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A Study of a Method to Determine Some of the Effects of Plant Competition

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A STUDY OF A METHOD TO DETERMINE
SOME OF THE EFFECTS OF PLANT COMPETITION

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THESIS ABSTRACT

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A study was made to determine some effects of competition for water on buffalo grass (Buchloe dactyloides (Nutt.) Engelm.). The primary objective of the investigation was to determine if effects of competition on buffalo grass, as determined in a greenhouse study, could be measured.

Sods containing buffalo grass, buffalo and blue grama grass (Bouteloua gracilis (H.B.K.) Lag.), buffalo, blue grama, and western wheatgrass (Agropyron smithii Rydb.), and buffalo, blue grama, western wheatgrass, and western ragweed (Ambrosia psilostachya Gray) were planted in phytometers to evaluate competitive effects.

Four watering series (from very dry to wet) were arranged to determine effects of varying moisture conditions on buffalo grass.

Buffalo grass plants were carefully studied to determine effects of competition with various species and effects of different moisture conditions. Factors included in the study of buffalo grass plants were: (1) leaf length; (2) stolon length; (3) root length; (4) date of flower appearance; (5) number of tillers; (6) number of lateral roots per cm. of main root; and (7) production of tops.

Greatest variation in growth and production were caused by different soil moisture conditions; however, some changes were caused by competition.

Leaf length was greatly reduced in the drier series and some reduction was generally found as competition increased. Buffalo grass

plants grown alone produced leaves which averaged 7.02, 7.65, 12.08, and 13.31 cm. long, respectively, from dry series to wet while competition with the three competitors reduced leaf length approximately one to two cm. Competitive effects for the other two competitive series were intermediate.

Stolon length was inconsistently affected by moisture conditions and gave no indication of being influenced by competition. Flower appearance was delayed in accordance with moisture conditions, the dry series showing considerable delay. Flower appearance was also delayed as competition increased.

Root length increased as moisture increased in practically every case; however, the effects of competition on root length were again quite variable.

The number of tillers per buffalo grass plant increased with increased moisture and, strangely, also increased with increased competition.

The number of lateral roots per cm. of main root increased with increasing dryness and, generally, also increased with increasing competition.

Production of tops was quite variable and indicated little consistent influence of moisture or competition. Generally, production was greatest for those buffalo grass plants growing under moist conditions and without competition.

Results obtained from the study indicate that the procedure used to determine competitive effects has many limitations and changes in the method used will be necessary to insure valid results.

ACKNOWLEDGMENT

The author wishes to express his appreciation to Dr. G. W. Tomanek for suggesting the problem, for help throughout the investigation, and for reading and criticizing the manuscript. Thanks are also extended to the members of my graduate committee, Drs. F. E. Kinsinger, H. C. Reynolds, and K. L. Marsi for reading and criticizing the manuscript. Thanks are also extended to F. Neil Folks, who took several of the photographs, and to several members of the Botany Department who helped in the field and laboratory work.

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INTRODUCTION

Plant competition is one of the most important ecological processes found operating in a plant community. Form, structure and even the presence of a given plant in a certain plant community are controlled by the severity of competition provided by associated vegetation.

The importance of plant competition prompted a study to learn if a simple method for determining competitive effects could be devised. Additional information should be derived from such a study and thought on this matter resulted in the formulation of three primary objectives: (1) to determine whether or not some effects of competition on a given species could be feasibly studied in a greenhouse; (2) to devise a laboratory method for studying some effects of plant competition; and (3) to determine some effects of competition on growth and development of buffalo grass (Buchloe dactyloides (Nutt.) Engelm).

Buffalo grass was chosen as the principal species because of its importance as a dominant in the mixed prairie. Buffalo grass and blue grama grass (Bouteloua gracilis (H.B.K.) Lag.) almost completely dominate the prairies located in the short grass disclimax of more xeric, western areas of the mixed prairie and are the dominant species of the upland in the eastern mixed prairie regions.

Two other common associates of buffalo grass are western wheatgrass (Agropyron smithii Rydb.) and western ragweed (Ambrosia psilostachya Gray). Because the latter two species are often associated with buffalo grass, all three were used as competitors to evaluate methodology in the investigation.

RELATED LITERATURE

Many studies concerning effects of competition on plant species have been made. Probably the most classic work on plant competition is the book, Plant Competition, by Clements, Weaver, and Hanson (1929) which includes a number of laboratory and field experiments with a great variety of plant species growing under various environmental conditions.

Plants compete for water, light, soil nutrients, carbon dioxide, and oxygen. Competition always occurs where two or more plants make demands for environmental factors in excess of supply (Weaver and Clements, 1938).

Clements, Weaver, and Hanson (1929) also found that competition is most severe between plants which are most similar (e.g., between plants of the same species).

Since competition is most severe between similar plants, evidently then, in a given community, competition between various species will be most severe during the seedling stage since, at this time, all plants, regardless of their mature form, will be fairly similar (Weaver and Clements, 1938).

To determine effects of competition on sunflowers, Clements, Weaver, and Hanson (1929) planted seeds 2, 4, 8, 16, 32, and 64 inches apart under uniform environmental conditions. The authors found that the degree of competition was proportional to the rate of planting. The most severe competition was exhibited by plants spaced 2 inches apart which, for example, produced, per plant, only 0.29 per cent of the foliage produced by plants spaced 64 inches apart. Similarly, seed production in the former averaged only 15 per head as compared with 507 and 1803 for those planted 16 and 64 inches apart, respectively.

In a phytometer experiment with sunflowers and wheat, Weaver, Clements, and Hanson (1929) found that light was the most important competitive factor. The authors stated that "with light intensity reduced five times, the leaf area was decreased a third, and the dry weight three times in Helianthus and Triticum." They further state that "the amount of photosynthate for the 'thins' was 50 per cent larger than for the 'thicks,' the sequence being in agreement with that of density and light values."

The previous study is in agreement with Brenchley (1919) who found that "the decrease in light caused by overcrowding is a most potent factor in competition even when an abundance of food supply and water is presented to each individual plant."

Clements (1949), in a controlled experiment with wheat (Triticum sativum), found that foliage, root, and seed production per plant decreased in relation to the planting rate. The wheat was planted at one-half normal, normal, twice normal, and four times normal rates in plots of uniform size. The height of stem, length of leaves, and total leaf area decreased rapidly from the half-normal to the four times normal density, the former producing twenty times as much leaf area, per plant, as the latter.

Similar results have been found for corn (Kiesselbach, 1923) and sudan grass (Peralta, 1935) planted in varying densities. Competition between the plants reduced top, root, and seed production in the various plantings, the effect being greatest in the dense plantings and least in the thinner ones. Morphological characteristics of blue grama and buffalo grass which permit successful competition in the upland mixed prairie are described by Mueller and Weaver (1942), Clements, Weaver, and Hanson (1929), and Albertson (1937).

Hertzer and McGregor (1951), in a study of prairie grasses, discovered that big bluestem (Andropogon gerardi) is a prairie dominant because of a dense, sod forming habit of growth, large size, and rapid development. Foliage produced by big bluestem effectively shades out invaders.

The effect of continued drouth on prairie vegetation and resulting competition between remaining plants have been thoroughly studied (Weaver, 1942, 1943; Weaver and Albertson, 1943, 1944).

Weaver (1942, 1943) stated that the true prairies of Nebraska were invaded by the xeric mixed prairie grasses to a distance of approximately 100 miles because of the extended drouth of the 1930's. True prairie species--big and little bluestem, switch grass, and tall dropseed--were replaced or considerably reduced in size and number by invasion of buffalo grass, blue grama grass, and western wheatgrass.

Blaisdell (1949), in studying grass reseeding in western states dominated by sagebrush (Artemesia tridentata), suggested that permanent grass establishment could be obtained only by removing the competing growth of sagebrush.

Similar results were found by Robertson (1947) who seeded seventeen species of native and exotic grasses into areas where sagebrush competition was severe, reduced, and completely lacking. Grass establishment could be assured only in those areas where the sagebrush plants were killed or removed.

Holmgren (1956) determined effects of competition by annuals on bitterbrush (Purshia tridentata), an important wildlife browse species in Idaho. Bitterbrush reseeding experiments often failed because of severe competition with cheatgrass brome (Bromus tectorum). The most effective method of eliminating cheatgrass brome competition was to remove a two-inch layer of soil from the area in the fall which removed weeds and weed seeds at the same time.

Undesirable woody brush and shrub plants reduce grass production in many California prairies (Shultz, Launchbaugh, and Biswell, 1955). Successful grass seeding can usually be accomplished if brush competitors are removed by burning, an economical method of brush elimination.

Competitive effects of crested wheatgrass (Agropyron cristatum) have been extensively studied.

Heinrichs and Bolton (1950) studied effects of crested wheatgrass on 12 perennial grasses, sedges, and forbs which are native to the prairies of southern Saskatchewan. They found that wild barley (Hordeum jubatum) and sweet grass (Hierochloe odorata) were completely eliminated by competition in two years. Other species were reduced or eliminated, but over a longer period of time.

In a study to determine effects of crested wheatgrass on weedy perennials in Canadian prairie, Pavlychenko (1942) sowed crested wheatgrass seed into mature stands of poverty seed, Canada thistle, quack grass, sow thistle, toad flax, and other undesirable weeds. In four seasons, perennial weeks were badly supressed or completely eliminated. Sow thistle (Sonchus arvensis) was completely suppressed in three years, Canada thistle (Cirsium arvense) in five years and quackgrass (Agropyron repens) was almost gone in four years. Poverty weed (Iva axillaris), leafyspurge (Euphorbia esula), field bindweed (Convolvulus arvensis), and hoary cress (Cardaria draba) had not disappeared after four years of competition but only weak plants remained.

Rummell (1946), in a greenhouse experiment, determined effects of competition with cheatgrass brome (Bromus tectorum) on crested wheatgrass and western wheatgrass. The annual grass reduced foliage production, root and rhizome production, number and length of roots, rhizomes and shoots, and number of tillers in both perennial species.

Weaver (1960) explains the differences in upland and lowland vegetation: "Mid-grasses of uplands cannot compete successfully with tall grasses on lowlands because of dense shade produced by them. Conversely, upland soils are usually not sufficiently moist to produce good development of tall grasses, especially in competition with mid-grasses."

In a study near Hays, Kansas, to determine the effect of competition of big bluestem (Andropogon gerardi) with forbs, Dwyer (1958) learned that rhizomatous forbs were more harmful competitors than were taprooted forbs. Five species of rhizomatous forbs reduced big bluestem production an average of 54.9 per cent while five taprooted forbs reduced production an average of 13.0 per cent.

Riegal (1944) indicated that western ragwood (Ambrosia psilostachya) reduced production of buffalo grass and blue grama grass in the mixed prairie of Kansas. Timmons (1950) discovered that many native grasses will completely eradicate or greatly reduce growth of field bindweed.

Hamilton and Buchholtz (1955) investigated competitive effects of quackgrass (Agropyron repens). Evans (1960) and Donald (1951) studied plant competition for soil nutrients.

Effects of weed competition on the spread of grass seedlings were studied by Hase (1941). Water usage of native Nebraska prairie grasses was studied by Weaver (1941) and the relative drouth resistance of seedlings of dominant prairie grasses was studied by Mueller and Weaver (1942).

Wilkins (1935) investigated competitive and survival rates of grasses and legumes sown in prairie meadows.

METHODS OF STUDY

Selection of Sods

In early January, 1961, sods containing the desired species were excavated from a typical upland prairie site in the Fort Hays Kansas State College pasture approximately 2½ miles west of Hays, Kansas.

Ten sods containing pure buffalo grass, ten containing buffalo grass and blue grama grass, ten containing buffalo grass, blue grama grass, and western wheatgrass, and ten containing buffalo grass, blue grama grass, western wheatgrass, and western ragweed were carefully selected. The sods were four inches deep and approximately six inches in diameter.

Selection was made on the basis of old plant parts still visible above the soil. An attempt was made to locate areas where an approximately equal abundance of each species could be obtained in a given sod. However, some difficulty in making such a selection was encountered because of the small area of the selected sods.

The soil, at the time of sod selection, was frozen and all plants were dormant. Soil moisture, because of a previous snow, was unusually high.

Greenhouse Procedure

Each sod was placed in a phytometer 6 inches in diameter and 26 inches deep, of galvanized sheet metal rolled into a cylinder and held at the top by a tin gallon container with both ends removed and at the bottom by a similar container with the bottom in place. Such arrangement facilitates root washing because the phytometer can be opened by removing the gallon containers with little disturbance to the column of soil.

Each phytometer was filled with a mixture of well-screened silty-clay loam soil of good moisture content and fine sand in the ratio of two-thirds soil to one-third sand. Such medium is not compacted as much as heavier soil and considerably reduces root-washing time. Soil used to fill the phytometers had a permanent wilting percentage of 5.38 as determined by the method described by Daubenmire (1959).

Sods were carefully trimmed so that they would just slip into the phytometers. Soil in the phytometers was slightly moistened to insure prompt rooting and the depth of soil was regulated so that a slight depression was left at the surface to prevent loss of moisture when the plants were watered.

Dead vegetation was clipped flush with the soil surface and all mulch was removed to facilitate examination of emerging plants. The sods contained an abundance of moisture and were, therefore, not watered immediately.

To obtain a record of temperature, relative humidity, and relative evaporation rate within the greenhouse a Bendix-Friez hygrothermograph and a Livingston-type clay atmometer bulb apparatus (Livingston, 1935) were located in close proximity to the phytometers (Fig. 1). Maximum and minimum daily air temperatures were averaged to obtain maximum and minimum weekly averages. Weekly evaporation rates were determined by refilling the atmometer bottle.

Watering series were arranged for each of the four competitive series to determine effects of competition in relation to soil moisture conditions: (1) Series I, the dry series, consisting of two phytometers of each species combination, each of which received 0.2 inch of water per week; (2) Series II, the intermediate dry series, consisting of two phytometers of each species combination, each of which received 0.4 inch of water per week; (3) Series III, the average series, consisting of four phytometers of each species combination, each of which received 0.6 inch of water per week; and (4) Series IV, the wet series, consisting of two phytometers of each species combination, each of which received 1.0 inch of water per week. The average series was based on the long-time rainfall average of 2.37 inches per month for the growing

Figure 1. Buffalo grass (Bda) on left and sods containing buffalo grass, blue grama grass (B[illegible]), western wheatgrass (Asm), and western ragweed (Aps) on the right. Instruments are hygrothermograph (left) and atmometer apparatus. Series I (8 phytometers) is nearest camera.

season of April through September at Hays. Sods were watered according to the amount of water needed to cover the surface of the sod to the prescribed depth (e.g., the Series IV sods were covered with water to the depth of one inch, each week). Ordinary tap water was measured with a graduated cylinder and was poured over the surface of the sod, a practice which undoubtedly prompted some inaccuracy because of spaces which developed between the sod and the phytometer wall in a few cases. Effective sealing of these spaces was nearly impossible to accomplish.

Sods were examined and watered weekly and the hygrothermograph record sheet was changed and the atmometer bottle was refilled with distilled water. Any annual grasses and forbs and undesirable perennial plants which appeared were carefully removed with a forceps and recorded. Measurements and observations of the buffalo grass plants in all phytometers were made weekly and records of average leaf length, stolon length, longest leaf length, number of tillers, and date of flower appearance were made. When the wet series buffalo grass plants started flowering prolifically, flower appearance was recorded twice weekly.

An attempt was also made to measure light intensity under the vegetation of the various sods. However, numerous inconsistencies in light intensity, caused by variations in the vegetative cover and by the small area which could be sampled, were found and this data has, therefore, been omitted.

A large number of grasshoppers and aphids appeared on some sods during February and all sods were, therefore, sprayed with an insecticide.

Photographs of the various competitive and watering series were taken on March 24, 1961. Basal and foliage cover of each species was estimated and recorded during April. Cover estimations were made by looking down on the plants and sketching the area covered by each species on a special sheet. The latter contained a six-inch circle marked off in square centimeters. A separate sheet was used for the basal and foliage cover of each phytometer and the area covered by each plant species was determined by counting and recording the number of cm. squares.

During April, the phytometers were opened and the soil was carefully washed from the roots by using a regular hose nozzle which was regulated so that a fine spray of water was emitted. Root systems and tops, thus removed intact, were carefully pressed and dried. Photographs were taken to show the extent of top and root growth of various series.

Final measurements of tops, roots, and stolons of buffalo grass were made and tops were weighed on a triple-beam balance scale accurate to the nearest 0.01 gram. Weight of foliage per unit of basal and foliage area was determined. A more workable figure was obtained of the resulting quotient by multiplying by 1000. Since weight per unit of foliage area seemed more accurate than weight per unit of basal area, only the former has been included. Final average leaf lengths were obtained by measuring 50 of the Series I and II leaves and 100 of the Series III and IV leaves where available.

Roots were also weighed but results were misleading because of the impossibility to effectively separate old, dead roots from newly produced roots. Root weights have, therefore, been omitted. The final number of tillers per plant and the average number of lateral roots per centimeter of main root were determined and recorded.

Scientific names of grasses and forbs used in this study are those of Hitchcock and Chase (1950) and Rydberg (1932), respectively.

To simplify tables and to eliminate repetition, the competitive series will be designated thus: (1) "A" will be the pure buffalo grass series (no competition); (2) "B" will be the buffalo grass-blue grama grass series; (3) "C" will be the buffalo grass-blue grama grass-western wheatgrass series; and (4) "D" will be the buffalo grass-blue grama grass-western wheatgrass-western ragweed series (severe competition).

EXPERIMENTAL RESULTS

Environmental Conditions

Records of temperature, relative humidity, and relative evaporation as determined by use of the hygrothermograph and atmometer apparatus are included to indicate some environmental conditions within the greenhouse during the time of plant growth. Average maximum temperature for the period was 91.7°F. and average minimum was 59.1°F. Average maximum relative humidity was 94.1 per cent and average minimum was 45.9 per cent. Average evaporation rate from a standardized Livingston's white-atmometer bulb was 115.02 ml. per week (Table I).

Vegetation Measurements

Weekly examination of the sods indicated that a great number of annual grass and forb seeds were present in the soil as germination of certain species continued throughout the growing period. Certain

Table I. Weekly average maximum and minimum temperatures (degrees Fahrenheit), relative humidity (percent), and evaporation (ml. per week) in a greenhouse, February to April, 1961.

Date	Temperature Max.	Temperature Min.	Humidity Max.	Humidity Min.	Evaporation
2-6	95.1	51.8	94.0	35.5	------
2-13	93.0	53.3	85.1	40.8	------
2-20	95.1	62.6	97.0	36.7	132.40
2-27	88.8	59.0	96.0	49.4	118.56
3-6	91.4	60.0	94.0	49.4	132.60
3-13	87.1	60.0	96.0	55.5	106.00
3-20	91.7	62.0	96.0	49.6	101.88
3-27	82.4	60.0	94.0	57.4	118.60
4-3	88.1	62.0	93.0	48.3	105.30
4-9	84.1	58.0	94.0	45.0	114.70
4-16	99.0	61.5	96.0	37.3	------
Average	91.7	59.1	94.1	45.9	115.02

perennial species also were found. Cheatgrass brome (*Bromus tectorum*) and Japanese brome (*B. japonicus*) were found particularly abundant in every phytometer. Below is a list of the species removed.

Common Name	Scientific Name
Japanese brome	Bromus japonicus
Cheatgrass brome	Bromus tectorum
Windmill grass	Chloris verticillata
Little barley	Hordeum pusillum
Fire weed	Kochia scoparia
Grooved flax	Linum sulcatum
Sand dropseed	Sporobolus cryptandrus
Salmon-colored mallow	Sphaeralcea coccinea
Wild alfalfa	Psoralidium tenuiflorum
Tumble grass	Schedonnardus paniculatus
Yellow foxtail	Setaria lutescens
Green foxtail	Setaria viridis
Bottle-brush squirreltail	Sitanion hytrix
Sheep-sorrel	Xanthoxalis stricta

Plants receiving less than the average amount of moisture produced far less foliage than plants of the more mesic series. At the end of each week leaves of the Series I plants would tend to roll and turn brown at the tips while the average and wet series plants continued to grow and remained green (Fig. 2).

Stolon production by the Series I and II plants was practically nil while Series III and IV plants started producing stolons almost immediately. However, considerable variation in stolon production

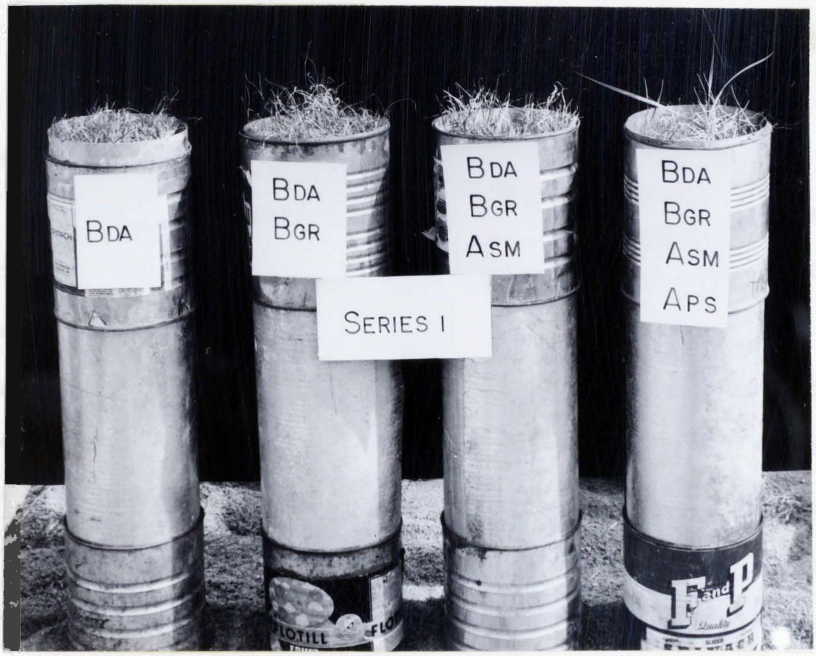

Figure 2. Selected Series I phytometers showing relative vegetative development of the plants of different competitive series. March 24, 1961.

occurred with plants of the wetter series and of the different competitive series. Some of the Series IV buffalo grass plants were prolific stolon producers while others of that series produced very few. Measurement of stolon internodes, however, proved that there was little difference in internode length which averaged about 4 cm.

Inflorescences. Different moisture and competitive conditions caused a remarkable variation in flower appearance but greatest variation was caused by variable moisture conditions. Sods were observed twice weekly after initiation of flowering and the date of flower appearance, whether staminate or pistillate, was recorded (Table II). The first staminate inflorescences appeared on the Series IV sods with no competition on February 10 and the first pistillate inflorescences on February 12, 27 and 29 days after planting, respectively. Average date of flowering for the Series IV buffalo grass plants with competition gave little indication that delayed flowering with increased competition was occurring. Average date of flowering for the Series IVB, IVC, and IVD plants was 35, 32, and 33 days after planting, respectively. Series IIIA, IIIB, IIIC, and IIID plants flowered 38, 37, 46, and 42 days after planting, respectively, the competitive rates again showing inconsistency in causing a delaying effect. A further delay in flowering, caused primarily by moisture conditions, was found in Series II plants, the respective dates of flowering after planting being 40, 38, and 48 days for the A, B, and C competitive rates. Series IID plants produced no flowers. Series IA, IC, and ID plants flowered 65, 81, and 82 days after planting, respectively. No flowers were produced by Series IB plants. The relative abundance of staminate inflorescences on March 24, 1961 can be seen in the accompanying photographs (Figures

Table II. Average date of flower appearance of buffalo grass grown under different moisture conditions and competitive rates

Series	Date of flowering	No. of days of growth prior to flowering
IA	3-20-61	65
IB	No flowers	--
IC	4-5-61	81
ID	4-6-61	82
Average		76
IIA	2-23-61	40
IIB	2-21-61	38
IIC	3-3-61	48
IID	No flowers	--
Average		42
IIIA	2-21-61	38
IIIB	2-20-61	37
IIIC	3-1-61	46
IIID	2-25-61	42
Average		41
IVA	2-11-61	28
IVB	2-18-61	35
IVC	2-15-61	32
IVD	2-16-61	33
Average		32

2, 3, 4, and 5).

Leaves. Final measurements of leaf length indicated that moisture and competitive conditions caused changes in vegetative form. Average leaf length increased with increasing moisture in every case and a reduction of leaf length was found to have occurred as competition increased, except in the Series IV plants where some inconsistent leaf measurements were recorded (Table III). Increased leaf length with increased competition in the latter Series probably resulted from elongation due to competition for light.

Average leaf length of the IA, IB, IC, and ID buffalo grass plants was 7.02, 7.12, 6.79, and 5.78 cm., respectively (Table III, see also Fig. 2). Respective length for IIA, B, C, and D sods was 7.65, 7.53, 7.22 and 6.85 cm. (Fig. 3). A great increase in average leaf length was noted for Series III plants. Respective length for the A, B, C, and D sods of this series was 12.08, 11.21, 10.37, and 10.21 cm. (Fig. 4). Average length for Series IVA, B, C, and D plants was 13.31, 12.06, 12.34, and 14.62 cm., respectively (Fig. 5).

Photographs of various competitive series were included to show effects of moisture conditions on each species (Figures 6, 7, 8, and 9).

A weekly measurement of the longest leaf of the buffalo grass plants in each phytometer was taken and an average was compiled.

Length of the longest leaf of the buffalo grass plants grown alone increased with increasing moisture. The longest leaf of Series I, II, III, and IV plants was 11.87, 16.42, 21.65, and 26.32 cm., respectively (Table IV). Competition with blue grama grass in the B competitive series reduced the longest leaf length somewhat with respective lengths from dry series to wet of 11.98, 15.92, 21.41, and

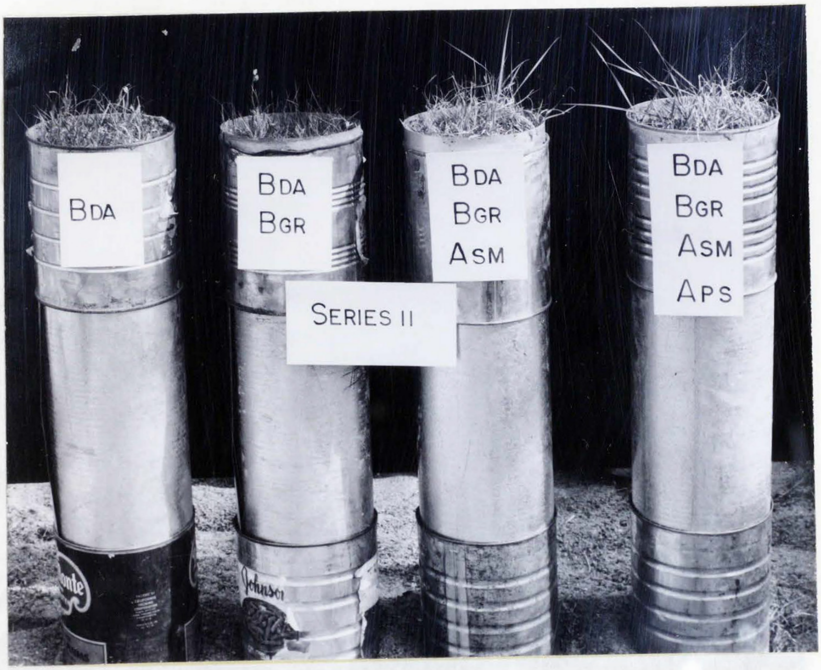

Figure 3. Selected Series II phytometers showing relative floral and vegetative development of plants of different competitive series. March 24, 1961.

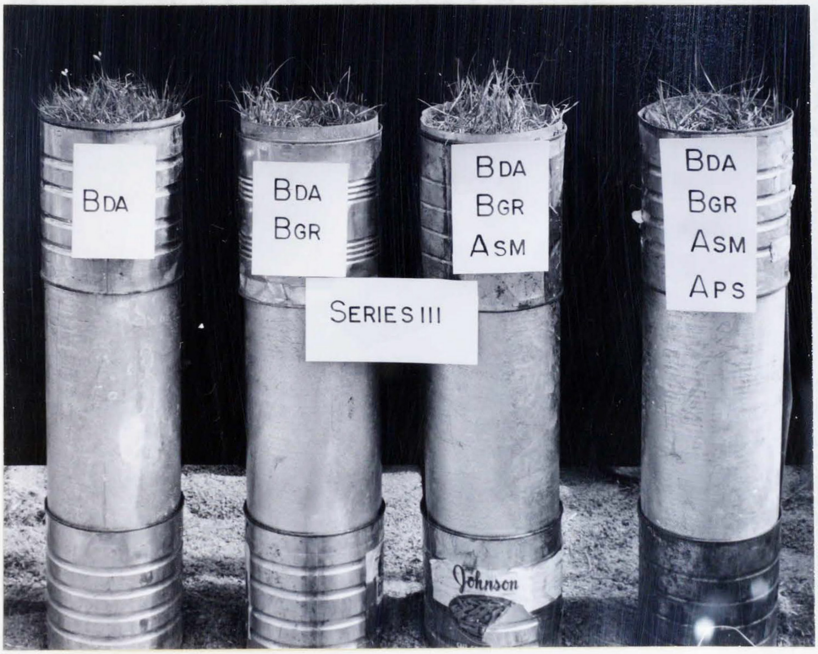

Figure 4. Selected Series III phytometers showing relative floral and vegetative development of plants of different competitive series. March 24, 1961.

Figure 5. Selected Series IV phytometers showing relative floral and vegetative development of plants of different competitive series. March 24, 1961.

Table III. Average leaf length (cm.) of buffalo grass grown under different moisture conditions and competition rates

Competitive series	Watering series			
	I	II	III	IV
A	7.02	7.65	12.08	13.31
B	7.12	7.53	11.21	12.06
C	6.97	7.22	10.37	12.34
D	5.78	6.85	10.21	14.62

Figure 6. Selected Series I, II, III, and IV phytometers of pure buffalo grass showing effects of different moisture conditions. March 24, 1961.

Figure 7. Selected Series I, II, III, and IV phytometers of buffalo grass and blue grama grass showing effects of different moisture conditions. March 24, 1961.

Figure 8. Selected Series I, II, III, and IV phytometers of buffalo grass, blue grama grass, and western wheatgrass showing effects of different moisture conditions. March 24, 1961.

Figure 9. Selected Series I, II, III, and IV phytometers of buffalo grass, blue grama grass, western wheatgrass, and western ragweed showing effects of different moisture conditions. March 24, 1961.

Table IV. Cumulative weekly length (cm.) of longest leaf of buffalo grass grown without competition under different moisture conditions

Date	Series I	II	III	IV
1-23	0.08	0.10	0.13	0.20
1-30	0.75	1.05	1.92	2.10
2-6	1.43	1.96	3.08	4.06
2-13	2.17	2.87	4.65	5.96
2-20	3.03	4.13	5.96	7.82
2-27	3.94	5.87	7.38	10.13
3-6	4.86	7.31	9.05	12.20
3-13	5.99	8.43	10.92	14.50
3-20	7.12	9.56	12.21	17.16
3-27	8.14	11.16	14.39	19.70
4-3	9.36	12.86	16.81	21.57
4-10	10.52	14.57	19.76	23.64
4-17	11.87	16.42	21.65	26.32

25.14 cm. (Table V). Competition with blue grama grass and western wheatgrass in the C competitive series caused a further reduction in length of the longest leaf. The respective length for the C series from dry series to wet was 11.45, 15.91, 20.99, and 24.72 cm. (Table VI). Some irregularities appeared in the D competitive series. Longest leaves for Series I, II, III, and IV buffalo grass plants in the D series were 9.21, 13.20, 18.20, and 34.05 cm. long, respectively (Table VII). The greatest length in the wet series was partly attributed to competition for light.

The average weekly increase in length of the longest leaf of buffalo grass in various series was compiled. The average increase in length was greatest for the more mesic series and, as a general rule, some decreased rate of increase was found as the severity of competition increased (Table VIII).

The average weekly increase in length for the A competitive series was 0.98, 1.36, 1.79, and 2.18 cm., respectivel , from dry series to wet. The B competitive series longest leaves showed average weekly increases of 1.00, 1.33, 1.79, and 2.10 cm., respectively, from dry series to wet while the C series increased 0.96, 1.33, 1.75, and 2.06 cm. per week. The D competitive series was unusual in that the increase in length in the dry series was greatly reduced while the wet series showed a greater average increase than any other series, with or without competition. The respective weekly average increase in length of the longest leaf of buffalo grass in the D series was 0.77, 1.10, 1.52, and 2.84 cm. from dry to wet.

Stolons. Stolon production was quite variable but indicated

Table V. Cumulative weekly length (cm.) of longest leaf of buffalo grass grown under different moisture conditions and competing with blue grama grass

Date	Series I	Series II	Series III	Series IV
1-23	0.07	0.09	0.13	0.18
1-30	0.63	0.94	1.67	1.93
2-6	1.16	1.85	2.63	3.86
2-13	2.11	2.62	4.27	5.98
2-20	3.14	4.11	5.81	7.67
2-27	3.97	5.62	7.24	9.95
3-6	4.91	7.19	8.92	11.99
3-13	6.05	8.45	10.87	14.33
3-20	7.15	9.32	11.96	16.87
3-27	8.21	10.91	14.02	19.12
4-3	9.52	12.70	16.57	21.03
4-10	10.66	14.39	19.30	23.17
4-17	11.98	15.92	21.41	25.14

Table VI. Cumulative weekly length (cm.) of longest leaf of buffalo grass grown under different moisture conditions and competing with blue grama grass and western wheatgrass

Date	Series I	Series II	Series III	Series IV
1-23	0.10	0.09	0.09	0.16
1-30	0.52	0.48	0.53	1.82
2-6	1.11	1.13	2.55	3.60
2-13	2.20	2.51	4.61	6.22
2-20	3.36	4.27	6.30	7.89
2-27	4.14	5.61	7.42	10.14
3-6	5.13	7.17	9.11	12.16
3-13	6.02	8.60	10.91	14.55
3-20	6.97	9.51	12.05	17.11
3-27	7.92	10.46	14.13	19.63
4-3	9.16	12.11	16.41	21.20
4-10	10.11	13.86	19.00	23.10
4-17	11.45	15.91	20.99	24.72

Table VII. Cumulative weekly length (cm.) of longest leaf of buffalo grass grown under different moisture conditions and competing with blue grama grass, western wheatgrass, and western ragweed

	Series			
Date	I	II	III	IV
1-3	0.05	0.06	0.09	0.19
1-30	0.37	0.41	1.69	2.15
2-6	0.99	1.07	2.73	4.22
2-13	1.83	1.92	4.02	6.34
2-20	2.79	3.11	5.37	8.11
2-27	3.51	4.98	6.63	11.04
3-6	4.46	5.91	7.90	12.97
3-13	5.39	7.36	9.12	15.79
3-20	6.18	8.50	10.73	18.63
3-27	6.98	9.61	12.06	22.06
4-3	7.87	10.91	14.01	26.39
4-10	8.14	11.93	16.15	30.21
4-17	9.21	13.20	18.20	34.05

Table VIII. Average weekly increase in length (cm.) of longest leaf of buffalo grass grown under different moisture conditions and competition rates

Competitive series	Watering series			
	I	II	III	IV
A	0.98	1.36	1.79	2.18
B	1.00	1.33	1.79	2.10
C	0.96	1.33	1.75	2.06
D	0.77	1.10	1.52	2.84

a general trend of increased production with increased moisture. Competition with the various species seemed to have little effect on the rate of stolon production or growth. In general, dry and intermediate-dry series buffalo grass plants produced few, if any, stolons. Some correlation between stolon production and moisture was observed in the Series III and IV plants.

No stolons were produced by any of the Series I or Series II buffalo grass plants with the exception of the C competitive series, the latter which produced stolons averaging 15.20 cm. in length. Final stolon length for Series III plants averaged 15.65, 9.44, 8.25, and 18.10 cm. for competitive series A, B, C, and D, respectively. Series IV plants produced stolons which averaged 36.20, 35.60, 7.64, and 26.10 cm. long, respectively, for competitive series A, B, C, and D (Table IX).

Tillers. The number of tillers per plant increased with an increase in moisture in every competitive series but there was no obvious correlation between competition severity and tiller production, as might be expected. Actually, with an increase in severity of competition there was a general corresponding increase in the number of tillers per plant (Table X). The average number of tillers per plant for competitive series A was 2.50, 4.00, 4.63, and 6.50 for the Series I, II, III, and IV phytometers, respectively. Plants of B competitive series produced 2.75, 5.00, 6.00, and 11.50 tillers, respectively, from dry series to wet. Tiller production per plant averaged 3.00, 4.00, 5.75, and 8.50 for C competition series and 4.00, 6.00, 6.40, and 9.50 for the D competition series from dry to wet, respectively.

Table IX. Stolon length (cm.) of buffalo grass grown under different moisture conditions and competition rates

Competitive series	Watering series			
	I	II	III	IV
A	0	0	15.65	36.20
B	0	0	9.44	35.60
C	0	15.20	8.25	7.64
D	0	0	18.10	26.10

Table X. Average number of tillers per buffalo grass plant grown under different moisture conditions and competition rates

Competitive series	Watering series			
	I	II	III	IV
A	2.50	4.00	4.63	6.50
B	2.75	5.00	6.00	11.50
C	3.00	4.00	5.75	8.50
D	4.00	6.00	6.40	9.50

Roots. During April, 1961, root systems were carefully washed out and preserved for future study. Different moisture conditions had a pronounced effect on root production and form but effects of competing plant roots on roots of buffalo grass were difficult to determine. General form, average length, and number of lateral roots per centimeter of main root of buffalo grass were determined for the various series.

Moisture conditions under which the plants were grown had a remarkable effect on root growth (Figures 10, 11, 12, and 13). Roots of most of the dry and intermediate-dry plants were much reduced and congested near the surface. The Series III and IV plants produced well developed root systems which extended to the bottom of the phytometers and, in many cases, coiled around the bottom several times (Figures 14, 15, 16, and 17). Root diameter was also generally larger in plants of the wetter series.

Average length of root systems of buffalo grass grown without competition was 35.00, 39.40, 62.00, and 61.53 cm., respectively, from the dry to the wet series (Table XI). Some difficulty in measuring the length of the roots of the Series IV plants was encountered because of the entanglement of roots in the bottom of the phytometers.

The number of lateral roots per centimeter of main root was observed and recorded for the buffalo grass plants of the various series. The number of laterals was found to increase with an increase in dryness. Little consistent evidence of the effect of competition on the number of lateral roots was found. The number of laterals per cm. of main root was 11.20, 10.02, 7.58, and 5.72 for buffalo grass

Figure 10. Selected Series I plants showing shoot and root growth of plants in four competitive series.

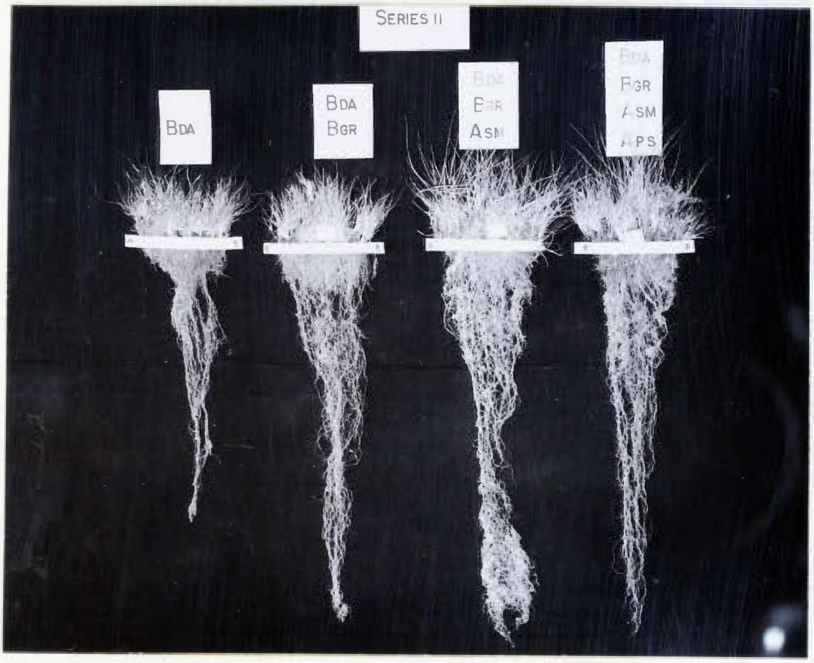

Figure 11. Selected Series II plants showing shoot and root growth of plants in four competitive series.

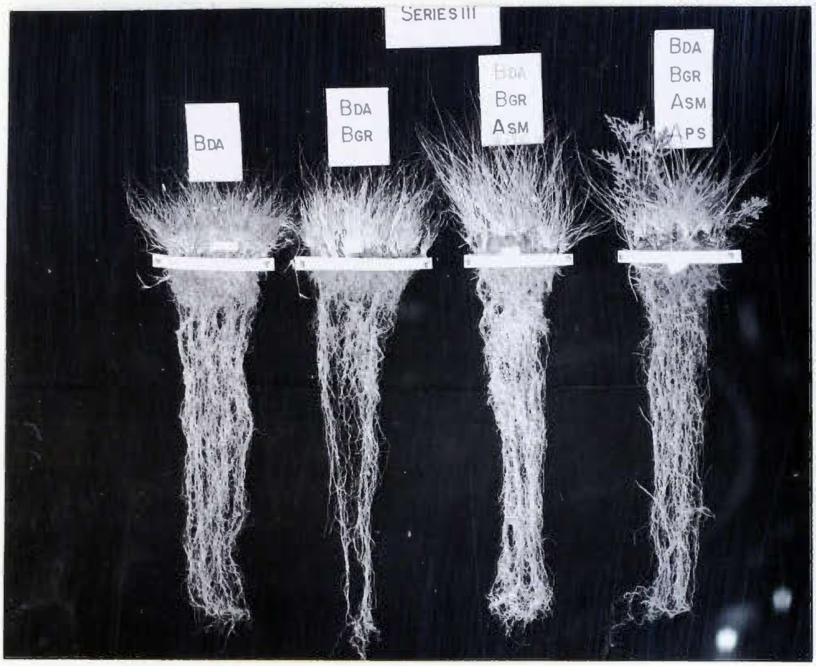

Figure 12. Selected Series III plants showing shoot and root growth of plants in four competitive series.

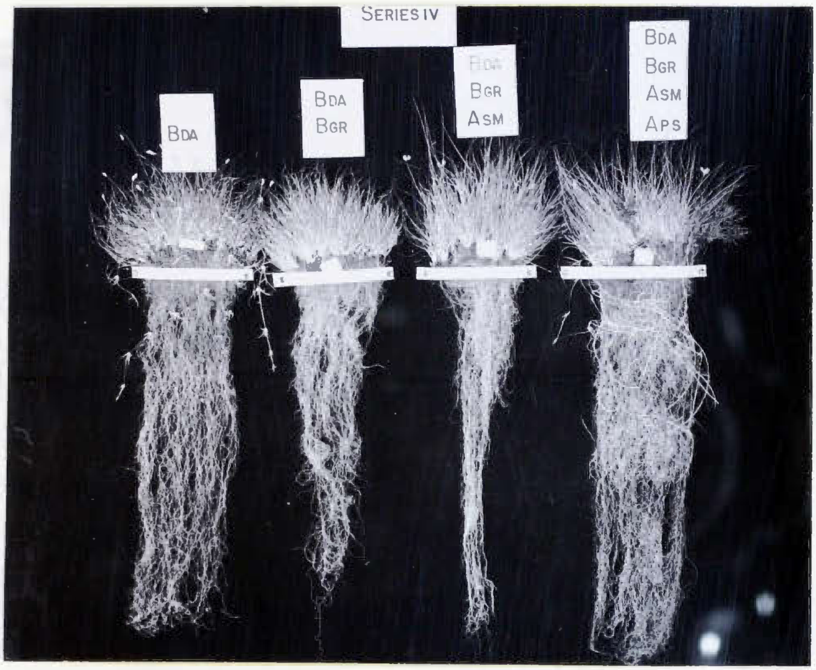

Figure 13. Selected Series IV plants showing shoot and root growth of plants in four competitive series.

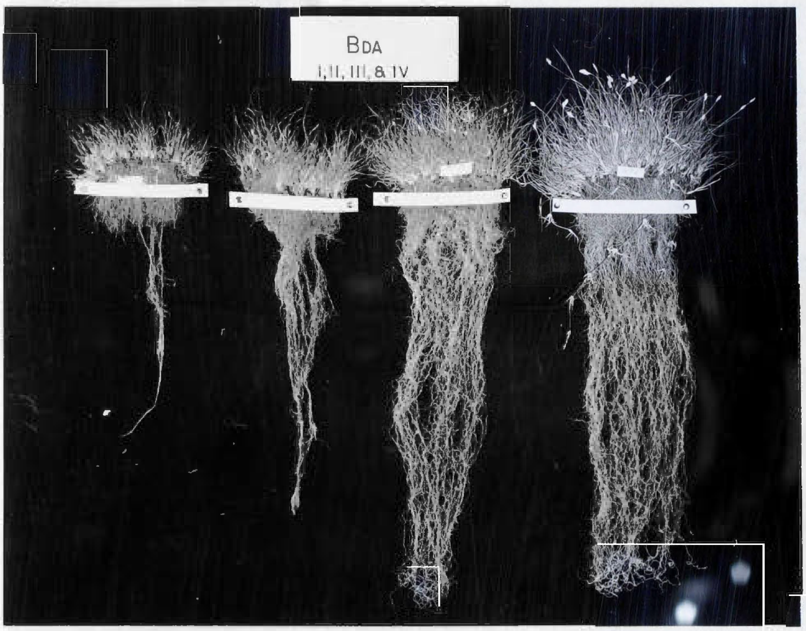

Figure 14. Selected Series I, II, III, and IV plants of buffalo grass grown alone showing shoot and root growth.

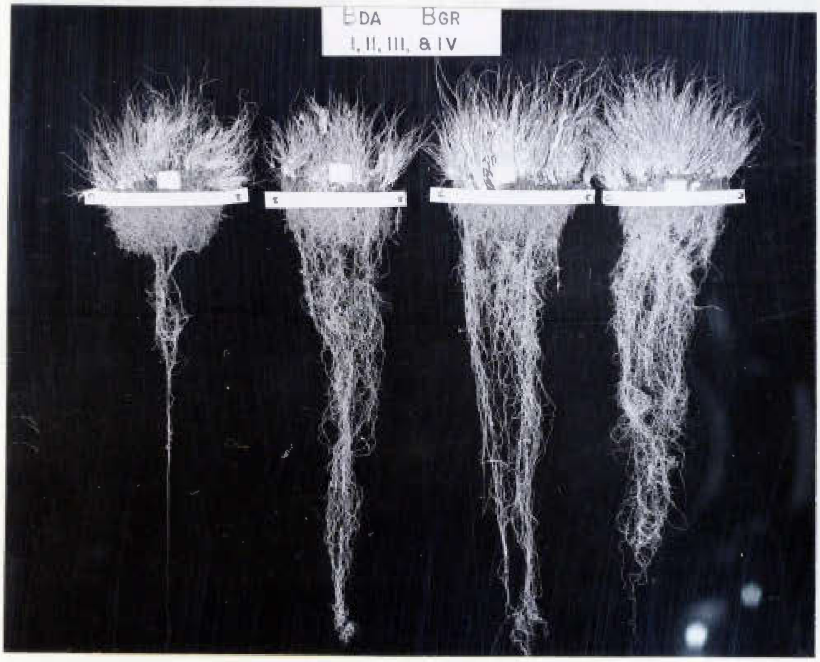

Figure 15. Selected Series I, II, III, and IV plants of buffalo and blue grama grass showing shoot and root growth.

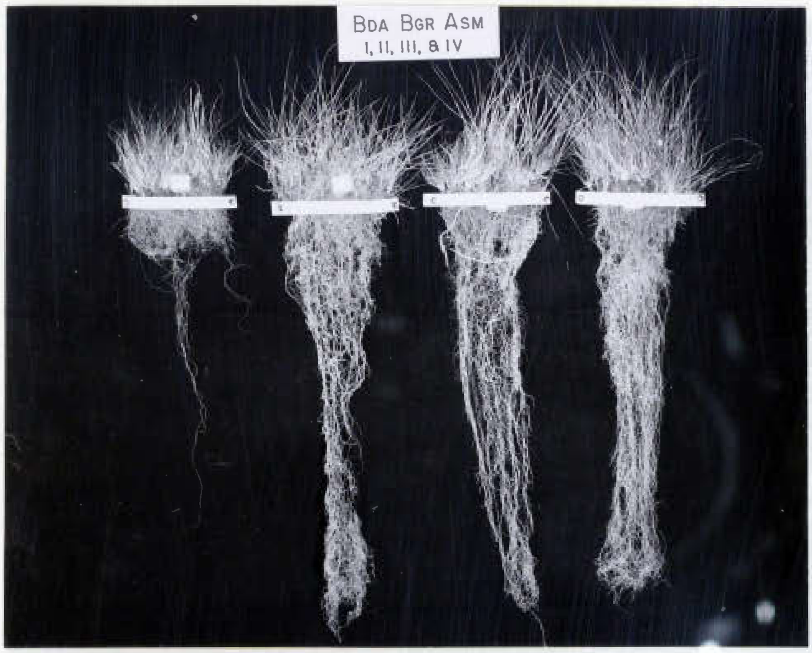

Figure 16. Selected Series I, II, III, and IV plants of buffalo, blue grama, and western wheatgrass showing shoot and root growth.

Figure 17. Selected Series I, II, III, and IV plants of buffalo, blue grama, western wheatgrass, and western ragweed showing shoot and root growth.

Table XI. Average length (cm.) of root systems of buffalo grass grown under different moisture conditions and competition rates

Competitive series	Watering series			
	I	II	III	IV
A	35.00	39.40	62.00	61.53
B	43.80	56.00	61.00	68.60
C	35.61	65.75	72.42	63.53
D	25.40	67.47	68.01	61.70

competing with blue grama grass from dry series to wet, respectively (Table XII). The respective number per cm. for C competitive series was 10.21, 6.89, 6.10, and 6.50 while D competitive series produced 8.09, 8.28, 6.50, and 3.94 per cm. from dry series to wet, respectively.

Yields. Production of buffalo grass was measured in terms of grams per square centimeter of foliage cover. To obtain more workable figures the resulting quotient was multiplied by 1000. Production data indicate many discrepancies in the method used to determine foliage cover; however, an attempt to measure production of buffalo grass under the different moisture conditions and competitive rates was necessary and the results are somewhat indicative of the conditions to which plants were subjected.

Production of buffalo grass grown alone was 44.85, 61.00, 43.30, and 75.25 grams per 1000 cm.^{2} from dry series to wet, respectively, while buffalo grass plants of B competitive series produced 34.95, 59.00, 60.50, and 68.75 grams, respectively, for the sam watering series (Table XIII). Buffalo grass plants grown in competition with blue grama and western wheatgrass produced 37.50, 32.80, 44.00, and 29.15 grams per 1000 cm.^{2}, respectively, from dry series to wet. Respective production of buffalo grass for the Series I, II, III, and IV plants of the D competitive series was 29.30, 50.35, 52.68, and 67.60 grams per 1000 cm.^{2} of foliage cover.

Table XII. Average number of lateral roots per cm. of main root of buffalo grass grown under different moisture conditions and competition rates

Competitive series	Watering series			
	I	II	III	IV
A	11.20	10.02	7.58	5.72
B	10.01	6.10	6.80	5.51
C	10.21	6.89	6.10	6.50
D	8.09	8.28	6.50	3.94

Table XIII. Production (gms./1000 cm.^{2}) of buffalo grass grown under different moisture conditions and competition rates

Competitive series	Watering series			
	I	II	III	IV
A	44.85	61.00	43.30	75.25
B	34.95	59.00	60.50	68.75
C	37.50	32.80	44.00	29.15
D	29.30	50.35	52.68	67.60

DISCUSSION

The procedure used in this study for determining some effects of plant competition has some merit. The method is relatively easy to arrange, environmental conditions can be controlled, and measurements of plant production and growth are easily obtained. Such a study can also be terminated in a comparatively short time.

There were, however, some serious limitations encountered and several important ecological measurements were omitted.

The first serious limitation of this study was made in the selection of the prairie sods. Selection of sods with a diameter of 6 inches which will contain equal amounts of a given plant is extremely difficult, if not impossible, and the difficulty increases with the number of species to be included in the sod. Sods used for the competition study were very carefully selected; however, in a number of the sods the desired species were not obtained because of failure of a given species to grow. This was especially true of the buffalo-blue grama grass competition series where the majority of sods contained little or no blue grama grass. In every case, dead tops of blue grama grass were included in the sods selected but, for some unexplained reason, many of the plants failed to grow. Presence of dead western ragweed tops in the sods where that species was desired was not absolute assurance of obtaining living western ragweed plants. However, an abundance of the species was obtained in most of the D competitive series sods.

Another limitation of selection of sods for use in a greenhouse project is that individual plants of a given species may show considerable variation in vigor, thus providing different degrees of competition for the species being studied, even if present in the same amount in all the original sods.

A further limitation in using small sods (6 in. diameter x 4 in. deep) is that root systems of all plants so obtained are seriously damaged and reduced. Since plants used in this study were in a dormant state and since they have similar root systems, the damage was expected to affect each plant similarly. One must realize however, that such plants do not represent natural field conditions and such damage to the roots may change the normal competitive balance in favor of the plants which can most quickly produce new roots.

Certain errors, perhaps inevitable, were probably incurred when watering the sods. Spaces between sod and phytometer wall sometimes developed, forming a pathway by which the water travelled down to the bottom of the phytometer. The water, rather than uniformly wetting the soil from top to bottom, probably remained near the bottom of the phytometer. Sealing the edges of the sod with soil would eliminate the problem and should be done as root form and size undoubtedly are affected by percolation of water to the bottom.

Certain important ecological and phenological measurements were omitted. A measurement of light, one of the most important factors for which plants compete, was omitted because the small size of the sods and variations in the vegetation cover in sods of the same series prevented valid measurement. Larger sods or samples would increase opportunities for making more acceptable measurements of light.

Measurement of soil temperature at the surface of the sods would have provided desirable data. The differences in insolation caused by differences in the amount of vegetation would have undoubtedly caused variation of temperature of the surface soil, especially when comparing different watering series.

The weekly increase in number of leaves per buffalo grass plant, an important part of the phenological data, was omitted by oversight. Differences, especially in the different watering series should have appeared.

To improve the method of studying competition that was followed in this paper the author suggests that: (1) larger and deeper phytometers be used; (2) seed rather than sods be planted; (3) the study be continued for at least one year; and (4) some quantitative method of determining plant cover be used.

Use of phytometers at least 4 feet deep and with a diameter large enough so that a vegetation sample of 0.25 square meter could be measured would greatly increase the success of the problem while, at the same time, would greatly increase the labor of r nning it.

Use of seed rather than sods would allow close control over the species and the number and spacing of each species. Use of seed would also eliminate the conglomeration of living and dead roots and crowns found in the sod and would greatly reduce the amount of time spent in washing out and examining root systems.

By continuing the study for at least one year, effects of competition for a longer period of time could be observed. In a year, a competitive balance would be established among plants and more reliable data would be obtained.

SUMMARY

Study of a phytometer method was made in a greenhouse to determine some effects of competition for water on buffalo grass. Buffalo grass was grown alone, with blue grama grass, with blue grama and western wheatgrass, and with blue grama, western wheatgrass, and western ragweed. The primary objective of the investigation was to determine if the effects of competition on a given species (buffalo grass), as determined by a greenhouse study, could be measured. To accomplish the objective a detailed study was made of the buffalo grass plants growing under various degrees of competition. Factors included in the study were: (1) leaf length; (2) stolon length; (3) root length; (4) date of flower appearance; (5) number of tillers; (6) number of lateral roots per cm. of main root; and (7) production of tops.

The four competitive series were designated "A", "B", "C", and "D" for the phytometers containing buffalo grass alone to the phytometers containing buffalo grass plus the three competitors, respectively. Ten phytometers in each of these competitive series were divided into four watering series: (1) Series I (dry); (2) Series II (intermediate-dry); (3) Series III (average); and (4) Series IV (wet).

Some environmental conditions within the greenhouse were relatively stable. Average daily maximum temperature was 91.7°F. and the average minimum was 59.1°F. Maximum and minimum relative humidity averaged 94.1 and 45.9 per cent. Average weekly evaporation was 115.02 milliliters.

Appearance of buffalo grass flowers was considerably delayed in the dry series and some additional delay was caused by competition.

Flowers appeared in Series I, II, III, and IV buffalo grass plants grown without competition 65, 40, 38, and 28 days after planting, respectively. In the D competitive series, flowers appeared 82, 42, and 33 days after planting on the Series I, III, and IV plants, respectively, no flowers being produced by the Series II plants. Delay of flower appearance in the B and C competitive series was intermediate, the latter generally showing the greatest delay.

A general reduction in leaf length was caused by reduced moisture and increased competition. Leaf length for buffalo grass plants averaged 7.02, 7.65, 12.08, and 13.31 cm., respectively, for Series IA, IIA, IIIA, and IVA phytometers while buffalo grass plants of B competitive series averaged 7.12, 7.53, 11.21, and 12.06 cm., respectively, from dry series to wet. Leaf length in C and D competitive series was 6.97, 7.22, 10.37, and 12.34 cm. for the former and 5.78, 6.85, 10.21, and 14.62 cm. for the latter, respectively, from dry series to wet.

Length of the longest buffalo grass leaf increased as moisture increased. With one exception, length decreased with increased competition. The longest leaf of Series I, II, III, and IV buffalo grass plants grown without competition was 11.87, 16.42, 21.65, and 26.32 cm., respectively, while plants of the D competitive series had longest leaf lengths of 9.21, 13.20, 18.20, and 34.05 cm., respectively, for the same Series. Longest leaf length of C and D competitive series was intermediate in every respect.

Stolon production was quite variable indicating that competition had little influence on stolon growth. With one exception, no stolons were produced by Series I or II plants. Some stolons were produced by most of the Series III and by all of the Series IV buffalo grass plants but measurements indicated only a general trend of increased length with increased moisture.

The number of tillers per buffalo grass plant increased with increased moisture and surprisingly, also showed a general increase as competition increased. The average number of tillers per plant was 2.50, 4.00, 4.63, and 6.50, respectively, in series A from dry to wet and 2.75, 5.00, 6.00, and 11.50 for competitive series B. Series C plants produced 3.00, 4.00, 5.75, and 8.50 tillers per plant from dry series to wet while 4.00, 6.00, 6.40, and 9.50 tillers were produced by competitive series D buffalo grass plants from dry series to wet.

Average length of root systems of buffalo grass was apparently not affected by competition but indicated a general increase with increased moisture. Average length of roots of buffalo grass grown without competition was 35.00, 39.40, 62.00, and 61.53 cm., respectively, from dry series to wet. Root systems of buffalo grass plants in other competitive series were of approximately the same length and generally indicated an increased length with increased moisture.

The number of lateral roots per centimeter of main root generally increased with decreasing soil moisture content but, again, little consistent change could be attributed to competition. The number of laterals produced by buffalo grass plants grown alone was 11.20, 10.02, 7.58, and 5.72 per cm. of main root, respectively, while plants of the B competition series produced 10.01, 6.10, 6.80, and 5.51 from dry series to wet, respectively. Plants of C competition series produced an average of 10.21, 6.89, 6.10 and 6.50 laterals per cm. and 8.09, 8.28, 6.50, and 3.94 laterals per cm. of main root were produced by D competitive series plants from dry series to wet, respectively.

Production of buffalo grass forage per unit of foliage area was determined. Many variations occurred but a general increased production was associated with increased moisture and a general decreased production with increased severity of competition. Buffalo grass plants grown alone produced 44.85, 61.00, 43.30, and 75.25 grams per 1000 $cm.^2$ of foliage cover from dry series to wet, respectively, while competition with blue grama grass decreased production to 34.95, 59.00, 60.50, and 68.75 grams for the same series. The C competition series plants produced 37.50, 32.80, 44.00, and 29.15 grams per 1000 $cm.^2$ of foliage area, respectively, for Series I, II, III, and IV while D competitive series plants produced 29.30, 50.35, 52.68, and 67.60 grams, respectively, from dry series to wet.

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