Response of root and shoot growth to decreases in soil water potential

Mark Edward Majerus

The University of Montana

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THE RESPONSE OF ROOT AND SHOOT GROWTH TO DECREASES IN SOIL WATER POTENTIAL

By

Mark E. Majerus

B.S., University of Montana, 1970

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for the degree of
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Approved by:

[Signatures]

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Chapter 1

INTRODUCTION

In central Montana the major grass species show differences in their site requirements. The stable communities serve to interpret the environmental conditions of the habitat. It seems apparent that available soil moisture is a major causal factor involved in species distribution and abundance. Frolick and Keim (1933) stated that the influence of the ground water and soil texture were the chief factors in determining the existence of distinct plant communities in the prairie hay district of Nebraska. Stager (1930), Patten (1963), and Dix (1958) all agree that water content of the soil is the most important factor in determining differences in the structure of prairie vegetation. This is further emphasized by the fact that some indirect factors such as soil, wind, salts, etc. can influence the plant only through their action upon the water regime. Water is no more indispensable to plants than is light or temperature, but it can be considered of great importance due to the involvement of water in a large number of vital functions.

In regions of wet winters and dry summers especially, the soil acts as the reservoir supplying water to the plant during the growth season. Water available for plant growth is supplied as rain and snow during the wet season, and where it is not maintained during the dry season by ground water, the supply is gradually exhausted. The rate of use and time of exhaustion of the available moisture supply depends greatly on the physical and physiological characteristics of the species. Shantz (1927) states that drought, in the proper sense, is correlated with soil
moisture and occurs when the available soil moisture is lowered to a point where the plant cannot absorb water rapidly enough to replace that lost to the air by transpiration.

Daubenmire (1956) stated that each vegetation type differs from its neighbor in the degree of summer drought, except at the wet end of the climatic gradient where low temperatures is more the decisive factor. McMinn (1952) supports this by showing that in the region of the northern Rocky Mountains, where precipitation is mostly in the winter months and summer drought occurs, different plant associations are correlated with different extents of soil drought. The time and extent of summer drought serves to limit the spread of some species while advocating spread of others. Depending on topography, exposure, and plant cover soil drought varies from one microclimate to another. It would be advantageous to know to what extent a plant could tolerate soil drought and this may be an indication of the site it will occupy.

By holding most environmental factors (light, temperature, soil characteristics, and photoperiod) approximately constant, the effects of the available soil moisture can be observed. This study was designed to make it possible to monitor root elongation and leaf elongation of three grass species while growing in soils with favorable moisture conditions (control) and soils with decreasing soil water potential (treatment) brought about by use of a nonrenewable moisture supply.

The species which were investigated were blue grama (*Bouteloua gracilis* (HBK) Lag.), western wheatgrass (*Agropyron smithii* Rydb.), and little bluestem (*Schizachyrium scoparium* (Michx) Nash), formerly *Andropogon scoparius* Michx).
The records taken in this study include: a) daily growth of leaves under control and treatment conditions, b) daily root growth under control and treatment conditions, c) daily changes in soil water potential at 8 cm intervals through the soil profile, d) correlation between soil water potential throughout the soil system and leaf elongation, e) soil water potential at the time of leaf growth cessation, f) correlation between soil water potential and root elongation in each of four soil levels, g) soil water potential at the time of root growth cessation in each soil level, h) comparison of cumulative values of per cent of average stem elongation and per cent of total root growth of the treatment and control plants. Each of the preceding is recorded for each of the three species and lends itself to interspecific comparison.
Chapter 2

LITERATURE REVIEW

Ecological distribution of species

In natural vegetation the position of plant species does not occur at random, but the plants are intermixed or controlled by the impact of the environment over a series of years. Within the mixed prairie of central Montana blue grama (*Bouteloua gracilis*), western wheatgrass (*Agropyron smithii*), and little bluestem (*Schizachyrium scoparium*) each appear to have distinct and different site requirements. Little bluestem has been reported as an important species of the mesic midwestern prairie, while western wheatgrass and blue grama are considered to be xeric species characteristic of the great plains (Weaver 1954).

Little bluestem is a major constituent of the uplands of the "prairie" region of the midwestern states. Northward and westward little bluestem forms a much-interupted sod (mats, tufts, and bunches) (Weaver and Fitzpatrick 1934). In Montana and North Dakota little bluestem is a minor species of the mixed prairie type. Hanson and Whitman (1938) found that in North Dakota little bluestem occurs on slopes where snow drifts accumulate on northern aspects of fairly steep slopes of hills and plateaus. Moisture conditions below the "steep" are more favorable than on the general slopes because snow tends to accumulate and run-off is retarded. Booth (1950) states that where moisture conditions are favorable, as in the midwest, little bluestem is usually considered a good forage grass while it is young and tender. In many drier types, such as in the mixed prairie, it is considered a pest.
The root system of little bluestem consists of a vast network of roots and masses of finely branched rootlets, some more than 30 inches in length and branched to the third order (Weaver 1958, 1961). Most of the roots extend off rather parallel with the soil surface or slightly oblique for long distances, where they end or finally turn downward. The lateral rooting system is well developed on all sides of the bunches in the surface 6 inches of soil. Below and inside of the laterals, at all angles to the vertical, are abundant roots which penetrate downward to depths of 2.5 feet in poorly disintegrated subsoil to as far as 8 feet in the Sandhills of Nebraska (Weaver 1920).

**Blue grama** is quite widely distributed; located in all the western states except possibly in the Pacific Northwest. It is especially characteristic of the short-grass areas of the Great Plains (Dayton et al. 1937). Coupland (1950) considers blue grama to be the most drought-resistant dominant in south-central Canada. It is adapted to habitats where, because of compact soil through which water percolated slowly, water loss from runoff is high. Under favorable moisture conditions it tends to form sod. In Montana it reaches its greatest prominence on the prairies of the eastern part of the state. It is often in pure stands on ridges or dry uplands where environmental conditions are too adverse for most other grasses (Morris et al.). The species is very drought resistant and has the ability to become dormant during dry periods and as soon as summer moisture is available it resumes growth (Booth 1950).

The root system of blue grama is well developed with great masses of fine roots occupying every cubic centimeter of soil to a depth of 1.5 feet and as far horizontally as 1.5 feet (Weaver 1920). Because of
extensive rooting in the surface soil blue grama is able to benefit from water furnished by light showers. Weaver (1920) studied root growth of blue grama in South Dakota, Colorado, and Nebraska and the maximum depth of penetration did not exceed 4.5 feet. Little difference in root distribution was found in several plant communities, except the marked development of widely spreading surface laterals so common in the more arid portions of the grassland formation was not found in the moister sites of the true prairie.

Western wheatgrass occurs in most parts of the western and mid-western states as well as in the southwestern part of Canada. Coupland (1950) found western wheatgrass in various soils of limited moisture content. It is adapted to gumbo flats, where moisture supply is moderate, and tolerates a fair amount of alkali. Dayton et al. (1937) says that it is best adapted to well-drained bottomlands, but is commonly found on open plains, hillsides, and benchlands. It occurs in considerable abundance, and on adobe soils is often the dominant grass over large areas. In Montana this grass is often the first to appear in quantity on abandoned, dry farm land (Dayton et al. 1937). Western wheatgrass is a perennial from creeping rootstocks, and under the most favorable conditions may grow in dense patches or even form a compact sod. The rhizomes are profoundly branched to the third and fourth order and thus furnish an excellent surface absorbing system (Weaver 1958). The vitality and growth habits of the rhizomes of western wheatgrass enables it to resist drought better than other prairie plants producing rhizomes, stolons or runners (Mueller 1941). Weaver (1958) showed that the depth of penetration varies with soil from 5 to 7 feet. The chief
difference in root habits of this grass in the true prairie, as compared
with the mixed prairie, were the lack of an extensive surface absorbing
system and the greater depth of penetration (8 to 9 feet).

Factors influencing vegetation distribution

Of the studies involving blue grama, western wheatgrass, and little
bluestem, the majority are ecological in nature and describe and list
the species of specific areas. Weaver and Fitzpatrick (1934) made an
extensive study of the vegetation of the "True Prairie". Weaver (1968)
summarized numerous ecological studies in the midwestern states.
Coupland (1950) described the vegetation pattern throughout southern
Alberta and Saskatchewan and later (Coupland 1961) classified vegetation
types into faciations based on dominant species of each type. He felt
that gradual changes of vegetation types were the result of topographic
position while abrupt changes in composition occurred in response to
changes in soil texture. Hanson and Whitman (1938) discussed the vege-
tation of western North Dakota. This area is primarily of the mixed
prairie type and basically more xeric than the true prairie regions of
the south. By studying relict areas (Cemeteries, protected lots, etc.)
Wright and Wright (1948) defined climax dominant types throughout the
southern portion of Montana. Relict areas were also found to be good
indicators of climax vegetation in South Dakota (Larson and Whitman
1942) and North Dakota (Quinnild and Cosby 1958).

Numerous people have given their explanation for vegetation patterns
and distribution. There is a question as to which environmental and/ or
physiological factor or combination or factors influence vegetation the most.

Heerwagen and Aandahl (1961) studies areas in the southern plains in which they found that soil types having closely related soil characteristics support essentially similar kinds of native plant communities. Therefore depending on the degree of plant community differentiation desired, they felt that it was feasible to group closely related soil types to express similar plant community potentials. In the Flint Hills it was found that the number of distinctive vegetational units was smaller than the number of soil units, but by grouping similar soil types, they defined six soil-vegetation types (Anderson and Fly 1955). In the Utah desert, Gates et al. (1956) made a study of possible soil texture-vegetation relationships. They found that there was some significant correlation between certain vegetation types, but no species was restricted to any specific soil types.

Steiger (1930) made extensive measurements of edaphic and aerial factors of the environment on both upland and lowland prairies. The water content of the soil showed the greatest and most consistant variation, and was the most important factor determining the structure of the vegetation pattern. White (1961) felt that little bluestem in southern South Dakota was not located on the more favorable moisture sites, but rather was on the more xeric microridges and related to soil texture and fertility. Contrary to this, Hanson and Whitman (1938) found little bluestem on northern aspects of ridges, but felt that because of snow drifts and percolation of moisture the ridges had favorable moisture conditions. Dix (1958) found that in the badlands of
North Dakota, grass species were located along a moisture gradient with blue grama and western wheatgrass at the drier end of the gradient and little bluestem at the wetter end of the gradient. Morris et al. (1964), in a plant-environment relation study, found soil moisture to be the most limiting factor, both as the total amount in the soil and distribution in the soil profile. Blue grama was found on variable textured soils with restricted moisture movement and relatively low moisture supply. Western wheatgrass occupied sites of variable soil texture with moderate soil moisture conditions. Little bluestem persisted on coarse, stony soils with moderately good moisture conditions. Patten (1963) used a total of 13 environmental factors in an attempt to explain vegetation type distribution. Of all the independent variables, soil moisture retention at 15 atmospheres tension and the clay content of the soil were the two most significant factors in influencing the diversity of the vegetational patterns. The vegetation in the badlands of North Dakota correlated significantly with apparent soil moisture (Dix 1958). McMinn (1952) felt that the presence of soil drought prevents the spread of an association into those areas where soil drought is more extensive than its constituent species can endure. Where soil drought does not exclude the species of an association the boundaries of their distribution may be set by their failure to compete successfully with species of other associations which are more tolerant to the environmental conditions.

**Water requirements of plants**

The fact that water is such an important factor in maintaining the plant has led to many investigations on the water requirements of various
forage and agronomic plant species. The water requirement was generally termed as the ratio of the weight of water absorbed by the plant during its growth to the weight of the dry matter produced (Weaver 1941, Shantz and Piemeisel 1929). Weaver (1941) determined the water requirements of seven prairie grasses including western wheatgrass (highest water usage) and blue grama and little bluestem (lowest water usage). Shantz and Piemeisel (1927) listed the water requirements of more than 20 agronomic crops of which cotton and a grass species (blue grama) made the most efficient use of water. Bailey (1940) studied three cool season grasses and found western wheatgrass to be one of the more efficient plants in water usage. Many others based their studies on the basic water requirements of various plants (Chamblee 1958, Biggs and Shantz 1913, Dillman 1931, Bol'shakov et al. 1968).

Early investigators considered water requirements to be closely correlated with drought resistance. A study of water usage and drought resistance of several southern grasses was conducted by Burton et al. (1957). Mueller and Weaver (1942) studied the drought resistance (expressed as per cent survival) of seedlings of dominant prairie grasses. They found that blue grama was by far the most enduring; little bluestem was intermediate and western wheatgrass was the least able to resist drought. Heat resistance as a factor in drought resistance was considered by Julander (1945). In natural conditions there is a series of wetting and drying cycles throughout a growing season. Repeated drought cycles were used by Todd and Webster (1965) to study the survival of cereal seedlings. Mueller-Dombois and Sims (1966) used a series of wettings followed by a drought cycle to see if three grasses would locate
themselves along a moisture gradient. *Andropogon gerardi* thrived on the very moist sites, *Calamagrostis canadensis* died back to the moist sites and *Koeleria cristata* survived at the drier levels.

Shantz (1927) broke the term drought resistance down into a series of more physiological categories: drought escaping (grows only where conditions are favorable), drought evading (limit growth or have efficient use of water), drought enduring (small amount of growth relative to available moisture), and true drought resistant (thick skinned species of the desert).

The water requirements and drought resistance of a plant are good criteria for explaining its distribution but they do not account for all the factors involved. There are many plant and soil factors which influence the availability of the moisture supply.

Jamison (1956) outlined factors which he felt governed soil moisture availability. Plant factors involved were a) plant condition, b) rooting habits, c) drought resistance. Environmental factors were a) moisture tension, b) osmotic pressure, c) ions present in solution, d) soil moisture conductivity, e) soil depth, f) soil stratification, and g) soil temperature.

**Soil water potential**

Hillel (1971) states that the amount and rate of water uptake depends on the ability of the roots to absorb water from the soil with which they are in contact, as well as on the ability of the soil to supply and transmit water toward the root at a rate sufficient to meet transpiration requirements. These, in turn, depend on properties of
the plant (rooting density, rooting depth, and rate of root extension),
as well as the physiological ability of the plant to increase its own
water suction sufficiently to continue drawing water from the soil at a
rate needed to avoid wiltin and properties of the soil (hydraulic con-
ductivity-diffusivity-matric suction-wetness relationships). According
to Brown (1970) the concept of the energy status of water in a system
best explains the availability of the water. The free energy of the
water in the soil can be expressed as the difference between the free
energy of pure free water and the free energy of the water in the system
at the same temperature and pressure; better known as water potential.
Water potential is affected by factors which change the free energy of
water molecules in the system. The presence of solutes, colloids, large
particles such as sands, silts and clays all decrease the water poten­
tial. The water molecules interact with these components and decrease
the free energy of the water below that of pure free water. Therefore
the total water potential is a combination of osmotic (due to the
presence of dissolved substances in the solution), matric (function of
the capillary or colloidal adsorptive forces by soil particles) and
gravitational (external gas pressure and gravity) (Hillel 1970, Brown
1970).

The preceding discussion of soil water potential is an indication
that soil moisture, salinity and alkalinity, and soil texture are all
included in a combined nature to produce soil water potential.

Wadleigh and Gauch (1948) found that leaf elongation of cotton
decreased as soil water potential decreased and it virtually ceased when
the soil reached a water potential of -13.8 to -15.1 bars. First
visible wilting of barley leaves was observed at soil water potentials between -1 and -5 bars (Millar et al. 1970). Others observed a decrease in growth as soil water potential decreased: flax and cereal (Bourget et al. 1966), tomato and loblolly pine (Brix 1962), and flax (Lehane and Staple 1962).

The effects of water potential on physiological aspects of the plant such as transpiration and photosynthesis were studied by Todd and Webster (1965). Rawlins et al. (1968) found that transpiration was unaffected by soil moisture potential until it dropped to -6 to -8 bars. Transpiration decreased linearly to a water potential of -37 bars and at -50 bars the transpiration rate was zero. Permanent wilting (the point at which the plants would not recover) was found to occur at soil water potentials of -20, -28, and -48 bars in tomato, privet, and cotton respectively (Slayter 1957). Eddleman and Nimlos (1972), using thermocouple psychrometers, studied growth response of *Agropyron spicatum*, *Festuca scabrella*, *Calamagrostis canadensis*, and *Carex geyeri* to soil water potential and atmospheric stress. Growth rates were generally lower under High Stress Atmosphere than the Low Stress Atmosphere. *A. spicatum*, *F. scabrella*, and *C. canadensis* ceased growth, in the High Stress Atmosphere, at -5.0, -8.5, and -12.5 bars respectively and, in the Low Stress Atmosphere, at -12.5, -12.5, and -27.0 bars respectively. *Carex geyeri*, under High Stress Atmosphere, ceased growth at -5.5 bars.

Osmotic potential, which is a component of soil water potential, can be an important limiting factor. Magistad (1945) showed how soil salts reduce water intake by roots because of salting out of cellular proteins, shrinkage of cell contents from cell wall, irreversibility of
hydration of cell contents and interference with ion accumulation. The salt content of soil is of major importance in the arid west in determining the total soil water potential (Kelley 1954).

Kaufman (1968), using pine seedlings, found that when the roots were subjected to severe stress they matured toward the tip and became dormant, resulting in less growth during subsequent drying cycles. Gingrich and Russel (1957) observed a marked reduction of moisture transmission when there was a development of soil water potential in the range from $-\frac{1}{2}$ through -12 bars. The reduction of moisture transmission was a function of the water intake by roots and the rate of movement of moisture through the adjacent soil to the roots. Peters (1957) used corn to demonstrate that uptake of water and elongation of roots are decreased as the soil water potential decreased and that the uptake of water and root elongation decreased as the moisture content per unit of water potential decreased. Burton et al. (1957) revealed that a much lower percentage of roots was needed to supply the nutrient needs than to satisfy the water requirements, thus more often water is the limiting factor.

Newman (1966) noticed a marked reduction in root growth of flax at -7 bars total water potential. At -15 bars root growth was reduced to 20 per cent of the original growth and some roots continued to grow under conditions drier than -20 bars. Both Davis (1940) and Bennett and Doss (1960) found that there was a selective absorption of water near the plant, when similar numbers of roots of the same plant were in soil of higher moisture content further from the plant, indicating a moisture absorption gradient in the root system. Moisture was first removed from
the top 6 inches of soil where root concentration was highest. As the soil water potential decreased near the surface, more moisture was extracted at successively lower depths. However, the rate of moisture extraction decreased with increasing depth. Plants usually wilted before the moisture content of the lower depths was reduced to a level comparable to the upper soil levels. This indicates that the activity of roots at the lower rooting depths was insufficient for the plant to extract moisture fast enough to maintain a normal transpiration rate. Since roots are dependent on their shoots for the carbohydrates essential to growth, whatever affects photosynthesis and the use of carbohydrates in the shoot will also affect root growth. Reciprocally, any injury to or inadequacy of the root system will hinder shoot growth. In general, root and shoot growth are rather closely related and, if the development of one is modified, growth of the other is likewise modified (Roberts and Stuckmeyer 1946).

Studies of roots

The study of roots is limited because of the difficulty of observing roots without destroying them. Weaver (1920) used deep trenches to observe rooting patterns and Weaver (1950) used the monolith method of root sampling. Kittock and Patterson (1959) used 2 inch Pyrex tubes to study root elongation of 10 grass species seedlings. Glass front boxes were used to observe root development under various treatments without disturbing the root-soil system. Muzik and Whitworth (1962) used a wooden root box with glass and a shutter clamped on one side of the box. To simulate natural conditions as closely as possible Lavin (1961) built sheet metal boxes with a glass front which slide into wooden frames
built below the soil surface. This provided natural darkness and temperature conditions. To study the affect of temperature, soil strength and pH on cotton seedling root growth Pearson et al. (1970) used boxes of acrylic plastic.

Differences in opinion exist concerning the ability of roots to grow into dry soil. Weaver (1920) and Weaver and Crist (1922) found that root penetration was greatest in the true prairie, less in mixed prairie, and least in the short-grass plains, which has so little rainfall that the soil is seldom wetted deeper than 1.5 to 4.0 feet. In plains regions where only the surface soil is wetted, roots do not penetrate below the hardpan which marks the lower limits of moist soil. Shantz (1927) found that certain trees of the African grassland possess roots capable of extending into dry soil, but most crop plants cannot do so. Some investigators found that roots growing in moist soil would extend into dry soils only a short distance (Muller 1946, Hendrickson and Veihmeyer 1931, and Hunter and Kelley 1946). In most cases, upon encountering dry soil the root growth ceased and the roots become suberized to prevent moisture loss.

The type of growth of the root system of seedlings of many species is firmly fixed by their heredity. This in turn has an important bearing on the plants ability to absorb water and hence survive drought. As seedlings grow older, the form of the root system often tends to be increasingly modified by environmental factors. Conspicuous differences do exist and are developed in the extent and form of root systems of plants (Weaver and Clements 1938). Cannon (1926) and Weaver and Clements (1929) believe that a relatively low water content, provided there is
(1929) believe that a relatively low water content, provided there is enough to insure good growth, stimulates the roots to greater development, resulting in a greatly increased absorbing surface. The additional absorbing surface is furnished by the development of secondary and tertiary branches. Where the soil profile is wet the rooting is shallow and not as extensively branched. This reduction in growth may be due, in part, to lack of aeration. Kramer (1949) felt that in general, larger root systems are produced in soil that contain an abundance of soil moisture if aeration is good, but a larger ratio of roots to shoots is obtained when there is a limited supply of water.

**Techniques for measuring soil moisture**

Several techniques are available for determining the water potential in the soil-plant system, but some of them have rather limited application; others are undesirable in view of recent advances in water relation technology. Some of the techniques for the measurement of soil water potential that are still in use but of limited applicability are as follows: tensiometers (Richards and Ogata 1961) which are capable of measuring matric potentials only between 0 and -1 bar, freezing point depression (Abele 1963) which has an upper limit of about -25 bars, electric-conductance method (Bouyoucas and Mick 1940) which has a sensitive range of -0.5 to -15 bars, dye-refractometric method (Knipling and Kramer 1967), soil culture method (Berstein and Pearson 1954), and Gray hydrocal hygrometer method (Bouyoucas and Cook 1968). Warring and Oleary (1967) used a pressure membrane which measures up to a pressure of one bar and a pressure plant which measures pressures to
-20 bars. In this mechanism the lower side of the soil sample is exposed to atmospheric pressure and the upper side is exposed to the pressure you wish to impose on the moisture within the soil sample.

Some observers have grown plants in solutions in which the osmotic potential can be changed by diluting the solution. Parmar and Moore (1966) and Kaul (1966) used Polyethylene glycol to study the affect of water potentials on growth of corn and cereal grains. Using Mannitol solutions McGinnies (1960) studied germination of range grasses at pressures ranging from -1/3 to -12 bars.

The thermocouple psychrometer method of measuring soil water potential is relatively new and is proving itself in many fields of science. Since the relative vapor pressure of soil water and plant tissue (which is directly proportional to water potential) with in the range of usual physiological significance (0 to -75 bars) lies very close to the saturated vapor pressure (95 to 100 per cent), the method used to measure this must be capable of detecting very small changes in vapor pressure (Brown 1970). Spanner (1951) first demonstrated that sufficiently sensitive measurements of the relative vapor pressure of water in the narrow range of interest can be made with small sensitive thermocouples. This method offers great sensitivity and accuracy and can be used either in the laboratory with very small samples or in the field over extended periods. Richards and Ogata (1958) suggested a modification of the Spanner (Peltier) psychrometer, consisting of a small silver ring attached to the ends of the chromel and constantan thermocouple wires, which holds a drop of water. Barrs (1965) and Zollinger et al. (1966) compared the two types of psychrometers and found that there was
more error in the Richards and Ogata (wet-loop) type.

Special techniques and precautions to follow during construction have been presented by Campbell et al. (1968), Weibe (1970), Merril et al. (1968), and Weibe et al. (1971).

Nimlos et al. (1971) explain construction and calibration procedures of the Peltier thermocouple psychrometers. One change in this construction procedure has been developed by Brown (1970). Instead of the thermocouple junction being covered by porous clay cups a cap of fine mesh stainless steel wire was developed. The screen covered psychrometers reach vapor equilibrium in about 30 minutes while the clay cup psychrometers require over 2½ hours to reach equilibrium.
Specimens of blue grama, western wheatgrass, and little bluestem were collected from an area 15 miles west of Lewistown, Montana along the Judith River valley.

The blue grama site was on the crest of a steep slope overlooking the river valley. The species composition of the site was almost pure blue grama along with a few plants of *Agropyron smithii*, *Artemisia frigida*, and *Opuntia* spp. This was the most exposed of the three sites.

The western wheatgrass site was located on the lower portion of a gentle southwest facing slope in the river valley. This species was found in association with *Koeleria cristata*, *Stipa comata*, and *Poa* spp.

The little bluestem site was on a steep north-facing slope and extended into a narrow draw. This species was in association with *Koeleria cristata*, *Agropyron spicatum*, and *Poa* spp. The sites were not only quite different in the location but in the soil texture also.

(Table 1)

<table>
<thead>
<tr>
<th>Site</th>
<th>Per cent 2 mm</th>
<th>Per cent 2 mm</th>
<th>Sand</th>
<th>Silt</th>
<th>Clay</th>
</tr>
</thead>
<tbody>
<tr>
<td>Little bluestem</td>
<td>27</td>
<td>83</td>
<td>40</td>
<td>39</td>
<td>21</td>
</tr>
<tr>
<td>Blue grama</td>
<td>55</td>
<td>45</td>
<td>36</td>
<td>37</td>
<td>27</td>
</tr>
<tr>
<td>Western wheatgrass</td>
<td>100</td>
<td>0</td>
<td>2</td>
<td>32</td>
<td>66</td>
</tr>
</tbody>
</table>
Plant specimens were collected by digging up clumps (blue grama and little bluestem) or closely associated individual stems (western wheatgrass). Specimens were collected early in the spring before any evidence of new growth. Once new growth started, the plant clusters were broken into smaller plants which were used as individual replications in the study. Clonal material was used to minimize the genetic variation between replications of each treatment.

**Growth Chamber Study**

A preliminary study was conducted in controlled environment growth chambers (Sherer CEL-3714) provided by the U.S. Forest Sciences Laboratory, Missoula, Montana. The methodology of this study was based on a similar study of bunchgrasses of western Montana conducted by Eddleman and Nimlos (1972). Individual plants were grown in 1 gallon plastic pots containing approximately 3,000 grams of air-dry sandy loam soil (48% sand, 41% silt, and 11% clay). A soil mixture of 3 parts (by volume) top soil and 1 part peat moss was used throughout the entire study. Fertilizers were not used. Four treatment replications and four control replications were utilized.

The growth chamber was set at the following environmental conditions. The "day" period of 15 hours has a temperature of 30°C and a relative humidity of 20%. The "night" period of 9 hours had a temperature of 20°C and a relative humidity of 45%. The incandescent lights turned on one-half hour earlier than the fluorescent lights and turned off one-half hour later to simulate sunrise and sunset. The average light intensity during the day period was approximately 4,000 foot-candles.
After the plants were transplanted to the pots they were allowed to grow for 7-10 days to renew active growth. The soil of the treatment pots was saturated on the first day of the experiment and no additional was added throughout the remainder of the test period. Transpiration, water utilization, and evaporation losses eventually exhausted the available moisture supply. Sphagnum moss was placed on the soil surface to reduce losses due to evaporation but still allow for gas exchange. The control plants were grown at very high soil water potential (0 to -1 bar), which was maintained by watering every 3 or 4 days.

Leaf growth measurements were taken once every 24 hours. The total elongation of leaf blades; sheaths and stem internodes of 5 stem was recorded. All measurements were taken from a fixed point near the soil surface. Measurements were made of all elongating leaf blades (distances between top of sheath to tip of leaf blade). The stem internode growth was expressed as the daily increase in the difference between the distance from the fixed point to the tip of the last leaf blade and the length of the last leaf blade. Daily soil water potential measurements were taken using two Spanner (Peltier) type thermocouple psychrometers at depths of 5 cm and 10 cm below the soil surface. All measurements were taken on both treatment and control plants until there was no further elongation on any of the 5 tagged stems in the treatment pots.

**Root Box Study**

A second study was conducted in a green house using glass-front root observation boxes (Figures 1 & 2). The soil depth of 40 cm in the root boxes, as compared to 15 cm in the pots, produced on increase in
Figure 1. Rear view of root observation boxes.

Figure 2. Front view of root observation boxes.
the available soil profile creating a greater distribution and elongation of the roots. The root boxes contained a soil volume of approximately 6,400 cm$^3$, as compared to 2,500 cm$^3$ in the plastic pots.

The boxes were fixed at a 30° angle to force root growth along the glass surface. The glass surface was divided vertically into four equal regions each 8 cm deep (Figure 3). A 4cm area on the top and bottom were ignored. The bottom area was mostly gravel which aided in the proper drainage of the boxes. The upper area, in most cases, was above the active rooting area of the plant.

Root growth measurements were made once every 24 hours. All root growth for the previous 24 hours period was measured and then covered with a white crayon mark (Figure 3). Root growth was recorded individually for each of the four soil depths.

Leaf growth measurements were taken at the same 24 hour intervals. Leaf blade, sheath and stem internode elongation of 4 tagged stems was measured from a fixed point near the soil surface, just as in the growth chamber study.

Soil water potential measurements were taken with thermocouple psychrometers. Four psychrometers were used for each treatment box. The instruments were inserted through the back of the boxes such that one psychrometer would be located in the middle of each of the four soil zones and close to the glass where the mass of the roots would be located (Figure 4). Soil temperature measurements were made each day for later use in converting voltmeter readings into bars of water potential.

An attempt was made to maintain relatively constant environmental conditions throughout the study of the three species. Only one species
Figure 3. View of root system with white crayon marks. Note the four soil zones on the glass surface.

Figure 4. Thermocouple psychrometers inserted into the treatment boxes.
was observed at a time because only 6 root boxes were available. Three boxes were used for treatment plants and three for control plants. Lights were kept on during the evening hours so that all the species would be exposed to the same photoperiod. The study of each species involved 40 to 50 days each, and this extended the study through the summer months and into the fall. With the long days total growth per 24 hour period was increased, thus exhausting the moisture supply earlier than with natural day lengths.

Growth measurements were begun when the plant started to produce new roots (usually 7-10 days). The treatment boxes were not watered after an initial saturation. Control boxes were watered every 3 or 4 days to maintain a high water potential in the soil system.

All measurements were taken until no further leaf or stem elongation was apparent on the four tagged stems of the treatment plants and no root elongation occurred in any of the four soil zones of the treatment boxes.
Chapter 4

RESULTS AND DISCUSSION

Growth Chamber Study

The main objective of this study was to test the hypothesis that there is a direct correlation between decreasing soil water potential and decreasing leaf elongation. Interspecific comparison can also be made with the resulting regression lines.

Control plants were maintained to furnish information on the growth patterns under favorable conditions. In all cases the daily leaf growth of the control plants maintained a constant or slightly increasing rate of growth (Figure 5). Under favorable conditions the daily production of foliage was quite different between species. Blue grama produced up to 32 mm (average per stem) of growth daily, western wheatgrass produced up to 37 mm daily and little bluestem reached a maximum of 16 mm of daily growth. There is no significant difference in the growth rates of the control and treatment plants until the decreasing soil water potential caused the treatment plants to decline in their foliage production. The rate of decline and the time involved in reaching a point of leaf growth cessation varied with the species (Figure 5). Blue grama required an average of 19 days to exhaust its moisture supply, western wheatgrass took an average of 12 days, and little bluestem took 13 days.

The decreasing soil water potential, expressed as negative bars, serves as a good indicator of the drying pattern of the soil mass (Figure 6). The soils of little bluestem and western wheatgrass dried at about the same rate, with little bluestem drying out the upper soil zone.
Figure 5. Average daily leaf elongation of the control (-----) and treatment (-----) plants from the beginning through the end of growth for treatment plants. (Growth Chamber Study)
Figure 6. Soil water potential at the two soil levels in pots (Growth Chamber Study) from beginning to end of growth for treatment plants. End of lines represents day on which plant growth ceased.
slightly more than western wheatgrass. The slow extraction of moisture by blue grama can be seen by the gentleness of the slope down to about -10 bars, at which time the drying rate is greatly increased. The end point of each of the lines indicate the soil water potential at which leaf growth was terminated. Table 2 lists the soil water potential of both soil levels when there was no further leaf elongation.

Table 2. Soil water potential at time of leaf growth cessation.

<table>
<thead>
<tr>
<th>Specie</th>
<th>Level 1</th>
<th>Level 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) blue grama</td>
<td>-63.3 b c1 /2/</td>
<td>-17.5 b c 1</td>
</tr>
<tr>
<td>b) little bluestem</td>
<td>-18.7 a c 2</td>
<td>-11.8 a 1</td>
</tr>
<tr>
<td>c) western wheatgrass</td>
<td>-12.9 a b</td>
<td>-13.3 a</td>
</tr>
</tbody>
</table>

1/ Letter indicate the species which are significantly different at the .05% level using a t-test of the replication means.

2/ Number indicate which level within a species are significantly different at the .05% level using a t-test of the replication means.

The water potential in the upper level of blue grama was significantly lower than both little bluestem and western wheatgrass. Little bluestem also had a significantly lower soil water potential than western wheatgrass. In the lower soil level blue grama again had a significantly lower soil water potential than little bluestem and western wheatgrass; the latter two having virtually the same soil water potential. If the species were ranked according to their tolerance of low soil water potential, they would be ranked with blue grama first, followed by little bluestem and western wheatgrass respectively.
In correlating leaf growth and soil water potential, all the data points described the curve form \( Y = a + b \log X \). As the soil water potential decreased the leaf growth rate decreased rapidly at first and then decreased at a slower rate at the low moisture potentials. Leaf growth which occurs in the range of 0 to \(-1\) bar were not used because of the great variability of the leaf growth response in this range. This was found to be true in a similar study (Eddleman and Nimlos 1972). No single part of the soil mass controlled the leaf growth, but rather a combined affect of the entire soil profile.

The comparison of the soil water potential in both soil levels with the leaf growth can be used to interpret the possible cause and effect relationship between soil water potential and leaf growth.

**Blue grama**—(Figure 7a). The more gentle slope of the line representing the correlation in the upper soil level shows that a unit decrease in the water potential of the upper level has a lesser affect on leaf growth than did a similar decrease in the water potential of the lower levels. The almost identical Y intercepts of each of the regression lines suggests that there was no reduction in leaf growth until there was soil water potential less than \(-1\) bar in both soil levels.

**Western wheatgrass**—(Figure 7b). The response of leaf growth to soil water potential was unique in this species in that the response of leaf growth to water potential was almost identical in both soil levels. This species extracted moisture very evenly from all parts of the soil mass.

**Little bluestem**—(Figure 7c). Unlike the other two species, leaf growth was reduced before the lower level experienced any decrease in
Figure 7. Correlation between average daily leaf elongation and daily soil water potential in both soil levels in the pots (Growth Chamber study).
the soil water potential below -1 bar. The growth rate was reduced from approximately 18 mm per day to approximately 10 mm per day before there was a significant reduction in the water potential in the lower soil level. The slope of the regression line representing the correlation in the upper level has a greater pitch, suggesting that decreases of soil water potential in the upper level resulted in greater decreases in leaf growth than did similar decreases of soil water potential in the lower level.

**Root Box Study**

Roberts and Struckmeyer (1946) emphasized the importance of the interrelationship between roots and shoots. What affects one consequently will have an affect on the other. The root boxes provide a means by which both the roots and shoots can be observed and measured while soil water potential is decreased.

The leaf growth is a result of the genetic base of the species and the environmental factors acting upon the plant. Little bluestem was found to produce far less foliage than either western wheatgrass or blue grama under treatment of control conditions (Figure 8). Blue grama and western wheatgrass reached a maximum stem elongation of about 34 mm per day, while little bluestem reached a maximum of only 20 mm per day.

In the comparison of leaf growth in the control and treatment boxes, blue grama exhibited the greatest difference (Figure 72). The treatment plants produced less growth starting with the second day of the experiment. The pattern of growth of the control plants reached a peak and declined toward the end of the study period. This decline is due in part to the maturation of the plant material. This was the only species which
Figure 8. Average daily leaf elongation of the control (-----) and treatment (-----) plants from the beginning through the end of growth for treatment plants (Root Box Study).
matured and produced seed stalks (Figure 9). For the first half of the study period, the leaf growth of the control and treatment plants were relatively constant. As the soil water potential decreased in the treatment boxes the leaf growth declined rapidly and the leaf growth in the control boxes continued toward a peak late in the study period. The pattern for western wheatgrass is nearly the same as blue grama, except no decline occurred in the control plants near the end of the study period.

The leaf growth of the control plants of little bluestem was quite static throughout the study period. The leaf growth of the treatment nearly coincided with that of the control for the first one-third of the study. The photographs of the treatment and control plants help to describe the magnitude of their differences (Figure 9).

The time interval involved in the drying varied more in this study than in the growth chamber study. Blue grama required an average of 32 days to exhaust its moisture supply. Western wheatgrass required an average of 26 days and little bluestem required an average of 21 days.

Although the roots that appear against the glass of the root boxes do not represent the entire root population, there is every indication that the visible roots are a relatively consistent representation of the total root mass. In all species the total root growth reached an early peak in growth and tapered off later in the study period (Figure 10). In the control plants secondary peaks of growth appeared. In the treatment boxes of little bluestem and blue grama, root production was higher than in the control boxes for the first half of the study period. This difference may be due to one of two factors or a combination of both:
Figure 9. Sample plants showing leaf production in the root boxes at the end of the study period.
Figure 10. Daily root growth of control (- - - -) and treatment (-----) plants from the beginning to cessation of growth of the treatment plants. (Root Box Study)
a) the drying soil of the treatment boxes may stimulate a higher than normal root elongation, or b) the wet soil of the control boxes may reduce root growth because of the reduced aeration or excess moisture supply. Unlike the other two species, western wheatgrass produced almost identical amounts of roots in the treatment and control plants during the early part of the study period.

The differences in root growth between species was even more variable than the leaf growth. Western wheatgrass produced a maximum of about 1,000 mm per day as compared with 700 mm per day for blue grama and 300 mm per day for little bluestem.

Leaf and root production was not terminated at the same time. Root growth of blue grama continued for an average of 2 days after the cessation of leaf growth. Little bluestem produced roots for an average of 4 days after leaf growth cessation. Only in western wheatgrass did root growth stop before leaf growth, averaging one day earlier. The photographs of total root production (Figure 11) aid in describing the differences between the control and treatment plants but as can be seen, the differences in root production is not as pronounced as that of leaf production.

The reason for the production of lateral roots cannot be interpreted from this study, but the variability in the lateral root production is interesting to note. In blue grama both the treatment and control plants developed lateral roots in all of the soil levels. In western wheatgrass lateral roots growth was distributed evenly through the soil of the control plants but found, in any abundance, only in the lower levels of the treatment plants. In little bluestem lateral growth was
Figure 11. Sample plants showing total root production at the end of the study period.
found throughout the soil profile of the treatment plants and only found in the upper levels of the control plants.

The breakdown of the root growth into the four soil levels serves as a better indication of the rooting patterns of the three species (Figures 12, 13, 14). The pattern of peak growth can be followed as it moves downward through each soil level. In blue grama and little bluestem it can be seen that the growth in the treatment plants is greater than for the control plants in all levels during the early part of the study period. In all cases the roots quite elongating in the first level the earliest followed by the second, third, and fourth level respectively. Because the soil usually dried out in the upper level first, then moved downward through each successively lower level, the cessation of root growth followed the same basic pattern.

The daily growth rate of the leaves and roots show quite well the general patterns of growth under favorable conditions and during a drought cycle, but the factor which causes the death of the aerial plant tissue must be considered, i.e., soil water potential. The drying pattern of the larger soil mass of the root boxes proved to be quite different than in the restricted soil system of the pots. Only one problem was encountered in the measurement of soil water potential. The upper soil level of blue grama dried out beyond the measurement capabilities of the thermocouple psychrometers used. The highest measurable value was about -80 bars. Although the thermocouple were incapable of measuring the low water potential reached in the upper level of blue grama, a projection of the trend suggest that the upper soil level of blue grama reached a water potential lower than -100 bars. The increases
Figure 12. Daily root growth of blue grama in each of four soil levels for control (striped bars) and treatment (plain bars) from the beginning through root growth termination in all levels.
Figure 13. Daily root growth of western wheatgrass in each of the four soil levels for control (striped bars) and treatment (plain bars) from the beginning through root growth termination in all levels.
Figure 14. Daily root growth of little bluestem in each of the four soil levels for control (striped bars) and treatment (plain bars) from the beginning through root growth termination in all levels.
in the water potential in the four levels provide a distinct pattern of moisture extraction for each species (Figure 15). The end points of each line indicate the water potential in that level when both root and shoot growth terminated.

The soil water potential at the time of leaf growth cessation can be used to rank the three species in their ability to extract moisture from a dry soil and still be able to produce foliage (Table 3).

**Table 3. Soil water potential (in bars) when leaf growth terminated.**

<table>
<thead>
<tr>
<th>Level</th>
<th>a) blue grama</th>
<th>b) western wheatgrass</th>
<th>c) little bluestem</th>
</tr>
</thead>
<tbody>
<tr>
<td>Level 1</td>
<td>-80.0 bc1/ 2342/</td>
<td>-30.0 ac 234</td>
<td>-24.3 ab 234</td>
</tr>
<tr>
<td>Level 2</td>
<td>-26.0 c 134</td>
<td>-23.6 c 134</td>
<td>-9.8 ab 134</td>
</tr>
<tr>
<td>Level 3</td>
<td>-11.0 bc 12</td>
<td>-16.8 ac 134</td>
<td>-3.4 ab 12</td>
</tr>
<tr>
<td>Level 4</td>
<td>-8.4 bc 12</td>
<td>-15.3 ac 12</td>
<td>-3.0 ab 12</td>
</tr>
</tbody>
</table>

1/ Letters indicate the species which are significantly different at the .05% level using a t-test of the replication means.

2/ Numbers indicate the levels within each species which are significantly different at the .05% level using a t-test of the replication means.

Blue grama tolerated the lowest water potential in the first soil level followed by western wheatgrass and then little bluestem. In the second level blue grama and western wheatgrass were similar but significantly lower than little bluestem. In the third and fourth levels western wheatgrass developed the lowest soil water potential followed by blue grama and little bluestem respectively. As seen in the preceding table western wheatgrass extracted soil moisture more evenly from the entire soil profile than did the other two species. Within the soil
Figure 15. Soil water potential developed at each soil level in days from the beginning of the experiment. End point of lines indicate soil water potential when all leaf and root growth terminated.
system of blue grama the water potential of the first level was signifi-
cantly lower than the other levels, followed by the water potential of
the second level and then the water potential of the third and fourth
levels, which were similar. The same differences are found in each of
the species, but the magnitude of the differences vary considerably.

There has been questions concerning the ability of roots to pene-
trate dry soils. The design of this study made it possible to detect
the soil water potential at which roots no longer elongate (Table 4).

<table>
<thead>
<tr>
<th>Table 4. Soil water potential (in bars) when root growth terminated.</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) blue grama</td>
</tr>
<tr>
<td>Level 1</td>
</tr>
<tr>
<td>Level 2</td>
</tr>
<tr>
<td>Level 3</td>
</tr>
<tr>
<td>Level 4</td>
</tr>
</tbody>
</table>

¹/ Letters indicate the species which are significantly different at
the .05% level using a t-test of the replication means.

²/ Numbers indicate the levels within each species which are signifi-
cantly different at the .05% level using a t-test of the replication
means.

The roots of blue grama were able to sustain growth at the lowest
level of water potential. The soil water potential in the soil of blue
grama were significantly lower than the soil water potential in the
first level of western wheatgrass and significantly lower than the soil
water potentials in the first, third and fourth levels of little blue-
stem. The soil water potential of western wheatgrass was significantly
lower than that of little bluestem in the lower two soil levels. In the
soil of blue grama all levels developed similar water potentials at the time of root growth termination. In western wheatgrass the roots which survived the lowest soil water potential were in the lower three levels. In the soil of little bluestem the roots which tolerated the lowest water potential were in the upper two levels. In western wheatgrass the water potentials of the lower three levels were similar and significantly lower than the water potential of the upper soil level. In little bluestem the water potential of the upper two levels was significantly lower than the water potential of the lower two levels.

The correlation of soil water potential with root growth in each of the four levels (Figures 16, 17, 18) was fairly good. There is a question as to the reduction of root growth being solely the result of decreasing soil water potential. As shown in Figure 10, root growth peaks early and drops off considerably. Thus some of the decrease in the root growth may be due to the general rooting patterns of these species.

The correlation of soil water potential in all soil levels with leaf growth cannot be used to pinpoint the region of the soil which is the most critical in controlling leaf growth, but the slope and position of the regression lines can be used to support some hypotheses.

**Blue grama**—(Figure 19a) Decline in the soil water potential of the upper soil level corresponds with very small reductions in leaf growth suggesting that the upper level contributed little to the reduction of leaf growth. The leaf growth was reduced to nearly 50% of the original before the soil water potential dropped below -1 bar in the third level. The low $r^2$ value for the regression line representing the third level was due mostly to the extreme variability in the leaf growth when the
Figure 16. Correlation between soil water potential and total daily root growth in each of the four soil levels for blue grama.

**Blue Grama**

**LEVEL 1**

\[ Y = 32.4410 - 25.0280 \log X \quad R^2 = 0.6339 \]

**LEVEL 2**

\[ Y = 78.7942 - 71.5662 \log X \quad R^2 = 0.6334 \]

**LEVEL 3**

\[ Y = 54.6301 - 3.7206X \quad R^2 = 0.2218 \]

**LEVEL 4**

\[ Y = 76.3601 - 5.2377X \quad R^2 = 0.6752 \]
Figure 17. Correlation between soil water potential and total daily root growth in each of the four soil levels for western wheatgrass.
Figure 18. Correlation between soil water potential and total daily root growth in each of the four soil levels for little bluestem.
Figure 19. Correlation between average daily leaf elongation and soil water potential in all four of the soil levels for all three species.
third level water potential was in the range of -1 to -3 bars.

**Western wheatgrass**—(Figure 19b) As illustrated in the graph all the regression lines originate at points where leaf growth was at its maximum (15-20 mm/day). This indicates that water potential decreased below -1 bar in all the levels before any reduction in leaf growth occurred. The upward sloping of the first two lines indicate that leaf growth was still increasing as the soil water potential decreased to as low as -5 bars in the upper two soil levels. The main source of moisture at this time had to be from lower levels. The similarity of the slopes of all four lines suggests that the water potential of all four levels contributed rather evenly to the reduction of leaf growth.

**Little bluestem**—(Figure 19c) The presence of decreasing water potential was apparent before there was any decrease in water potential of the second level. Leaf growth was reduced to one-third that of the original growth before the water potential decreased below -1 bar in the third soil level. The water potentials reached in the lower two levels, before leaf growth terminated, was still very high as compared to the upper soil levels. Soil moisture should still have been available to the plant. The possibility of a shut-off system or induced dormancy may be involved in the termination of growth. Bennett and Doss (1960) found that when plants wilted there was usually available moisture in the lower soil levels, but the plant was incapable of efficiently extracting this moisture.

Most of the $r^2$ values of the correlation between leaf growth and soil moisture potential were relatively good. Much of the variation was due to the difference between replications of each species in spite of
the attempt to use clonal material to reduce genetic variation.

Foth (1962) found that in corn, early development was characterized by rapid growth of both roots and shoots. The weight of the shoots increased more rapidly and caused an increase in the top-root ratio. This period was followed by one in which extensive brace root development caused a decline in the top-root ratio. The same root-shoot relationship can be interpreted from a comparison of the per cent of the total root growth with the per cent of average cumulative stem growth. The percentages were calculated by accumulative addition of growth each day and determining the per cent of the final total. Increases in root growth and leaf growth can be interpreted from this comparison in both the treatment (Table 5) and the control (Table 6) plants.

In the treatment plants of blue grama and western wheatgrass a greater per cent of the roots are produced in the earlier part of the study period. Blue grama produced half of its roots before one-third of the leaves were produced. Little bluestem produced leaves at a slightly faster rate than roots. When 90% of the leaves were produced only 75% of the roots were produced. The growth pattern of the leaves and roots were quite different in the control plants (Table 6).

The control plants of little bluestem produced roots and shoots at about the same rate all the way through the growth period. Western wheatgrass produced roots much quicker than leaves. When 75% of the roots were produced only a little more than half of the leaves were produced. Therefore a great portion of the total leaf production occurred in a short time near the end of the growth period when daily leaf production was at its highest. Leaf production of blue grama
started out slow but near the end of the growth period was greater than root production.

### Table 5. A comparison of % total root growth with % cumulative average stem growth for the treatment plants.

<table>
<thead>
<tr>
<th>Root Growth</th>
<th>25% Leaf Growth (blue grama)</th>
<th>27% Leaf Growth (western wheatgrass)</th>
<th>34% Leaf Growth (little bluestem)</th>
</tr>
</thead>
<tbody>
<tr>
<td>25% root growth</td>
<td>10% leaf growth (blue grama)</td>
<td>27% leaf growth (western wheatgrass)</td>
<td>34% leaf growth (little bluestem)</td>
</tr>
<tr>
<td>50% root growth</td>
<td>28% leaf growth (blue grama)</td>
<td>40% leaf growth (western wheatgrass)</td>
<td>60% leaf growth (little bluestem)</td>
</tr>
<tr>
<td>75% root growth</td>
<td>62% leaf growth (blue grama)</td>
<td>60% leaf growth (western wheatgrass)</td>
<td>92% leaf growth (little bluestem)</td>
</tr>
</tbody>
</table>

### Table 6. A comparison of % total root growth with % of cumulative average stem growth of the control plants.

<table>
<thead>
<tr>
<th>Root Growth</th>
<th>25% Leaf Growth (blue grama)</th>
<th>18% Leaf Growth (western wheatgrass)</th>
<th>18% Leaf Growth (little bluestem)</th>
</tr>
</thead>
<tbody>
<tr>
<td>25% root growth</td>
<td>7% leaf growth (blue grama)</td>
<td>18% leaf growth (western wheatgrass)</td>
<td>18% leaf growth (little bluestem)</td>
</tr>
<tr>
<td>50% root growth</td>
<td>34% leaf growth (blue grama)</td>
<td>30% leaf growth (western wheatgrass)</td>
<td>40% leaf growth (little bluestem)</td>
</tr>
<tr>
<td>75% root growth</td>
<td>81% leaf growth (blue grama)</td>
<td>57% leaf growth (western wheatgrass)</td>
<td>75% leaf growth (little bluestem)</td>
</tr>
</tbody>
</table>
Chapter 5

SUMMARY AND CONCLUSION

The three species involved in this study were deliberately chosen because of the habitats they occupy. Blue grama is usually the dominant species on dry harsh sites. Little bluestem appears to thrive on wet north-facing slopes. Western wheatgrass is found on a variety of sites ranging from zeric to mesic and appears to be an intermediate species in its moisture requirements.

One characteristic of each of these species which must be considered is their season of growth and maturation. Blue grama and little bluestem have both been termed "warm season" grasses while western wheatgrass is a "cool season" grass. The growth of blue grama begins during the last week of April or first week in May. Culms appear during June or favorable years. Flowering takes place by the end of August and seed shatter occurs during September. Little bluestem has very similar phenology, but may be as much as a week later than blue grama. The growth of western wheatgrass begins early in April. Spikes appear during the first half of June and flowering occurs about two weeks later. Seeds mature during July and are shed during August. Western wheatgrass in most cases, has produced its foliage and set seed before the low moisture conditions of the summer months begin.

Because the growth chamber study and the root box study had only soil water potential and leaf growth in common, these are the only criterion on which a comparison can be based upon. Although the pots had only two soil levels and the root boxes had four levels, there is a pattern of
similarity between the two soil systems. (Tables 2 & 3) The soil water potential in the top two levels of the root boxes of blue grama were comparable to the two levels of the pots. The same is true for little bluestem. In western wheatgrass the two levels in the pots were comparable to the two lower soil levels of the root boxes. This comparison may be an indication that the soil water potential of the upper two soil levels of blue grama and little bluestem are important in contributing to the reduction of leaf growth. In both cases the lower levels still contain moisture which should be available to the plant. The lower two levels of western wheatgrass are apparently the limiting factors in leaf growth reduction because of the similarity with the soil levels in the pot which were the controlling factors in that study.

Using three species of clover, two species of alfalfa, orchard grass, tall fescue, and Reed canary grass, Bennett and Doss (1960) found that as the soil water potential decreased near the soil surface, more moisture was extracted at successively lower depths. However, the rate of moisture extraction decreased with increasing soil depth. Plants usually wilted before very much available moisture was depleted at the lower levels. In studies of corn (Davis 1940, Russel et al. 1940) and pears (Aldrich et al. 1935) it was found that there was selective absorption of water near the plant, indicating a moisture absorption gradient in the root system. In the light of these studies the failure of blue grama and little bluestem to extract all the available moisture from the soil levels can be understood. Western wheatgrass extracted moisture with the same basic pattern except it did not extract moisture from the upper levels as extensively as expected but rather extracted moisture
from the lower levels more extensively than the other two species.

In a study by Bennett and Doss (1960) the actual rooting was investigated using three soil moisture levels. With the exception of Reed canary grass, the greatest rooting depths were found at the lowest soil moisture levels and the shallowest rooting was in the highest soil moisture levels. Most of the roots were concentrated in the upper six inches of soil. In my study blue grama and little bluestem produced more roots (in terms of visible elongation) in the drier soil than in the favorable soil conditions of the control soil. Western wheatgrass was an exception. This species produced relatively similar amounts of root in both the wet and dry soils, just as Reed canary grass did in the previously mentioned study.

Weaver (1941) determined the water usage (number of pounds of water lost from the plants and soil together divided by the number of pounds of dry matter produced) of seven prairie grasses. The water usage of western wheatgrass was found to be 3,229 pounds/pound of dry matter, as compared to 1,075 pounds for blue grama and 1,017 pounds for little bluestem. This means that western wheatgrass used up to three times more water than the other two species in the production of its foliage. In my study neither leaf production nor water usage was measured by actual weight, therefore efficiency could not be determined. However, just the nature of the rapid removal of moisture from all levels of the soil system and the failure to dry the upper levels extensively, suggests the inefficiency of western wheatgrass. Both blue grama and little bluestem reduced leaf production as soon as the soil water potential began to decline. This cut back in leaf production was probably an adjustment
by the species to conserve moisture. I feel that the results found by Weaver (1941) do describe the moisture efficiency of these species well.

In ranking these species according to their tolerance to decreasing soil water potential, blue grama would have to be ranked first followed by western wheatgrass and little bluestem respectively.

The soil water potentials which were reached in the four soil levels before leaf growth cessation occurred were: blue grama ( -80, -26.0, -11.0, -8.4 bars respectively), western wheatgrass (-30.0, -23.6, -16.8, -15.3 bars respectively), and little bluestem (-24.3, -9.8, -3.4, -3.0 bars respectively).

The soil water potentials which were reached in each of the four soil levels before root cessation occurred in that particular level were: blue grama (-16.6, -14.7, -10.7, -14.5 bars respectively) western wheatgrass (-7.8, -10.6, -9.6, -13.8 bars respectively) and little bluestem (-9.2, -11.1, -5.0, -5.0 bars respectively).

Weaver (1954), Dix (1958) and Morris (1964) felt that blue grama, western wheatgrass, and little bluestem were located along a moisture gradient with blue grama at the drier end of the gradient, western wheatgrass was in the range of dry to intermediate, and little bluestem on the wetter end of the gradient. The findings of my study support this theory. Blue grama and western wheatgrass tolerated low soil moisture potentials while the water potentials endured by little bluestem were relatively higher.


