetation, though later they list the reaction of a large number of shrubs to 2, 4-D, but no mention is made of their importance in the vegetation, and no other grasses are mentioned.

Another area of sand sage vegetation occurs in west Texas. A. S. Jackson, a game biologist, has discussed the area in relation to bobwhite management (Jackson 1965). Unfortunately, his discussion of the vegetation is negligible, but he does make some valuable observations on two Spring fires which burned in 1962. In one area, the fire was followed by a good supply of summer moisture and by late August the grass-forb association included "sandsage, Texas croton, sandlily, sand dropseed, western ragweed, and sand bluestem." He concluded that except for Chickasaw plum (Prunus angustifolia) and aromatic sumac (Rhus aromatica), neither of which had fully recovered, the vegetation by late August closely resembled that of an adjacent unburned area. The other fire occurred in a different locality and was followed by a poor supply of summer moisture. After two growing seasons, Jackson concluded that the Chickasaw plum and the aromatic sumac had been "permanently retarded." No mention, however, was made of the recovery of sand sage, but he did note its importance in contributing to the hot fire. Presumably, he would have mentioned it with the other shrubs if it had been similarly damaged.

Ramaley (1939) has conducted the only intensive ecological investigation of sand vegetation in Colorado. He lists Artemisia filifolia as the dominant and Muhlenbergia pungens, Oryzopsis hymenoides, Sitanion hystrix, and Sporobolus cryptandrus as "frequent species," plus 34 "other species." He believed that the sand sage vegetation formed a "semi-permanent community on level to slight rolling ground where soil is more compact and contains more humus than that which favors [the] Muhlenbergia pungens community ." He adds that the sand sage [community] is "more advanced ecologically than the Muhlenbergia community (sand-hills mixed community), " and apparently he meant by this that it is successionally later. Ramaley also indicated that fire and overgrazing may "degrade sand prairie (Stipa-Andropogon-Calamovilfa community) to the sand-sage stage."

The sandhills of Saskatchewan, which have been described by Hulett et al. (1966), merit attention as they too occur in the central North American grassland. Unlike most sand vegetation studies, including Ramaley's, quantitative techniques were employed in this study.

Hulett et al. (1966) divide the dunes on the basis of physiographic categories into "active complexes," "stabilized blowouts," "stabilized dunes," "dune depressions," and "sand flats." Since sand sage does not occur as far north as Saskatchewan (Ramaley 1939), and since the description of the "stabilized dunes" makes it appear the most similar to the Colorado sand sage vegetation, the data from this physiographic category are used for comparison (see Results).

It is worthwhile to contrast the adjacent hardland vegetation in eastern Colorado with the sand sage vegetation. As with the sand sage vegetation, the hardland vegetation has been inadequately investigated, and thus it is impossible to give more than a general description for the entire area. Though the vegetation of the western sector of the Colorado plains near the mountains has been subdivided (Shantz 1923 and Morris and Dix 1971), this has not been done for the eastern sector of the hardlands.

Weaver and Albertson (1956) describe the hardlands as "short-grass type" or "grama-buffalo grass type" as does Shantz (1923). Other than blue grama and buffalo grass, which may provide as much as 90 percent of forage (Klipple and Costello 1960), the other perennial grasses include squirreltail (Sitanion hystrix), red three awn (Aristida longiseta), tumble grass (Schedonnardus panniculatus), and western wheatgrass (Agropyron smithii).

CHAPTER V

RESULTS

Sand sage vegetation on the Colorado plains can be visualized as sagebrush shrubs scattered throughout a tall-grass matrix (Figs. 2 and 3). The shrubby habit of sand sage makes it the most conspicuous species, and small soapweed (Yucca glauca), the only other shrub encountered, is similarly obvious when present. The ground cover includes a large number of mid and tall grasses which impart a distinctive appearance to the vegetation, especially in late summer. The most common grasses are sand dropseed (Sporobolus cryptandrus), blue grama (Bouteloua gracilis), needle-and-thread (Stipa comata), sand reed (Calamovilfa longifolia), and sand bluestem (Andropogon hallii). Notably, over one-half of the grasses (12 of 21) are listed by Rydberg (1922) as either commonly associated with, or restricted to, sandy soils. Blue grama is the only common grass not among the twelve. Thus the flora is distinctly arenaceous. Forbs, though numerous, are usually widely scattered and inconspicuous when not in flower.

The family composition of the sand sage vegetation was found to resemble that found in other grasslands by Steiger (1930) and Dix and Butler (1960) with Compositae contributing the most species (25%), Gramineae was second (20%), followed by Chenopodiaceae (12%) and

Figure 2A. Sand sage (*Artemisia filifolia*), about one meter tall in eastern Colorado. Note *Stipa comata* in foreground. (Photograph taken during July, 1971, 2 miles north and 2 miles east of Eckley, Colorado - center of Section 18, T. 2 N., R. 45 W.)

2B. Sand bluestem (*Andropogon hallii*), about one meter tall, and sand sage (*Artemisia filifolia*), in eastern Colorado. Note amount of cover on right of photograph. (Photograph taken during August, 1971, along Colorado highway 96, $\frac{1}{4}$ mile north of Big Sandy Creek - southeast quarter of Section 36, T. 18 S, R. 46 W.)

Figure 3A. Over-grazed area of sand sage (Artemisia filifolia) vegetation in northeastern Colorado. Note physiognomy, especially the lack of tall-grasses. (Photograph taken during July, 1971, 7 miles south of Holyoke along Colorado highway 51 - northwest quarter of Section 17, T. 6 N., R. 44 W.)

3B. Native sand sage (Artemisia filifolia) vegetation near Eckley, Colorado. Foreground area is not grazed, while area beyond the fence is grazed by cattle. (Photograph taken during July, 1971, 2 miles north and 2 miles east of Eckley, Colorado - center of Section 18, T. 2 N., R. 45 W.)

Leguminosae (5%). Ascelpidaceae, which commonly contributes a large number of species to grassland floras, was represented by only one species (1%).

A total of 84 vascular plant species were recorded in the quadrats of the study (Table 1), 43 of which were defined as "significant" (i.e., frequency $\geq$ 15% in at least one stand) and are listed in Table 2. A great dissimilarity in importances of species between the northern and the southern study areas can be seen by inspection of the Tables. In particular, such species as sand reed and needle-and-thread, which are so important in the north, do not occur in quadrats in the south. Because of these differences, the two areas will be described separately.

The most important species in the northern stands are sand sage, sand dropseed, sand reed, Carex spp., and needle-and-thread. Blue grama, narrow-leaved goosefoot (Chenopodium leptophyllum), spiderworth, (Tradescantia occidentalis), sand bluestem, and prairie sunflower (Helianthus petiolaris) are all common as well. Most of the variation within the northern stands can be accounted for by slope and exposure effects. Figures 4 and 5 illustrate their effects on selected species. The species in Figure 4 are ordered from those which reach their maximum importance on north and east facing slopes to those which reach their maximums on west and south facing slopes. In Figure 5, the species are arranged in three groups: those which are

Table 1. List of all species found in the quadrats of the study, showing the number of stands in the north (total = 21) and in the south (total = 10) in which each species was recorded. Complete species lists for the stands were not recorded.

Species	N	S	Species	N	S
Abronia elliptica	0	1	Chrysopsis villosa	0	1
Agropyron smithii	3	0	Cirsium plattensis	2	0
Allium cernuum	1	0	Conyza canadensis	4	2
Ambrosia coronopifolia	6	4	Croton texensis	2	0
Andropogon hallii	17	1	Cyperus schweintzii	1	0
Andropogon scoparius	3	0	Descurainia sophia	1	0
Apocynum sibiricum	2	0	Erigeron bellidiastrum	9	2
Argemone intermedia	1	1	Erigeron sp.	1	0
Aristida fendleriana	3	0	Eriogonum microtheca	1	0
Artistida longiseta	2	5	Erigonum effusum	1	0
Artemisia filifolia	19	10	Euphorbia glyptosperma	1	1
Artemisia ludoviciana	9	0	Evolvulus nuttaliensis	4	2
Ascelpias ascelpidoides	1	0	Festuca octoflora	6	0
Astragalus sp.	2	0	Gaura coccinea	2	3
Bahia oppositifolia	1	0	Haplopappus gracilis	0	1
Bouteloua curtipendula	0	2	Haplopappus spinulosus	4	5
Bouteloua gracilis	16	10	Helianthus petiolaris	20	5
Bouteloua hirsuta	2	3	Hymenoxys odorata	1	0
Bromus tectorum	5	0	Ipomea leptophyllum	1	2
Buchloe dactyloides	0	1	Kochia scoparia	2	0
Calamovilfa longifolia	19	0	Koleria cristata	2	0
Carex spp.	10	0	Lappula redowskii	2	2
Chenopodium alba	2	0	Lepidium montanum	2	0
Chenopodium dessicatum	1	0	Lesquerella ludoviciana	4	0
Chenopodium leptophyllum	18	2	Lesquerella montana	1	2

Table 1. (Continued)

Species	N	S	Species	N	S
Lithospernum incisum	2	0	Physaria australis	1	0
Lithospernum ruderale	1	0	Plantago purshii	11	2
Lygodesmia juncea	2	1	Polygonum ramosissimum	1	0
Lysimachia ciliata	1	0	Psoralea lanceolata	3	5
Melilotus offinale	1	0	Redfieldia flexuosa	9	1
Mentzelia nuda	9	3	Salsola kali	12	6
Mirabilis linearis	3	0	Solidago sp.	2	1
Muhlenbergia pungens	11	0	Sorgastrum nutans	3	0
Munroa squarosa	0	1	Sphaeralcea coccinea	0	3
Oenothera nuttalii	1	0	Sporobolus cryptandrus	21	10
Opuntia humisfera	12	4	Stipa comata	19	0
Oryzopsis hymenoides	4	0	Thelesperma trifidum	1	0
Panicum virgatum	0	2	Tradescantia occidentalis	16	2
Penstemon ambiguus	6	0	Tragopogon parvifolia	1	0
Penstemon angustifolia	0	2	Vicia americana	11	0
Phlox hoodii	10	0	Yucca glauca	4	4
Physalis lanceolata	2	0			

Table 2. Mean frequency of occurrence and number of stands of occurrence (≥) for all species with frequency 15% in one or more stands. Ordered from species characteristic of the northern stands to those characteristic of the southern stands.

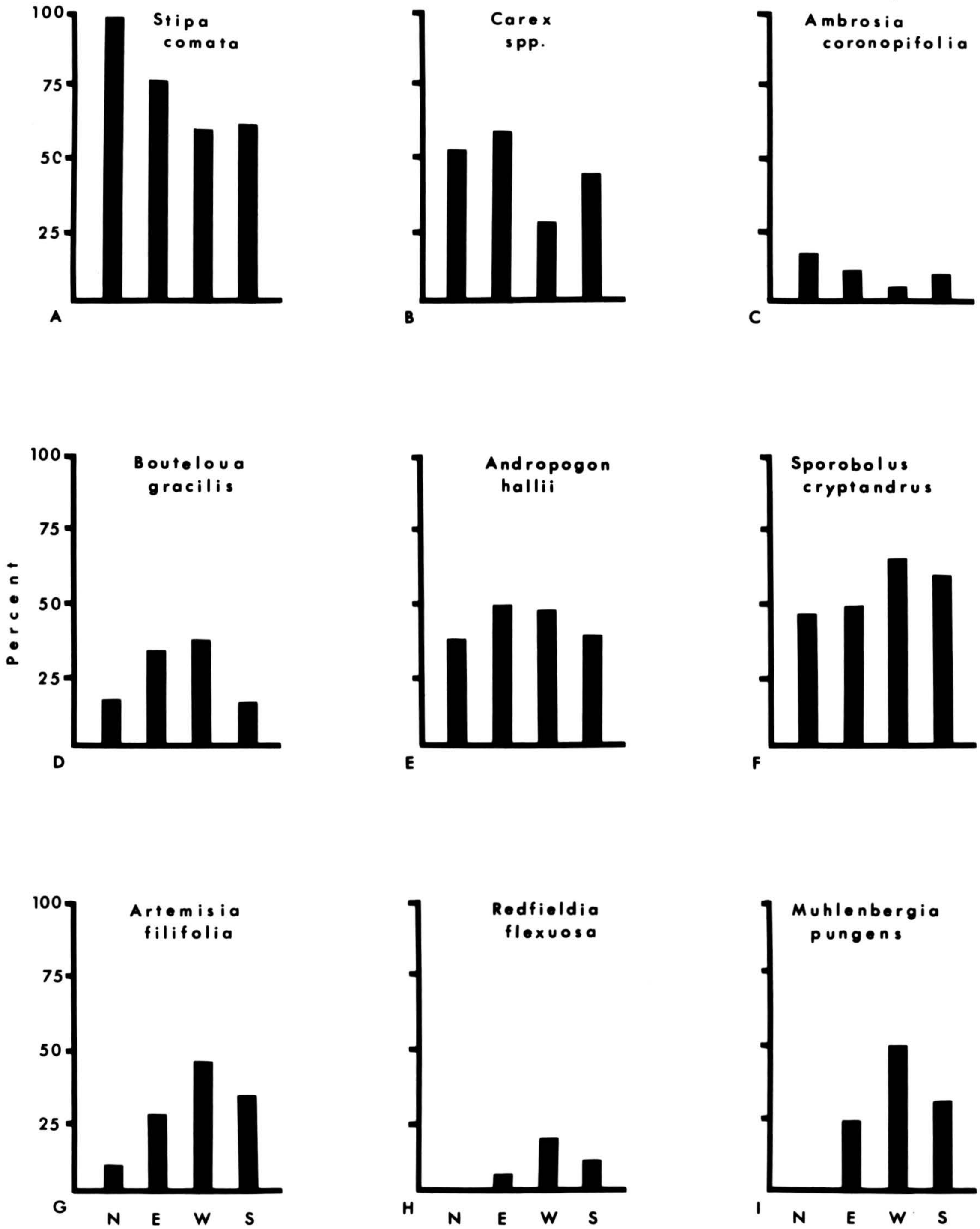
Species	Northern Stands (total = 21 stands)	Southern Stands (total = 10 stands)
Stipa comata	66 (19)	(0)
Calamovilfa longifolia	60 (19)	(0)
Carex spp.*	49 (10)	(0)
Chenopodium leptophyllum	46 (18)	10 (2)
Tradescantia occidentalis	37 (16)	7 (2)
Andropogon hallii	41 (17)	65 (1)
Helianthus petiolaris	33 (20)	8 (5)
Muhlenbergia pungens	32 (11)	(0)
Artemisia ludoviciana	33 (9)	(0)
Salsola kali	21 (12)	8 (6)
Phlox hoodii	12 (10)	(0)
Erigeron bellidiastrum	17 (9)	8 (2)
Redfieldia flexuosa	12 (9)	11 (1)
Festuca octoflora	18 (6)	(0)
Penstemon ambiguus	19 (6)	(0)
Opuntia humisfera	9 (12)	6 (4)
Sorghastrum nutans	31 (3)	(0)
Andropogon scoparius	26 (3)	(0)
Agropyron smithii	19 (3)	(0)
Koleria cristata	15 (2)	(0)
Lepidium montanum	13 (2)	(0)
Mirabilis linearis	10 (3)	(0)
Kochia scoparia	12 (2)	(0)
Thelesperma trifidum	24 (1)	(0)
Eriogonum microtheca	16 (1)	(0)
Artemisia filifolia	32 (19)	31 (10)
Sporobolus cryptandrus	51 (21)	62 (10)
Lappula redowskii	4 (2)	18 (2)
Ipomea leptophyllum	8 (1)	30 (2)
Conyza canadensis	5 (4)	16 (2)
Lesquerella montana	24 (1)	54 (2)
Bouteloua hirsuta	18 (2)	40 (3)
Psoralea lanceolata	10 (3)	11 (5)
Haplopappus spinulosus	5 (4)	24 (5)
Aristida longiseta	6 (2)	27 (5)

Table 2. (Continued)

Species	Northern Stands (total = 21 stands)	Southern Stands (total = 10 stands)
Plantago purshii	10 (11)	93 (2)
Ambrosia coronopifolia	9 (6)	54 (4)
Bouteloua gracilis	37 (16)	73 (10)
Chrysopsis villosa	(0)	18 (1)
Buchloe dactyloides	(0)	44 (1)
Panicum virgatum	(0)	34 (2)
Spharalcea coccinea	(0)	25 (3)
Bouteloua curtipendula	(0)	48 (2)

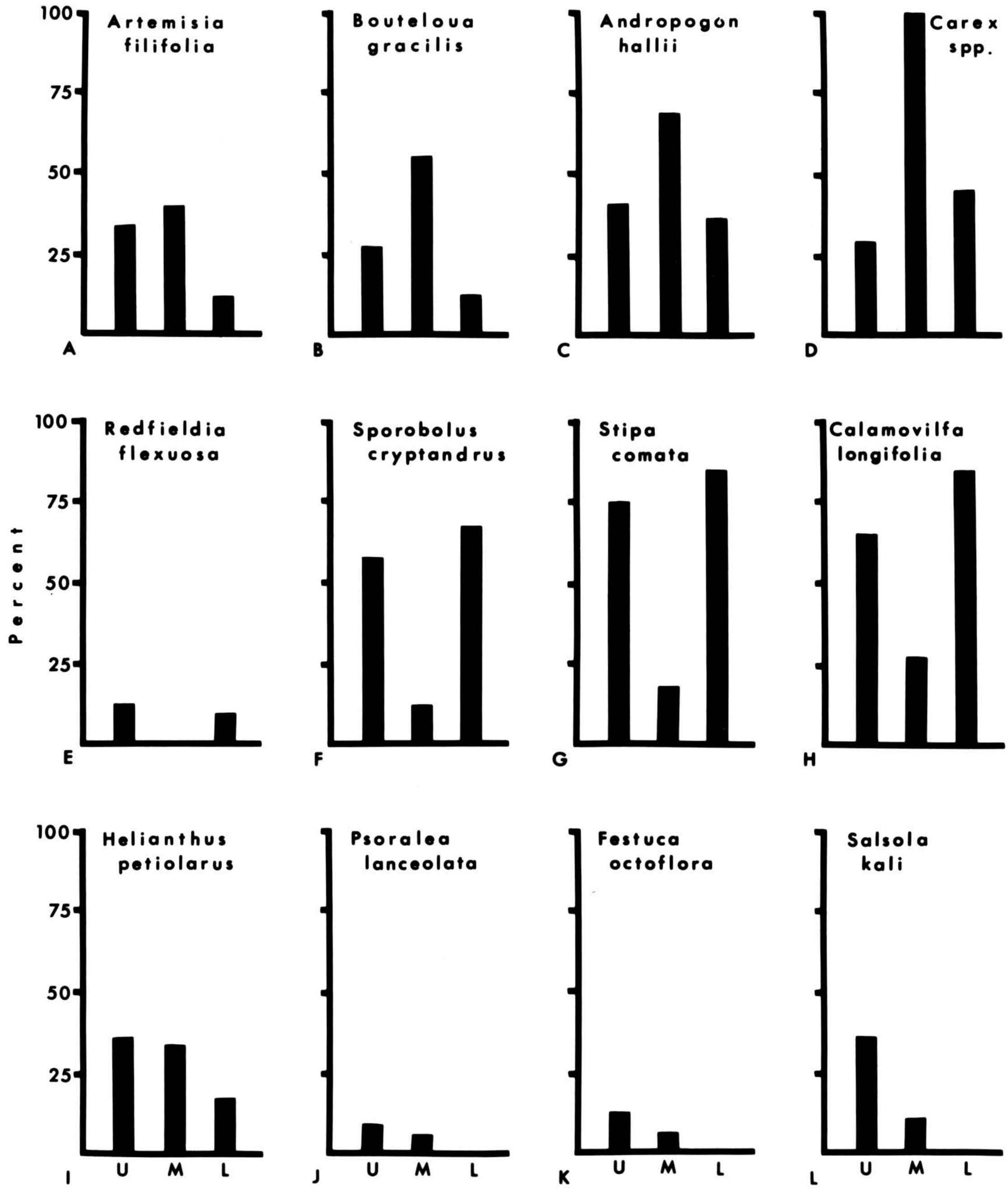
*Carex spp. = C. heliophila + C. eleocharis

Figure 4. Mean frequency of occurrence for selected species plotted against exposure, ordered from species which are most frequent on north and east-facing exposures to those which are most frequent on west and south-facing exposures. Categories are as follows: N = north and northeast-facing slopes, E = east and southeast slopes, S = south and southwest-facing slopes, and W = west and northwest-facing slopes.



100
75
50
25
Percent
Stipa comata
A
Carex spp.
B
Ambrosia coronopifolia
C
Bouteloua gracilis
D
Andropogon hallii
E
Sporobolus cryptandrus
F
Artemisia filifolia
G
Redfieldia flexuosa
H
Muhlenbergia pungens
I
N
E
W
S

Figure 5. Mean frequency of occurrence for selected species plotted against slope position, illustrating the three major patterns (see text).



100
75
50
25
Percent
Artemisia filifolia
A
Bouteloua gracilis
B
Andropogon hallii
C
Carex spp.
D
Redfieldia flexuosa
E
Sporobolus cryptandrus
F
Stipa comata
G
Calamovilfa longifolia
H
Helianthus petiolarus
I
U M L
Psoralea lanceolata
J
U M L
Festuca octoflora
K
U M L
Salsola kali
L
U M L

most common on the mid-slope position (Figs. 5A, B, C, and D); those which are uncommon on mid-slope positions compared to their behavior on upper and lower slopes (Figs. 5E, F, G, and H); and those which are common at one end of the slope gradient and whose importances gradually decrease along the gradient. These Figures illustrate that some of the more important species respond to slope or exposure: needle-and-thread is comparatively common on upper and lower slopes which have northerly exposures (Figs. 4A and 5G); sand reed is similarly common on upper and lower slopes, but shows less response to exposure (Fig. 5H). This pattern contrasts with that of blue grama and sand bluestem which are most common at mid-slope positions with mesic exposures (Figs. 4D, E, and 5B and C). These species, except blue grama, are about as common on level ground as on upper or lower slopes. Blue grama, however, reaches its maximum development on the level with an average frequency of 78 per cent. Generally the forbs show much less response to slope and exposure and thus few were included in Figures 4 and 5. Even the ones which were included, show less response than most of the graminoids.

Only five of the ten southern stands have slope and exposure (the rest are "level"), hence, interpretation of the effects is tenuous. Furthermore, within those five stands, responses to slope and exposure are not nearly as pronounced, nor as consistent, as in the north.

Therefore, graphs are not shown for the south as they were for the north. Briefly, blue grama is the dominant grass in the south and has a frequency value of 100 per cent in at least one stand in each slope category. In some cases, however, its frequency drops as low as 30 per cent, showing the inconsistent nature of blue grama's response to slope and exposure. Sand dropseed does about equally well on all exposure and slope positions, and it too is present in all stands. Its frequency, however, while variable between stands, is more consistent than that for blue grama. Significantly, both blue grama and sand dropseed reach their maximum expression in level stands. Side-oats grama and hairy grama, in contrast, do well only at the upper slope position with west or northwest exposures. It appears that exposure may be more important than slope position in these cases because both species fail to occur in other stands with upper slope positions, but differing exposures. Red three awn does well only on the level, and not consistently well there. Thus it can be seen that while slope and exposure do effect species behavior in the southern stands, as well as in the northern ones, the effects are less pronounced and more inconsistent. It appears that in the south there are more important factors than slope position and exposure to which the species are responding.

Soil analyses were conducted to determine if the two study areas varied in selected soil properties. Mechanical analysis revealed that the southern area had relatively less sand and relatively more silt and clay compared to the northern area (Table 3). Field capacity was also determined for representative samples, since, if the soil texture differences had any influence on the vegetation, it would probably be indirectly through their effect on soil moisture properties. The differences (Table 3) are slight and cannot account for the differences in species composition between the areas.

Climatic data (from secondary sources, Table 4) were examined to determine variations between the areas which might be significant for plant growth. This data show that important differences do exist between the two areas and this may well account for some of the dissimilarity in species' importances (Table 2). Furthermore, if the grasses are classified according to Gould (1968) (Table 5), the Subfamilies show some geographical separation, thus supporting the hypothesis that climatic differences are significant. The Subfamily Eragrostoideae is well represented in both areas, notably by sand dropseed and blue grama; the Subfamily Panicoideae is less evenly distributed, being more important in the northern stands, but still represented in the southern stands; but, significantly, while six species in the Subfamily Festucoideae occurred in samples in the northern area, none was found in samples in the southern stands. Gould (1968) believed that most members of the Festucoideae evolved in a "cool to cold" climate, and their absence in the southern stands is felt to reflect the warmer, drier climate in that area.

Table 3. Comparison of northern and southern stands based on soil texture and field capacity. All values are in per cent, and standard error of the means is indicated "S. E."

	Soil Texture					
	Sand	S. E.	Silt	S. E.	Clay	S. E.
Northern Stands	93	1.3	4	1.1	4	.9
Southern Stands	83	2.2	9	1.6	8	.8

	Field Capacity	
	Field Capacity	S. E.
Northern Stands	7.8	.2
Southern Stands	9.8	.9

Table 4. Climatic comparison of northern and southern study areas. Data for northern area from Akron, Colorado, and for southern area from Springfield, Colorado. Source: U.S. Weather Bureau: Climatic Summary for the U.S., Supplement 1931-1952, unless otherwise indicated.

	growing season* (days)	mean no. mo. with snowfall= 0.0 or T	mean annual precip. (in.)	minimum annual precip. (in.)	mean Jan. temp. °C (°F)	mean July temp. °C (°F)	mean annual evap. ** (in.)
Northern Area	143	3	18	10.0	-3°(26°)	23°(73°)	47
Southern Area	169	5	14	7.0	0°(31°)	24°(75°)	73

* Source: Climate & Man, Yearbook of Agriculture 1941, data for southern area from Two Buttes, Colorado.

** Source: for northern area, U.S. Central Plains Field Station, Akron, Colorado (mimeo.), 1951-1960; for southern area, John Martin Dam, U.S. Weather Bureau: Climatic Supplement 1951-1960.

Table 5. Classification of all grasses according to Gould (1968).

Panicoideae	Festucoideae	Eragrostoideae
Andropogon hallii	Agropyron smithii	Aristida fendleriana
Andropogon scoparius	Bromus tectorum	Aristida longiseta
Panicum virgatum	Festuca octoflora	Bouteloua curtipendula
Sorgastrum nutans	Koleria cristata	Bouteloua gracilis
	Oryzopsis hymenoides	Bouteloua hirsuta
	Stipa comata	Buchloe dactyloides
		Calamovilfa longifolia
		Muhlenberia pungens
		Munroa squarosa
		Redfieldia flexuosa
		Sporobolus cryptandrus

I thought that some of the species composition differences might be due to the substrate stability differences. This parameter has often been reported as profoundly effecting dune vegetation (Cowles 1899, Pound and Clements 1900, Pool 1914, Ramaley 1939, Tolstead 1942, Gimingham 1951, Olson 1958a, b, Chadwick and Dalke 1965, and Hulett et al. 1966). It is difficult to ascertain relative stability since most indicators rely on the vegetation which leads to circular reasoning if used to explain the vegetation. The geologic literature can be of help since geologists employ other measures, such as rates of movement, parent material weathering rates, and climatic data, to determine stability. Some geological information is available for the areas of my sites (Hill and Tompkin 1953 and Scott 1968). They indicate that the northern area is not yet stable, and that the dunes in the area are slowly migrating southeastward. In contrast to this, the southern dunes appear to be stable and non-migrating, except along the stream courses (Trimble 1972). Substrate stability differences, therefore, appear to be an important factor and undoubtedly contribute to the differences in vegetation in the areas.

Another factor contributing to the dissimilarity in vegetation could be a fortuitous difference in the choice of stands in the two areas, especially with regard to slope and exposure. However, while the areas do differ in per cent of stands in most exposure and position categories, the differences are not large enough to account for the differences in species composition.

Therefore, the variations in substrate stability and climate appear to be environmental factors of major importance in explaining the vegetational differences between the northern and the southern study sites.

Two other areas of dune vegetation in North America are of particular interest to the present study because they offer comparative data: the Nebraska Sandhills and the sandhills of southwestern Saskatchewan. Vegetational comparisons were made to evaluate the relationships of these three areas. An "*Artemisia filifolia* formation" has been described for Nebraska (Pound and Clements 1900), but the area lies southwest of the main Sandhills and has received no detailed studies. The comparisons with Nebraska use information from the description of the vegetation by Pound and Clements (1900). The Sandhills in Saskatchewan have recently been studied by Hulett *et al.* (1966). Sand sage does not occur in Saskatchewan. The nearest "physiographic category" of Hulett *et al*. (1966), and therefore the nearest ecologically, is their "stabilized dunes", and the data from those stands are used for comparison with Colorado.

Several species occur in all three areas: sand reed, hairy golden aster (*Chrysopsis villosa*), prairie sunflower, lance-leaved psoralea (*Psoralea lanceolata*), and needle-and-thread. If Nebraska and Colorado are considered alone, several more species are found in common: sand bluestem, little bluestem (Andropogon scoparius), sand sage, sandhill muhly (Muhlenbergia pungens), Thelesperma trifidum, and little soapweed. If Colorado and Saskatchewan are compared, blue grama, Lygodesmia juncea, Hood's phlox (Phlox hoodii), and sand dropseed are added to the list. However, floristic comparisons are difficult to interpret, especially when complete species' lists are unavailable. Furthermore, they are confusing because of ecotypic variation (McMillan 1959), chance, and phytogeographical problems (see Literature Review). Hence, it was decided to compare the areas using life-form systems.

Table 6 shows the comparisons of Colorado, Nebraska, and Saskatchewan using Raunkiaer's system of classification (as described by Cain and Castro 1959). The "typical" (Cain 1950) steppe community, taken from Paulson's (1911) data from near Akron, Colorado (Cain 1950), and Raunkiaer's "normal spectrum" (Cain 1950) are included for comparison. No significant differences could be seen between the two Colorado areas using this system, and hence the two are combined to represent Colorado.

One of the major inadequacies of Raunkiaer's system is that to be general enough to allow comparisons between highly different vegetational types, and still remain simple, it cannot be specifically adapted for use within a single vegetational type. Thus, Gimingham

Table 6. Comparison of selected vegetations using Raunkiaer's life-form classification system (see text). Species source information for Nebraska, Saskatchewan, steppe, and "normal" spectrum given in text.

	Phanerophytes	Chamaephytes	Hemicryptophytes	Cryptophytes	Therophytes
Colorado	3	3	44	38	12
Nebraska	11	8	33	46	0
Saskatchewan	14	14	41	31	0
Steppe (Akron)	0	19	58	8	15
Normal	46	9	26	6	13

(1951), examining two areas of dune vegetation in Scotland, used Raunkiaer's system, and finding it not completely satisfactory, developed a special growth-form system for sand vegetation.

Using Gimingham's system (1951), I compared the three areas once again (Table 7), but this time I separated the two Colorado study sites since differences between them are apparent. The Colorado vegetation, particularly that of northern Colorado, is characterized by small, dense growth-forms (e.g., by "small tussocks," "small branched," and "small erect" forms), whereas the vegetation of Saskatchewan, and especially that of Nebraska, differs from in possessing high percentages of large, open growth-forms (e.g., "large branched" and "large erect" forms). Gimingham (1951) found a similar pattern of differences in the two areas he examined in Scotland, and he showed that the small, dense habit was typical of less stable areas, I believe that the growth-form spectra in Colorado, Nebraska, and Saskatchewan reflect stability differences, with northern and southern Colorado being similar, the former being the less stable, and Saskatchewan and Nebraska being similar, the former being the less stable.

Table 7. Comparison of selected vegetations using Gimingham's system of growth-form characteristics. Figures are in percent. Species source information for Nebraska and Saskatchewan as in text.

	# species	large tussock	small tussock	large branch	small branch	large erect	small erect	large rosette	small rosette	prostrate	rhizomes
Colorado-N	32	0	44	9	15	9	19	0	0	3	34
Colorado-S	22	0	36	14	18	9	18	0	0	5	36
Nebraska	24	0	29	29	0	29	0	4	4	4	24
Saskatchewan	29	0	38	28	3	27	0	0	3	0	28

CHAPTER VI

DISCUSSION

Sand dropseed, blue grama, and needle-and-thread are among the most important species in the Colorado sand sage vegetation, and they all occur as important elements of the native vegetation in other parts of the Great Plains (Larson and Whitman 1942, Weaver and Albertson 1956, Hulett _et al_. 1968, and Nicholson and Hulett 1969). This suggests that the Colorado sand sage vegetation is not a distinct community, but more properly should be considered an edaphic variant of the mixed-grass prairie. Furthermore, examination of the changes in species' importances between the northern and the southern stands (Table 2) shows that the southern stands support a less arenaceous vegetation. It appears, therefore, that the more stable the substrate, the more closely the sand sage vegetation resembles the vegetation of finer textured soils, which supports the hypothesis that this vegetation is a variant of the mixed-grass prairie. I believe that if stands could be examined along a greater part of the stability gradient (e.g., stands intermediate in stability between my southern stands and the surrounding finer textured soils), especially in a restricted area where climatic variables would be eliminated, they would show that species compositions vary continuously along this gradient. This would be an appropriate test of my contention that the Colorado sand sage vegetation is a variant of the mixed-grass prairie. Unfortunately, my field observations indicate that the existence of more than a very few stands, still in native vegetation, with such intermediate conditions is quite doubtful.

The northern stands have many species with high mean frequencies and high presence values compared to the southern stands. Recent investigators have placed communities along gradients from "physically controlled systems" to "biologically accommodated communities" (see especially Dunbar 1968 and Woodwell and Smith 1969). Separation rests on the predictability of the environment; if the physical environment oscillates irregularly, the system tends to be dominated by the physical environment, but if the environment is either nearly stable, or oscillates regularly, the system tends to be dominated by species interactions, that is "biologically accommodated" (Dunbar 1968 and Slobodkin and Sanders 1969). In the former case, species normally adapt to environmental factors rather than to competition, and competition is normally minimized (Miller 1969 and Wilson 1969).

I suggest that the unstable sandy conditions, such as in the northern stands, are properly placed near the "physically controlled" end of the gradient since environmental oscillations are irregular. Supportive of this hypothesis are the data (Table 2) which show the importance of arenaceous species, such as sand reed, spiderwort, sand bluestem, sandhill muhly, blow-out grass, and sand bluestem, whose principal adaptations, such as rhizomes, extreme potential for culm elongation, ability to withstand periods of root exposure or stem burial, and small, dense growth-forms (Cowles 1899, Pound and Clements 1900, Gimingham 1951, Salisbury 1952, and Olson 1958a, b), are adaptations to withstand the oscillations of the physical environment.

The southern stands, with more stability and, consequently, more environmental predictability, and with a less arenaceous vegetation, tend to be less physically controlled and more biologically accommodated. As a system become more biologically accommodated, species interactions increase (Wilson 1969), and consequently, competitive exclusion becomes an important factor (Miller 1969 and Wilson 1969). The increase in competitive exclusion may lead to either of two possibilities: (1) dominance of the community by one or a few species to the near exclusion of all others, or (2) a reduction in niche sizes and the coexistence of more species (Miller 1969 and Slobodkin and Sanders 1969). If the first possibility occurred, it would be expressed as relatively few species with high mean frequencies and high presence values. Table 2 portrays this situation in the southern stands; a few species, such as sand dropseed and, especially, blue grama, appear to be so dominant that they can keep the number of species with high importances (high frequencies and high presence values) low by being strong competitors. In comparison, the northern stands, which are physically dominated, have several species with high importances (Table 2); hence, the dominance appears to be shared by several species. I believe that the more stable environment in the southern stands which permits increased competitive exclusion to occur is the best explanation for the fewer number of species with high frequency and high presence values in this area.

Differences between the northern and the southern stands are not simply differences in relative amount of species present, but in many cases, species common in one area are completely absent in the other (Tables 1 and 2). Of particular interest, six Festucoid grasses (classification according to Gould 1968) occurred in quadrats in the north, while none was found in samples in the south. This is not because the southern area is completely out of their range, it certainly is not, but I do feel it reflects the regional climatic change (Table 4), and perhaps a tension zone between the northern and the southern Great Plains lies through central Colorado. No detailed studies of vegetation of finer textured soils are available to determine if a similar pattern could be discerned there, but it should definitely be looked for in the future.

Figures 4 and 5 show species' responses of selected species to exposure and slope. In most cases, these patterns can best be interpreted as normal, or parts of normal, curves which suggests the usual situation of species' tolerance patterns (Curtis 1955). Blow-out grass, sand dropseed, needle-and-thread, and sand reed, though, exhibit anomalous responses to slope by reaching their maximum importances at the upper or lower slope position, but rarely occur at the mid-slope position (Figs. 5E, F, G, and H). Olson (1958b) has done the most thorough investigation of wind velocities on dunes, especially on vegetated dunes, and he found that winds at mid-slope positions, on leeward slopes, were anomalously still. Investigation of this phenomenen showed that the dune, acting as a wind break, caused eddying effects on the leeward side at mid-slope, and hence, wind velocity was essentially zero at this location. Significantly, the mid-slope stands in the northern area have leeward exposures considering that the most important winds for sand movement in northern Colorado are the northwesterly winter winds (Ramaley 1939). If this is the explanation for the species' responses described above, then this position should support a less psammovfilous, more hardland, vegetation, and indeed it does. Blue grama reaches its maximum importance here, as do the sedges (Figs. 5B and D). Sand bluestem also does best here (Fig. 5C) which may appear unusual until it is recognized that sand bluestem, though characteristically found on sand, rarely grows on unstable sand in Colorado, but is usually found as a member of the "sand prairie" (Ramaley 1939), which is probably the most stable sand habitat.

Life-form comparisons (Table 7) with the sand sage vegetation in southwestern Nebraska and with the "stabilized dunes" of Saskatchewan indicate that the northern and the southern Colorado study areas are very similar, but the northern area has a slightly less stable substrate, and the "stabilized dunes" of Saskatchewan and the sand sage vegetation in Nebraska are very similar, with the former having the slightly less stable substrate. Colorado is warmer, has less available moisture, and is more subject to drought than the other areas (Borchert 1950, 1971). Hence, cover is probably less and the substrate consequently less stable. The "stabilized dunes" of Saskatchewan are the most stable of the sand communities there (Hulett et al. 1966) and, therefore, it is not surprising that they are more stable than the sand sage area in Colorado. The sand sage in Nebraska occurs in the southwestern part of the State in the "tablelands of the foothill region" which is the most stable area in Nebraska which supports arenaceous vegetation (Pound and Clements 1900). This probably explains why the area of the Nebraska sand sage vegetation is the most stable of the three areas.

This study clarifies the successional position of the native sand sage vegetation in eastern Colorado. Since only stands free from grazing were sampled, the implication that sand sage vegetation may be a grazing "disclimax" (Ramaley 1939 and Weaver and Albertson 1956) is challenged. Furthermore, some of the more important species in the northern stands, including sand bluestem and needle-and-thread, quickly disappear with grazing (Weaver and Albertson 1956). Under moderate grazing, then, these species would probably be much reduced and ultimately disappear, and others, such as sand reed, sand dropseed, and blue grama, would probably increase as would sand sage. Although sand sage may increase under grazing, the species composition of the sand sage vegetation would change markedly and, therefore, the native sand sage vegetation as I have described it is not a "disclimax." If grazing were heavy, especially in dry years, enough cover might be removed that the substrate would become unstable and sandhill muhly and blow-out grass would become more important than at present.

Borchert (1971) has predicted a major drought in the Great Plains commencing in the mid to late 1970's. He distinguished the drought of the 1930's from the one in the 1950's on the basis of wind erosion risk, which was much greater in the former case. Hence, the effect of the hypothesized drought of the 1970's will be quite different depending on whether conditions are more similar to the 1930's or to the 1950's (Borchert 1971). This is especially true for sandy areas. Evidence from studies completed on the 1930's drought (Weaver and Albertson 1956 and Albertson and Tomanek 1965) shows that many of the grasses which occur in the sand sage vegetation, including blue grama, hairy grama, side-oats grama, switch grass (Panicum virgatum), western wheatgrass (Agropyron smithii), and sand dropseed, are drought resistant. However, other grasses, including little bluestem, the three awns (Aristida spp.), Junegrass (Koleria cristata), and six weeks fescue (Festuca octoflora), readily succumb to drought and recover only slowly, if at all. Indirect effects of drought may magnify the effects of drought. Grasshoppers, for example, did extensive damage to the vegetation during the 1930's (Weaver and Albertson 1956) and could do so again. Bronson and Tremeir (1959) found that black-tailed jack rabbit populations increased in sandy areas in Kansas during dry periods, and, hence damage from them also increased. Another indirect effect of significance is that a reduction in per cent cover, which was especially great during the 1930's drought, leaves much soil bare and subject to blowing. On sand areas, the removal of cover would probably have a pronounced effect. Thus both grazing and drought can be expected to have a great impact on the species composition of the native Colorado sand sage vegetation.

The effect of fire on sand sage vegetation has scarcely been investigated, but coupled with drought or over-grazing, its effect would be especially important (Jackson 1965). Sand sage itself is probably not destroyed by fire (see Literature Review), nor are the grasses, but a reduction in the per cent cover could have serious effects by exposing the surface to wind erosion.

Summarily, the Colorado sand sage vegetation is considered here to be a climax, edaphic variant of the mixed-grass prairie. Widespread species include sand dropseed, blue grama, sand sage, and prairie sunflower, but species composition varies greatly between the northern and the southern stands. Relative substrate stability and regional climatic differences appear to be the causal factors of the variation. Comparisons with the sand sage vegetation of southwestern Nebraska and with the "stabilized dunes" of Saskatchewan (Pound and Clements 1900 and Hulett *et al*. 1966) indicate a stability difference between the less stable Colorado sand deposits and the more stable Saskatchewan and Nebraska sand areas.

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