STEM STRUCTURE OF GRASSES ON THE JORNADA EXPERIMENTAL RANGE

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(WITH EIGHT FIGURES)

Introduction

The orthodox description of the grass family contains the phrase "stems usually hollow," which has been generally accepted as meaning that all mature grasses other than the genera of the Andropogoneae and Nazieae have hollow stems. Early in 1927, when certain grasses not members of either of these tribes were examined, they were found to have solid stems. Continued investigation showed that a very high percentage of the mature grasses native to the semi-arid Jornada plain have solid internodes.

BEWS (1) states that the stems of grasses are usually hollow, but that a number of "types" have solid stems, including the Andropogoneae and many of the Paniceae. VAVILOV (6) also refers to a solid stemmed variety of *Agropyrum cristatum* Beauv., which he reports as being widely distributed over European and Asiatic Russia.

JORNADA EXPERIMENTAL RANGE.—This area is a branch of the Southwestern Forest and Range Experiment Station, and includes approximately 300 square miles of semi-arid lands located near Las Cruces, New Mexico, some 50 miles north of the Mexican border. The region is typical of the south-central New Mexico grasslands. The greater part of it is a flat to slightly rolling mesa with elevations ranging from 4100 to 4700 feet. In addition, there are about 73 square miles of mountainous country which include the foothills and western slopes of the San Andres Mountains. Elevations vary in this area from 4700 in the foothills to 8000 feet on the higher peaks.

CLIMATE.—Climatically the Jornada region is one of the most arid in the southwest. The average annual rainfall for the 17-year period covered by the Jornada Experimental Range precipitation records is 8.99 inches, with a maximum of 17.73 inches and a minimum of 3.54 inches. Annual rainfall for seven of the seventeen years was above the average for the period, and for ten of the years was below the average.

Usually the first effective summer rains fall late in June or early in July. A general beginning of plant growth takes place after this rainfall and continues through a season of about 100 days. This period, which includes July, August, and September, is commonly referred to as the growing season. According to the Jornada records the average precipitation for the period of growth is 4.64 inches. Of the seventeen years included, six were above the average and eleven were below it. During this period of record the maximum summer seasonal was 8.53 inches and the minimum was 2.34 inches.

The average date of the last spring frost is April 9, and the average date of the first fall frost is October 26; 200 days is the average frostless period. Temperatures as high as 106° F. and as low as −8° F. sometimes occur. The average wind velocity is 7.1 miles per hour.

Recent measurements made at the Jornada headquarters show that a 0.5-inch daily evaporation loss from a free water surface is common during the summer and early fall months. A combination of hot dry winds and low relative humidity, sometimes as low as 10 per cent, gives a high rate of evaporation and a correspondingly high rate of transpiration in the vegetation.

The most prominent climatic characteristic is of course the ever-recurring periods of insufficient soil moisture. SHANTZ (5) states: "True drought can occur only when the available soil water has been exhausted." It is also accepted as fact that the individual plant represents the sum of all the factors which have affected its growth, of which available water is one. Drought is therefore a specific condition which can be detected in observable effects on the vegetation. The character of the effects from true drought are such as would, if continued for a sufficient time, eliminate the plants concerned from the area under consideration.

The writer (3) has previously offered a definition of drought which is believed to be sufficiently precise for range purposes. Drought was defined as a condition in which the water requirements of the established dominant plants of the highest successional stage exceed

[1] The climatic data are taken from the records of the New Mexico A. & M. College, located 20 miles south of the Jornada Experimental Range.

the available water supply, and which, if continued beyond the life span of these plants and beyond the duration of the viability of their seeds, would result in the extinction of the species. Drought in the Jornada region may be separated into two classes, general and stratified. General drought affects the whole of the soil profile utilized by plants; stratified drought occurs in horizontal layers within the soil profile and affects only the plants which have their roots mainly in the dry layer.

In connection with the climatic conditions, the sand storms which occur with unfailing regularity during the spring and early summer months are of importance. In addition to the damage incident to erosion and deposition of soil, the abrasive action of the sand blast increases the difficulties under which the succulent vegetation makes its struggle for an existence.

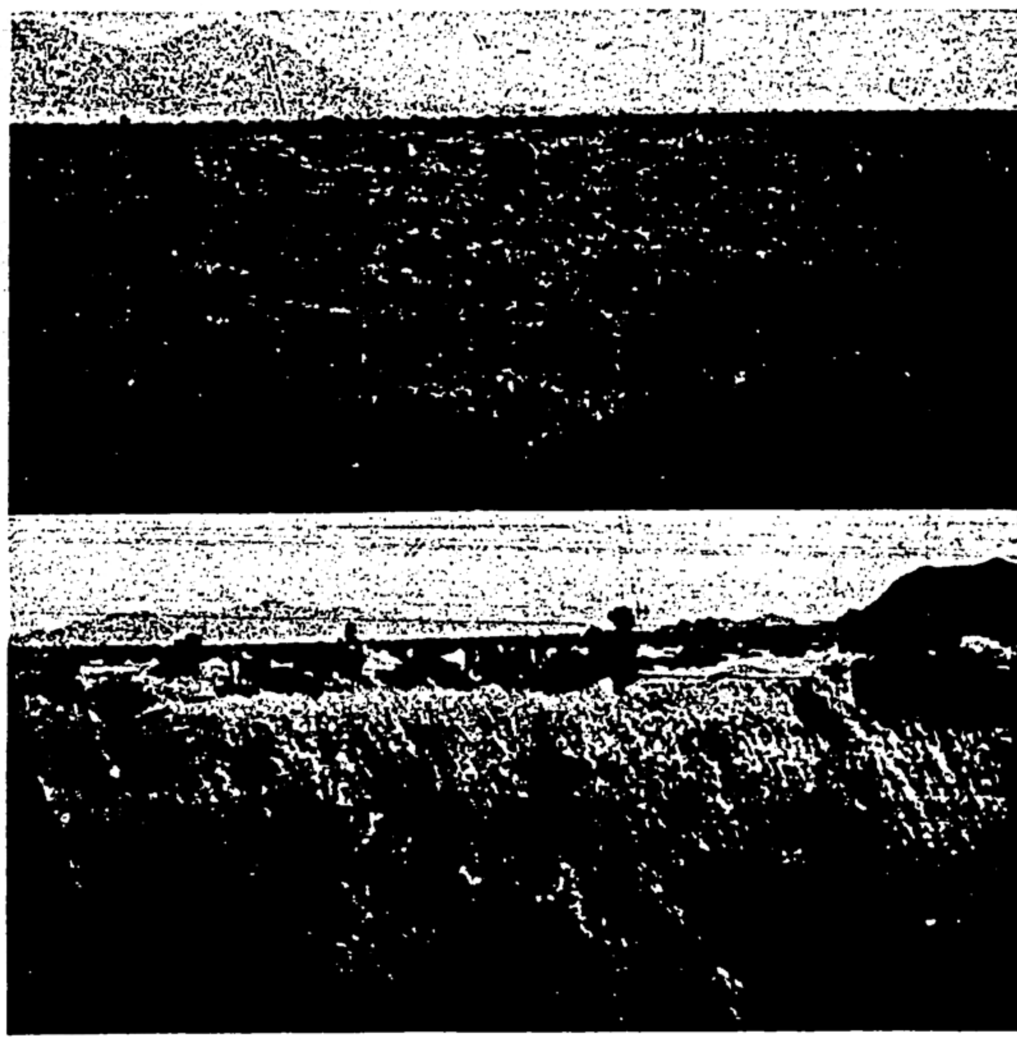
VEGETATION.—In spite of the climatic conditions, the Jornada grasslands produce abundant crops of forage. Figures 1 and 2 show typical range conditions in a year of average seasonal rainfall. The native vegetation consists of herbaceous plants and shrubs which are capable of maintaining an existence under conditions of low rainfall, high temperature, and a dry atmosphere. The more common plants take advantage of periods of abundant moisture, either by completing their growth in one usually short, wet period or by alternating rapid growth with dormancy through the succeeding wet and dry periods until maturity is attained.

CANFIELD (4) separates the grasses occurring in this region into four divisions or classes, based on the order of their development. The influence of the stem structure is apparent in these groups.

One class is composed of the annuals which complete growth early in the season, during a period of available moisture when the temperatures are low and the relative humidity is high enough to retard transpiration. The proportions of grasses with solid and with hollow stems are about equal in frequency in this group; nevertheless the solid stemmed species contribute materially to the plant cover while the hollow stemmed species occur infrequently.

A second group, composed chiefly of the perennial *Aristida* and *Hilaria mutica*, produce a mature crop of plants at any time during the frostless season when an unbroken period of available moisture of sufficient length occurs. A spring crop of these grasses followed by one or more summer crops is not an uncommon event. The members of this group are solid stemmed without exception.

A third group, represented by *Bouteloua eriopoda* and species of *Sporobolus* and *Muhlenbergia*, occurring on the well drained sandy or



FIGS. 1, 2.—Fig. 1 (above), range in early summer before growing season begins. Fig. 2 (below), range in fall after a good growing season.

gravelly soils, make their growth by stages. These grasses develop rapidly during periods of abundant moisture and high night temperature, although usually they are unable to attain maturity in one unbroken period. In the droughts which usually intervene between the rains, these grasses suspend activity and remain in a dormant condition, bursting into growth when the next soil-saturating rain comes. An almost immediate response to moisture is an outstanding characteristic of this group. Two members of the third group, *Bouteloua eriopoda* and *Muhlenbergia porteri*, are notable because of their true perennial habit of growth. Stems of these grasses remain green throughout the winter and leaf out again the following year. All species falling into this group are solid stemmed.

A fourth group contains *Koeleria cristata* and other grasses, most of them hollow stemmed, which are nearing the lower limits of their ranges. These species occur only in the more favorable situations, such as depressions, intermittent stream beds, and sheltered spots where moisture is present for longer than the usual periods.

Artificial planting of foreign grasses has resulted in failure. Grasses from distant arid lands which come highly recommended have not survived a single season.

Investigation

FIELD METHODS.—Field investigations on the stem structure of grasses were started in the late summer of 1927, and carried through each succeeding summer and fall up to and including the 1930 seasons. Mature plants of the various species were selected and a well developed culm was taken from the specimen. The culms were cut transversely through at a point about equidistant from two nodes, and an examination made with a hand lens. Should a stem be of very small diameter, or if for any other reason there was doubt as to the determination of the nature of the structure with the hand lens, material was selected in the field and preserved for microscopic study in the laboratory.

Identification of the species was established by making a study of each grass and comparing specimens collected in the field with authentic specimens in the Jornada Experimental Range herbarium. All specimens in this herbarium have been identified by the United States Bureau of Plant Industry.

LABORATORY METHODS.—Material collected in the field for laboratory use was immediately placed in a small individual vial of formalin acetic alcohol. The vial was temporarily labeled and numbered in the field. Later each specimen received a permanent label, placed inside the vial, which was then corked and sealed with paraffin.

Considerable difficulty was encountered in preparing the material for imbedding and sectioning. The high silicon content of the grass stems was a serious obstacle which prevented their successful sectioning. In attempts to remove the silicon, the material was immersed in solutions of hydrofluoric acid of different concentrations for varying periods of time. At last it was found that the use of 100 per cent hydrofluoric acid with an immersion period of one week was about right for the greater part of the material.

Further difficulties developed in sectioning. Good sections could not be secured by the usual alcohol stages of dehydrating and the usual paraffin method of imbedding. When the material was run through the alcohols using a 5 per cent solution as a beginning and advancing by 5 per cent stages to absolute, however, the result was satisfactory. The stems were then imbedded in celloidin.

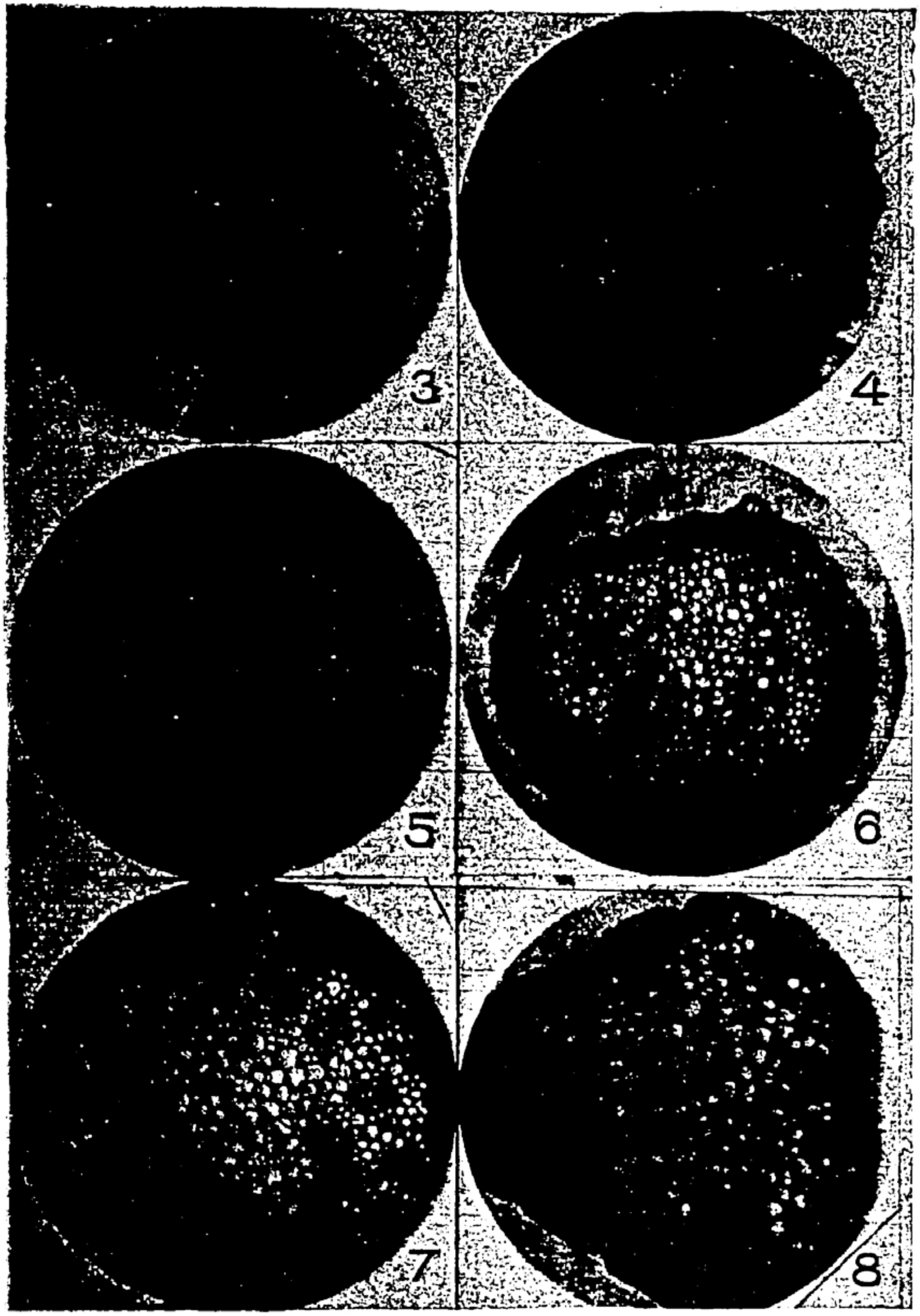
The formula used in making transverse sections of grass stems is as follows:

1. Kill in formalin acetic alcohol solution.
2. Immerse in 100% HF one week.
3. Wash in running water 24 hours.
4. Dehydrate using alcohol stages 5% to 100%, 5% in each step, changing at 4-hour intervals.
5. Imbed in celloidin, 2% to 16%, 12 hours in each solution.
6. Stain sections in iron-alum haematoxylin.
7. Mount in thin balsam.

Figures 3–7 show the stem structure of a few representative specimens of solid and hollow stemmed grasses. The cross-sections were made at a point about equidistant from two nodes and are typical of the species which they represent. In making the slides from which the photomicrographs were taken, it was necessary to cut the sections much thicker than usual to avoid tearing the thin walled cells in the central portion of the stems. These cells had become fragile from exposure to the strong acid used in removing the silicon.

Since it was desired that the photographs show the cell structure in the central parts of the stems, it was necessary in most instances to throw the heavy walled cells of the outer portions of the stems out of focus.

No attempt is made in this paper to enter into a detailed discus-



Figs: 3–8.—Transverse sections of grasses: Fig. 3, *Leptochloa fascicularis*, hollow stemmed annual grass occurring only in favored locations where moisture is available for longer than the usual periods. Note large central cavity. Fig. 4, *Hilaria mutica*, solid stemmed perennial grass (solid stems would be expected in this genus) occurring only on heavy clay soils and thriving only on areas subjected to periodic summer flooding. Fig. 5, *Scleropogon brevifolius*, perennial grass described by CAMPBELL (2) as a pioneer occurring on denuded clay flats. Fig. 6, *Muhlenbergia porteri*, perennial grass once common but now sparse, probably because stems are perennially green and therefore much sought by grazing animals. Fig. 7, *Sporobolus cryptandrus*, solid stemmed perennial grass occurring on dry sandy ridges and plains. Fig. 8, *Cyperus uniflorus*, a sedge requiring moist or wet soil as its habitat, included here to show similarity in stem structure to grasses of the semi-arid mesas.

sion of the differences in cell structure and cell arrangement which are apparent under the microscope. However, the thin walled cells of the central portions of the solid stemmed grasses and the arrangement of the vascular bundles are interesting items.

In the following list of species, all the grasses known to occur on the Jornada Experimental Range have been classified as to whether the stems are solid or hollow.

Solid stemmed annuals (7 species)

Nazieae, Tribe III
- Nazia aliena (Spreng.) Buckl.
- N. racemosa (L.) Kuntze

Paniceae, Tribe V
- Cenchrus pauciflorus Benth.

Agrostideae, Tribe VIII
- Aristida adscensionis L.

Chlorideae, Tribe X
- Bouteloua aristidoides (H.B.K.) Griseb.
- B. barbata Lag.
- B. parryi (Fourn.) Griff.

Hollow stemmed annuals (8 species)

Paniceae, Tribe V
- Panicum barbipulvinatum Nash
- P. hallii Vasey
- P. hirticaule Presl.

Chlorideae, Tribe X
- Leptochloa fascicularis A. Gray (fig. 3)

Festuceae, Tribe XI
- Eragrostis pilosa (L.) Beauv.
- Festuca octoflora Walt.
- F. octoflora hirtella Piper
- Munroa squarrosa (Nutt.) Torr.

Solid stemmed perennials (44 species)

Andropogoneae, Tribe II
- Andropogon saccharoides Swartz

Nazieae, Tribe III

Hilaria mutica (Buckl.) Benth. (fig. 4)

Paniceae, Tribe V

Echinochloa crus-galli (L.) Beauv.
E. crus-galli mitis (Pursh) Peterm.
Panicum obtusum H.B.K.
Paspalum distichum L.
Chaetochloa macrostachya (H.B.K.) Scribn. & Merr.

Agrostideae, Tribe VIII

Aristida divaricata Humb. & Bonpl.
A. glauca (Nees) Walp.
A. havardii Vasey
A. longiseta robusta Merr.
A. pansa Woot. & Standl.
A. purpurea Nutt.
A. schiediana Trin. & Rupr.
Epicampes emersleyi (Vasey) Hitchc.
E. rigens Benth.
Lycurus phleoides H.B.K.
Muhlenbergia arenicola Buckl.
M. monticola Buckl.
M. pauciflora Buckl.
M. porteri Scribn. (fig. 6)
M. repens (Presl.) Hitchc.
Oryzopsis hymenioides (Roem. & Schult.) Ricker
Sporobolus airoides Torr.
S. asperifolius (Nees & Meyen) Thurb.
S. auriculatus. Vasey
S. cryptandrus (Torr.) A. Gray (fig. 7)
S. flexuosus (Thurb.) Rydb.
S. giganteus Nash
S. nealleyi Vasey
Stipa eminens Cav.

Chlorideae, Tribe X

Bouteloua breviseta Vasey
B. curtipendula (Mich.) Torr.
B. eriopoda Torr.

B. gracilis (H.B.K.) Lag.
B. hirsuta Lag.
Chloris virgata Sw.
Leptochloa dubia (H.B.K.) Nees

Festuceae, Tribe XI
Distichlis spicata (L.) Greene
Eragrostis cilianensis (All.) Link
E. erosa Scribn.
Scleropogon brevifolius Phil. (fig. 5)
Triodia mutica (Torr.) Scribn.
T. pilosa (Buckl.) Merr.

Hollow stemmed perennials (10 species)

Paniceae, Tribe V
Leptoloma cognatum (Schult.) Chase
Valota saccharata (Buckl.) Chase

Agrostideae, Tribe VIII
Agrostis verticillata Vill.
Muhlenbergia rigida (H.B.K.) Kunth
Stipa columbiana Macoun
S. scribneri Vasey

Aveneae, Tribe IX
Koeleria cristata (L.) Pers.

Chlorideae, Tribe X
Capriola dactylon (L.) Kuntze

Festuceae, Tribe XI
Pappophorum wrightii S. Wats.
Triodia pulchella H.B.K.

Discussion

The terms solid stemmed and hollow stemmed refer to the condition of the grass stems at maturity. Due consideration has been given to the natural condition of the growing stem, and only mature stems have been used in this study. It is a recognized fact that nearly all grass culms have no hollow space in the internodes during the early periods of growth. This condition is especially true of the meristematic regions just above the nodes.

This study of the Jornada grasses includes seven tribes which are represented by 30 genera and 69 species. Of the total number, 51 species (74 per cent) have solid stems while only 18 species (26 per cent) have hollow stems.

ANNUAL GRASSES.—The annual grasses consist of 15 species of which seven are solid stemmed and eight are hollow stemmed. Annual grasses, because of their scattered occurrence and their short stature, constitute only a small fraction of the Jornada forage crop.

The solid stemmed annual species make their growth at any time during the growing season when the top layer of soil furnishes moisture for a period of sufficient length for them to complete development. These grasses belong in the class which completes growth in one unbroken interval. Although the rate of development may be perceptibly slowed down at times, either by a decrease in the depth of the moist top layer of soil or by an increase in the rate of transpiration to a point which is almost equal to the rate of absorption, in no observed instance can these grasses be said to have passed through a period of dormancy and to have resumed their growth with the return of favorable conditions.

The hollow stemmed annual grasses rely on a rapid development from germination to maturity for the maintenance of the species. Their period of growth generally is restricted to a short rainy interval in the early part of the season, at which time the days are cool and the relative humidity is high. However, an occasional plant may be found later in the season in sheltered spots or in catch basins, where the required climatic conditions are maintained by unusual factors beyond the regular season.

There is overwhelming evidence in practically all the species which have been observed that the hollow stemmed annual grasses of this semi-arid region thrive only under climatic conditions which are somewhat similar to those of the humid regions where the grasses are chiefly hollow stemmed.

PERENNIAL GRASSES.—The perennials are represented by 55 species, of which 45 (82 per cent) are solid stemmed while only 10 species (18 per cent) are hollow stemmed.

Native perennial grasses produce the major part of all the forage on Southwestern plains. In the Jornada region the species of five genera, *Bouteloua*, *Sporobolus*, *Aristida*, *Hilaria*, and *Scleropogon*, furnish 85 per cent or more of the forage derived from grasses. All the species representing these genera are able to withstand to a marked degree protracted drought with grazing. They have the ability to exist in the less favorable situations, as well as in the more favorable ones. Observed representatives of these genera native to this region are without exception solid stemmed grasses.

The hollow stemmed perennial grasses furnish very little forage. They are sparsely scattered throughout the region, being restricted to the more favorable sites. Even in these more favorable locations, such as the bottoms of intermittent streams or the higher elevations where precipitation is greater, the hollow stemmed species generally exist under the protection of some jutting rock or in the shade of some hardy shrub.

Summary

1. In the species of grasses observed, the types of stem structure in the Jornada Range grasses apparently reflect the moisture requirements and the periods of growth.

2. The solid stem is characteristic of the grasses which are apparently best able to survive under the semi-arid conditions of the Jornada region.

3. Almost three-fourths (74 per cent) of the grasses collected have solid stems.

4. Tribes commonly reported as having solid stems, Andropogoneae and Nazieae, are represented by one genus each.

5. Solid stemmed perennial grasses produce 85 per cent or more of the forage.

6. Hollow stemmed grasses either grow only in the more favorable locations or escape drought by completing their growth during a few weeks of highly favorable moisture conditions.

7. Hollow stemmed grasses have not the ability to withstand the long dry periods.

8. There are strong indications that the solid stem is an index which may be employed in the selection of grasses for introduction into semi-arid regions.

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