WATER RELATIONS OF SOME GRASSES WITH PHREATOPHYTIC PROPERTIES

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure Page

CHAPTER I

GENERAL INTRODUCTION

The role of water in the ecology and physiology of plants has long been widely acknowledged. It has been an accepted fact that there can be no plant existence without a basic required level of available water in the soil. Although water deficiency is no problem to areas of the world which are gifted with a plentiful water supply by rivers or regular and sufficient rainfall, the problem is well manifested when excessive loss of this water is caused by evaporation or improper consumption by plants. The problem is aggravated when water shortage is accompanied by prevailing high evaporative power of the air such as is characteristic of arid and semi-arid areas of the world.

In the arid and semi-arid regions of the Western States phreatophytes waste more than 25 million acre-feet of water into the atmosphere annually (Robinson, 1952). Phreatophytes, plants that depend upon ground water for their water supply, have a direct root connection with the water table. During the growing season they satisfy their needs for water by drawing on the ground-water reservoir, somewhat like a pump. In fact each plant may be considered as a miniature pumping unit, operating at varying rates according to its needs. The withdrawals of water deplete the ground-water reservoir with the result that ground-water levels are lowered.

Phreatophytes grow largely, although not entirely, along the banks of streams, in their flood plains, and in the delta areas at the heads of reservoirs. Here the ground-water reservoir has a direct connection with the water in the stream, such that stream flow reflects the effect of the draft on the ground-water reservoir. As the draft increases, there is a reduction in the stream flow; as a consequence, in the water that is readily available for man's use.

The economic value of most phreatophytes is low, and the water used by them is largely wasted. Water used in this way is known as nonbeneficial consumptive use and more recently has been referred to as consumptive waste (Robinson, 1958). Ground water that is consumptively wasted by phreatophytes is available for salvage. Salvage, as applied to the phreatophyte problem, is converting consumptive waste to beneficial consumptive use.

In order to plan a salvage project, information is needed concerning the magnitude of consumptive waste. This involves a knowledge of the species growing in the project area and the climatic and hydrologic conditions. A comparative investigation including plants which are known not to have phreatophytic capabilities would be vital in decision making as to the future of the project area. According to Robinson (1964a), three general methods are followed in salvage trials: (1) taking the plants away from the water (eradication, of which there are several ways), (2) taking the water away from the plants (here again, there are several ways), and (3) substituting plants of higher beneficial use in the project area.

Among plants indicated in the literature as phreatophytes are salt cedar (*Tamarix gallica* L., *Tamarix pentandra* Pall.) and inland saltgrass (*Distichlis stricta* (Torr.) Rydb.). Greasewood, Rabbitbrush, willow, and wildrose are common in the Humboldt River Valley, Nevada (Robinson, 1964b). Mesquites, cottonwood, and baccharis are quite abundant in the Caballa Reservoir area, New Mexico. Alkali sacaton and mesquite together with saltgrass and salt cedar grow in the bottom land of the Acme-Artisia reach of the Pecos River, New Mexico, and consume tens of thousands of acre-feet of water each year (Mower et al. 1964). Saltgrass, pickleweed and greasewood are the major phreatophytes responsible for immense losses of water from the lowlands around the southern end of Great Salt Lake and on the flood plains of the Jordan River in Utah. Removal of Tamarisk growing in central Arizona was found to reduce fluctuations in the water table (Gary, 1962).

In the state of Oklahoma, the problem of phreatophytes is well manifested in the Great Salt Plains area. A recent study of the vegetation in this area (Baalman, 1965) revealed that saltgrass and salt cedar are abundant especially in areas subject to frequent flooding. Based on Baalman's survey, I chose to study the water relations of these two plants and to investigate their ecological amplitude in the area. In the preliminary survey of the distribution of these two plants, it was found that not only water but also soil salinity is a major factor in their distribution. It was decided that a study of their water relations in the laboratory must cover the salinity effect too. Laboratory studies of the problems of water stress and salt tolerance of the two plants necessitated the elimination of salt cedar from this investigation since it required the establishment of a permanent water table in the soil. Therefore, studying the effect of water stress on the water relations of this plant is irrelevant to the problem. Consequently, it was decided that information gathered from the field concerning the ecological habitats of the plant are adequate to the purpose of this study. However, the study on saltgrass was completed in the laboratory and two more plants were included in the investigations, for the purpose of comparison. Alkali sacaton (Sporobolus airoides (Torr.) Torr.) was chosen for laboratory investigation on the basis that it has been known to have phreatophytic properties (Mower et al. 1964) as well as salt tolerance to some extent. Blue grama (Bouteloua gracilis (H.B.K.) Lag. ex. Steud.) was also chosen as it is known to be an abundant grassland plant with moderate water requirements and was common to the general area.

The present study is directed toward obtaining information on: (1) the ecological characteristics of the habitats in which saltgrass and salt cedar are found, particularly the moisture conditions and chemical properties of the soil, (2) the amounts of transpirational water loss from the two plants in their natural habitats as compared to water loss from the soil by direct evaporation and to study the variations in the relative turgidity (that is, relative water content) of their leaves in the different sites studied, (3) the effect of increasing moisture stress or salinity in the soil on transpiration of saltgrass, alkali sacaton and blue grama under controlled conditions in the laboratory, and (4) possible mechanisms that enable the plant to stand different degrees of stress by salinity or moisture deficiency such as the osmotic pressure and turgidity changes in the leaf.

CHAPTER II

REVIEW OF THE LITERATURE

Work on phreatophytes, particularly in western United States has been reviewed by Robinson (1959, 1964). The literature is fairly rich in works concerning survey of phreatophyte vegetation cover as well as methods of control and elimination of undesired phreatophytes. Few pieces of work have dealt with the water relations of such plants and these have been concerned mainly with evapotranspirational losses from areas covered by more than one species under field conditions. A lack of information concerning the limits of tolerance to desiccation or salinity is indicated by the few pieces of work reported.

Studies on salt cedar conducted by Horton (1959, 1964), Horton et al. (1960, 1962), Decker (1961) and Gary (1963) indicate that its seeds germinate very readily when moist, but the seedlings require continuously wet soil for several weeks in order to survive. Cuttings of tamarisk sprout vigorously when partially covered with warm, moist soil but lose sprouting ability very quickly when dried for short periods of time. The studies also indicate that _Tamarix_ _pentandra_ Pall. is the abundant species in the southwest and that T. _gallica_ L. has become agressively naturalized only in the humid areas around the Gulf of Mexico. The ecology of salt cedar (_Tamarix_ _gallica_ L.) was studied by Tomanek and Ziegler (1960) in Kansas, Texas and New Mexico. Their studies revealed that its seeds germinate optimally in solutions that had a pH of between 5.6 to 7.0 and were weakly saline. Seedling survival and growth was greatest in sodium chloride solutions of 0 to 3,000 ppm. The seedlings withstood concentrations of up to 4,000 ppm, but at 5,000 ppm all seedlings died.

In a study by Mower et al. (1964) along the Pecos River in New Mexico, salt cedar could replace phreatophyte grasses such as saltgrass and sacaton by a rate of 21.1 per cent over a two-year period (1956 - 1958). This was accompanied by an increase of water consumption by 21.8 per cent over the same period (from an average amount of 66,500 acre-feet to 81,000 acre-feet). From this, they inferred that if salt cedar growth continued to be uncontrolled, the rate of evapotranspiration might have risen to 170,000 acre-feet annually in a few years. Tomanek and Ziegler (1960) estimated transpiration from salt cedar to be 3.80 grams per square decimeter leaf area per day. This is compared to 5.80 grams for cottonwood and 8.23 grams for willow. However, they indicated that the total water output is greater from salt cedar due to the greater leaf area. Decker et al. (1962) indicated that tamarisk uses more water than a bermudagrass sod. Van Hylckama (1962) observed a variation in transpiration of salt cedar planted in pots with an artificially maintained water table. The variation was dependent on the depth of the water table.

Apparently there has not been as much attention given to saltgrass as that given to salt cedar. Unpublished work by V. I. Myers (cited by Robinson 1964a) indicated that saltgrass yield was nearly ten times greater and the evapotranspiration nearly four times greater in one location than that occurring at another location having almost identical climatic conditions during the growing season. He implied from this that consumptive use of phreatophytes should be related to stand densities or yields. Dylla et al. (1962, 1964) studied collectively the evapotranspiration of native meadowgrasses growing in areas of shallow water tables of the Humboldt River basin in Nevada. Grasses--predominantly sedges, bluestem, and saltgrass--were grown in evapotranspirameters (polyvinyl plastic-lined tanks) 10 feet square and 7 feet deep. A water table was maintained by controlling the water supply of the tanks. Their findings showed that grasses subjected to a simulated wet meadow (fluctuated higher water-table) conditions produced less hay per unit of water used than when grown under a constant shallow (4 feet) water table.

A vigorous controversy has continued for a number of years on whether the "available soil moisture" is equally available for plant growth between field capacity and the wilting point or whether this water is taken up with such increasing difficulty that plant growth functions are retarded before the wilting point is reached. Arguments on this issue are widely discussed by Veihmeyer et al. (1950), Richards et al. (1952), Slatyer (1957), Jamison (1956), Veihmeyer (1956) and Vaadia et al. (1961). Most of the work done was mainly relating soil moisture to plant growth and metabolism, usually excluding measured and unmeasured plant or climatic factors that are necessarily involved in studies of water relations. Evidences existing tend to relate the reduction in growth to water deficits within plant tissues. The degree to which growth is checked depends on the relative deficits developed within the plant. Vaadia et al. (1961) pointed out that:

> . . .internal water deficits are not necessarily related

> directly to soil moisture. Rather they depend at any given time on the balance between water lost from the shoot and that absorbed by roots. Whenever loss exceeds absorption, some deficit develops. If water deficits developed in plant tissues within diurnal cycles are not restored during the night, then progressive decrease in growth should be observed.

Under natural conditions, where there is a plentiful water supply in the soil, it is now generally accepted that the transpiration rate is determined by the weather. Several formulae have been determined to estimate the transpiration rate from standard meteorological data assuming an adequate supply of water (Penman 1948; Slatyer and McIlroy 1961). As the soil dries out, the actual transpiration will, at some stage, fall below the potential rate (Closs, 1958). It is that "stage" referred to by Closs that was subject to investigations by many workers.

Some investigators believe that transpiration is maintained at the potential rate until the soil moisture tension reaches the wilting point value and thereafter transpiration is very small, (Hendrickson et al., 1945; Thornthwaite, 1954; Veihmeyer et al., 1955 and Penman, 1956). Others point out an early decrease of transpiration with soil moisture dropping immediately below field capacity (Schopmeyer, 1939; Slatyer, 1956; Rutter and Sands, 1958; Watanabe, 1959; Bahrani and Taylor, 1961; Denmead and Shaw, 1962; Bennett and Doss, 1963; and Brouwer, 1963). Closs (1958) showed that the stage at which transpiration decrease starts depends on the prevailing air humidity. For mustard plants, an early decline of transpiration rate begins at low moisture tension especially when atmospheric humidity is low (31 per cent R. H.). The decline started later (that is, at higher soil moisture tension) in atmospheres of higher humidities (60 per cent

R. H.). Denmead and Shaw (1962) indicated that the stage of soil moisture at which transpiration began to decline depended on the prevailing light intensity and humidity.

According to Gardner (1965) "it appears quite adequate, for many purposes, to assume a linear relationship between transpiration rate and soil-water content." Transpiration rates of wheat, barley and oat seedlings were studied by Salim and Todd (1965). They found that the relationship between transpiration rate and soil moisture content was a linear function, at least within the range from near the wilting point to 50 per cent available soil moisture. The stage at which sharp drop in transpiration rate started was different among the genera. This difference was apparent under greenhouse conditions and in the growth chamber. However, many workers reported that with decreasing soil water potential, the transpiration rate decreases in a curvilinear fashion with a rapid initial decline followed by a more gradual reduction in rate (Bahrani et al., 1961; Denmead et al., 1962; Jarvis et al., 1963 and Perrier et al., 1961). Increase in soil moisture tension causes a progressive increase in leaf water deficit and decrease in stomatal opening (Rutter and Sands, 1958; Brouwer, 1963). However, Watanabe (1959) reported that the water content of leaves of Acacia mollisima is not affected by soil moisture until it was reduced nearly to the permanent wilting point.

Iljin (1957) pointed out that "the role of osmotic pressure in the life of plants is not fully understood. The osmotic values found cannot save the vegetative organs from desiccation under conditions encountered in nature." A relative humidity of 92 to 70 per cent consitutes the limit at which vacuoles of the cells, in isolated leaf tissues of most species of plants, lose all of their water, and the cells readily perish in such conditions. According to Iljin, species of the temperate zone have an average osmotic pressure of 10 atm., and those in the Arizona desert have an average osmotic value of 70 atm. An osmotic value as high as 50 atm. is rarely encountered; the maximum observed was that of Atriplex confertifolia grown on alkaline soil, which was 202.5 atmospheres. Wheat leaves attain a higher osmotic pressure in a dry atmosphere even when the soil moisture was kept favorable for best growth. Iljin (1916) showed that when environmental conditions are varied, a given species is able to change its osmotic value to a large extent. However, he later (1957) pointed out that:

> . . .the osmotic value is not an indispensable criterion of resistance to drought among all species of plants. It is only one of the means of defense against drought that is inherent in each species to a different degree. The increase of osmotic pressure can favor a better provision of soil water to the roots and also to the movement of water within the plants to parts where it is deficient.

From the physiological point of view, some of the earliest work concerned the influence of water deficits on carbohydrates. The accelerated conversion of starch to sugars during water deficits has been observed by many workers (Eaton et al., 1948; Wadleigh et al., 1945; and Woodhams et al., 1954). However, the rapid starch reduction is not compensated for by corresponding increases in sugars (Woodhams et al., 1954). This suggests that respiration rates might have increased because of water deficits. Several investigators have found this to be the case for some species (Petrie et al., 1938; Schneider et al., 1941; and Upchurch, 1955).

Some studies have been carried out on the relationship between water deficits and protein metabolism. Mothes (1956) showed a relationship between water content and proteolysis. Petri et al. (1938) observed that the net formation of proteins from amino acids decreased as moisture deficits increased.

At the present time, there is a general agreement in the literature that the exposure of plants to substrate solutions or soil containing soluble salts, or other osmotically active solutes in excess of those required for normal growth usually result in decreased water absorption, disturbed nutrient uptake and metabolism, and a reduced plant growth (Slatyer, 1961). A saline soil has been defined by Hayward and Bernstein (1958) as "that which contains sufficient soluble salts to affect adversely the growth of plants."

The U. S. Salinity Laboratory at Riverside, California, early started a series of experiments to determine the tolerance of crop plants to the salts commonly found in irrigation waters and soils, and to what extent climate modified these effects (Magistad et al., 1943). Hayward and Long (1941) gave reports on the ranges of salinity in sand cultures which plants can tolerate under normal climatic conditions. The U. S. Salinity Laboratory suggested a lower limit of salinity of soils to be "solutions of electrical conductivity (EC_e) of four to two mmhos, which is equivalent to about two grams of sodium chloride per litre at field capacity" (Hayward and Bernstein, 1958). Regardless of the salt used, Hayward et al. (1946) pointed out that increase in concentrations of salts resulted in decreased vegetative growth or in death when the osmotic pressure of the substrate solution exceeded five atmospheres.

The effects of osmotically active soluble salts of the soil on plants are referred to generally as of two main types (Magistad, 1945;

Hayward et al., 1949; Bernstein et al., 1958): (1) partly due to direct osmotic effects of increased soil or substrate water stress, and (2) partly to specific toxic effects of individual ions. Hayward and Spurr (1944a; 1944b) pointed out that the presence of excessive concentrations of soil salts may affect plant growth through the osmotic pressure of the soil saline solutes, thus, tending to restrict the uptake of water by the roots. Lagerwerff and Eagle (1961) gave a detailed discussion about specific-, non-specific-, osmotic- and physiological effects and their mechanisms of influence on plant activities.

The influence of the direct osmotic effects is the subject of my study. Evidence of such osmotic effects on plant growth is quite clear from two types of experimentation. First are those studies on the influence of increasing total soil moisture stress on plant growth, in which the effect has been the same regardless of whether the total stress consisted mainly of soil moisture tension or of an osmotic potential in the solution (Wadleigh and Ayers, 1945; Wadleigh et al., 1946; and Ayers et al., 1943). The concept of "physiological dryness" of saline soils is a reflection of this view. Second are those experiments conducted with iso-osmotic concentrations of different mineral salts and organic solutes in which the degree of inhibition of growth has effectively been the same regardless of the solutes employed (Eaton, 1941; Long, 1943; Gauch et al., 1944; Hayward et al., 1944a, 1944b; and Magistad et al., 1943).

As pointed out by Bernstein and Hayward (1958), some plants are much more sensitive to salinity during germination and early seedling growth than during later stages of development. The same authors suggested that the entry of ions and solutes not required for normal growth is restricted by the endodermis. This indicated that appreciable quantities of solutes enter the plant (Slatyer, 1962). However, Walter (1955) considers that if the substrate osmotic potential is balanced by the intake of solutes, then there can be no increase in water stress or osmotic inhibition of growth. In an attempt to reconcile these two divergent views, it has recently been suggested that a vapor gap may occur at the root-soil interface (Bonner, 1958 and Philip, 1958). It was proposed that in wet soils, with root-soil liquid phase continuity, Walter's view would be valid but; as the soil dried, soil and root shrinkage would lead to the development of a vapor gap which could provide an ideal differentially permeable membrane so that the opposing idea would apply. However, this interpretation is unsatisfactory since, not only are the effects apparent in culture solutions, but rates of vapor transport across such a gap appear to be inadequate to supply the amounts of water required by the plant (Bernstein et al., 1958).

CHAPTER III

THE ECOLOGICAL AMPLITUDE OF SALTGRASS AND SALT CEDAR IN THE GREAT SALT PLAINS OF OKLAHOMA

Introduction

The Great Salt Plains of Oklahoma are located in Alfalfa County. They constitute a wide variety of ecological habitats ranging from areas with alluvial soils rich in fine matter as a result of flooding to immense salt flats of remarkably permanent salt crust that prevents any plant growth. Included also are areas of coarse to fine sand with a water table ranging from less than 12 inches to more than 4 feet deep. Such a variety of habitat reflects naturally a wide variation in vegetation cover. This has been recently studied by Baalman (1965). Saltgrass exists in a variety of these habitats with a slight degree of variation in relative vigor. Salt cedar is more or less limited in distribution to sandy areas with an obvious tendency to invade areas where the water table is near the ground surface.

Materials and Methods

Selection of Study Sites

Prior to any decision regarding the sites chosen for study and sampling, the area was thoroughly surveyed. The work of Baalman (1965) was very often referred to in order to check on the distribution and any information concerning the ecological habitat of both saltgrass and salt cedar in the area. Selection of the study areas was based mainly on a representation of various types of growth of saltgrass and only the seedling stage of salt cedar up to about one year old.

Nine sites were chosen for the study. Some of the sites contained only one of the plants; others contained mixed stands. A description of sites and their locations is as follows:

Site 1: A rather elevated alluvial stretch of land on the bank of one of the tributaries of the Salt Fork of the Arkansas River. The soil is greyish and fine textured and the water table was deep (more than two feet). Only vigorously growing saltgrass exists together with some other grasses and forbs.

Site 2: Gently sloping area lying about ten feet below the south-southwest margin of the area of site 1 and extending about 300 yards. The soil is a sandy loam, coarse to fine sand on the surface changing to reddish sandy loam below the upper six inches. This site has only saltgrass almost in a pure population and it has good growth. The water table was one foot deep.

Site 3: This is an extension of about 600 yards on the same slope of site 2 to the south and west. Soil texture is coarse to fine sand all over the depth of the profile. Both saltgrass in good growth and salt cedar seedlings are found in this area. The water table is ten inches deep.

Site 4: At the bottom of the slope and extends for about 600 yards to the southeast of site 3. Salinity seems to be high at this site as indicated by a slight salt crust on the surface. Water table was ten inches deep. Soil is fine textured, brownish and consists of silt and loam. The only plant here is salt cedar.

As described above, sites 1 to 4 represent a vegetation intergrading from high density cover of saltgrass at the top of a slope through a mixture of both saltgrass and salt cedar to a pure population of salt cedar at the bottom of the slope.

Site 5: Located about six miles south of site 4 at the southeast quarter of section 26 (map designation of the Wildlife Refuge Office in the plains area is T26 N R 10 W). Soil is brownish and fine textured all the way down to two feet deep. Water table was deep (below two feet). This site is dominated by saltgrass only in dense and vigorous growth.

Site 6: Located about one-half mile west of site 5 in the southwest quarter of section 26 (map designation of the Wildlife Refuge Office). Soil is sandy, coarse to fine throughout the profile. Water table was more than one foot deep. Salt cedar occurs in good growth as seedlings and older plants. Saltgrass is also present. A thin salt crust is apparent on the margins of this site, indicating possible high soil salinity.

Site 7: Located one and one-half mile south of site 4. Soil is sandy. Salt cedar is dominant. Water table was 18 inches deep.

Site 8: About 300 yards east of site 7. Soil is sandy loam. Saltgrass is dominant. Water table was 12 inches deep.

Site 9: Located about one-half mile east of site 1 on the north side of State Highway 11. Soil is fine clay (alluvial) and seems to have been deposited by flooding of this low level area. Saltgrass is dominant. Water table was deep (at more than two feet).

It is important to mention that saltgrass exhibits vigorous and dense growth in fine clay soil (sites 1 and 9), where it forms either dense mats of considerable cover or isolated patches of pure stands of the grass. In sandy soil it forms more or less evenly scattered tufts.

Soil Moisture Content in the Study Sites

Root penetration of saltgrass was found not to exceed six to eight inches. The rhizome extends only about one to two inches below the soil surface. Roots of salt cedar seedlings which are one year old or younger were found to be about five to eight inches deep. Thus, it was decided that a ten-inch profile sampling would be fairly representative of the root zone. Also, sampling below that was practically impossible in some sites because of the shallow water table. This profile was arbitrarily divided on sampling into three horizons: (1) zero to two inches deep, (2) two to five inches deep, and (3) five to ten inches deep. For moisture content determinations, appropriate size samples were secured in air-tight aluminum cans. These were immediately weighed in the field and kept to be oven-dried on getting back to the laboratory. The moisture content was expressed on soil dry weight basis.

From the same depths of the profile in each site, sampling was secured for chemical analysis of the soil. The samples were air dried at room temperature and then mixed well and ground to pass a two mm. screen to be ready for analysis.

Sampling Plants for Osmotic Pressure Determination

Just a few hours before returning to the laboratory, plant samples from the sites studied were secured. The plants were collected with their roots intact in soil cores and the cores were tightly wrapped in polyethylene bags to reduce their moisture loss by evaporation. In the laboratory, the stems were cut and quickly freeze-dried in a lyophilizer for about 24 hours. The samples were then kept in a desiccating chamber in the cold room until the time of extraction. Before extraction, each sample was finely ground to pass a No. 60 mesh of a Wiley Mill.

Measurement of Relative Turgidity and Water Content of Leaves

The method of Weatherly (1950) was used to determine the relative turgidity in punched leaf discs. A further examination of the relative turgidity technique was carried out by Weatherly and Barrs (1962) to correct mainly for continued uptake of water by leaf discs after attaining full turgidity due to growth. It was found that keeping the floating discs at low temperature (3°C) and under low light intensity reduced this error. However, the uptake in response to initial water deficit was slowed by cold. This could be overcome by keeping the discs floating on water for a longer time under this low temperature and in the dark.

This precaution was taken earlier by Slatyer (1957) on testing the relative turgidity of the arid zone species Acacia aneura F. Muell., in which he kept the floating discs in a refrigerator at 5 to 7°C to secure more or less a constant temperature. The precaution was based originally on a study by Werner (1954) in which he found that the amount of uptake was directly influenced by fluctuations in water temperature.

The above results suggest that floating previously weighed fresh leaf cuts on distilled water in the refrigerator is the best procedure for determining relative turgidity. Saturation was attained in 24 to 36 hours. Leaf cuts were blotted dry, weighed immediately, oven dried at 85°C for 24 hours and re-weighed.

The relative turgidity of leaves was expressed as a percentage and evaluated according to the equation:

$$\text{R.T.\%} = \frac{\text{Water Content of the Fresh Leaf Tissue}}{\text{Water Content of the Same Tissue at Full Saturation}} \times 100$$

The water content of leaves was expressed on a fresh weight basis and calculated as follows:

$$\text{W.C.\%} = \frac{\text{Leaf Tissue Fresh Weight - Leaf Tissue Oven-dry Weight}}{\text{Leaf Tissue Fresh Weight}} \times 100$$

Determination of the Osmotic Pressure of Plants

Plant samples which had been previously freeze-dried and finely ground were extracted with boiling water. Two hundred to four hundred milligrams of the ground plant material were extracted in 15 ml of de-ionized water in a plastic centrifuge tube for 15 minutes on a boiling water bath. The tube was swirled every five minutes to secure good mixing of the contents. After 15 minutes, the sample was centrifuged. The extraction process and centrifugation of the sample was repeated three more times using 15 ml of de-ionized water each time and the extracts were pooled in a 100 ml Erlenmeyer flask. The total extract was concentrated on a rotary evaporator to 10 ml for subsequent determination of the osmotic pressure. Duplicate samples from each site were prepared.

The osmotic pressure of the extracts was determined by the cryoscopic method described by Walter (1949). The osmotic pressure was calculated from the equation given by Lewis (1908) which relates the osmotic pressure of the extract to the depression in the freezing point below that of distilled water as follows:

$$\text{O.P. in atmospheres} = 12.06\Delta - 0.021\Delta^2$$

where Δ is the lowering of the freezing point.

Very often the samples were super-cooled during the determination, which might have lead to change in the value of the freezing point of the extract. A correction for super-cooling was given by Harris and Gortner (1914) which is:

$$\Delta = \Delta_1 - 0.0125\, U \Delta_1$$

where Δ and Δ_1 are the true and observed lowering of freezing point respectively and U is the number of degrees of super-cooling.

The osmotic pressure of the sample extract was calculated back to the actual osmotic pressure in the leaf by taking into consideration the water content in the leaves of the fresh sample. An example of such calculation is as follows: For an extract of 0.2 g plant dry material in 10 ml water the dilution now is 50 fold. If the water content of the fresh leaves was 40 per cent and the osmotic pressure of the extract was 2.0 atmospheres, therefore,

$$\text{Actual O.P.} = 2.0 \times 50 \times \frac{60}{40} = 150 \text{ atmospheres}$$

Measurement of Evaporation and Transpiration in the Field

Careful study of the sites revealed that site 3 was the most suitable to make a fairly representative evaluation of the daily amount of water loss from the soil and from both plants considered. The choice was based on the fact that the two plants exist together in a fairly good growth condition at this site. In addition, the soil is representative of the predominant sandy areas in the plains. The shallow water table suggested that measurement from this site was likely to represent maximal water expenditure to be met with in the area.

To maintain a minimal disturbance of the soil, cores containing either the saltgrass, salt cedar, or bare soil were secured from the site. The size of the core was made to fit cans four inches in diameter and eight inches deep. To have a fairly good representation of the soil conditions in the site, four cores were secured for each plant and for bare soil. The choice was based on selecting from patches of vegetation of homogeneous and representative distribution. Measurement of water loss was secured by periodically weighing the cans containing the soil cores. Loss in weight was taken as either evaporation from potted soil or evapotranspiration from planted cans. At times between weighings, the cans were kept imbedded in the soil in such a way that the soil surface inside the can was at the same level as the ground surface outside. In this way, the soil inside the can was kept at approximately the same temperature of the soil outside. Measurement was made at 1:00 p.m. each day for five days in June, 1966, and for three days in July of the same year. The three day measurement in July was found adequate to represent water expenditure during that month since the weighing procedure followed indicated that the moisture content of the soil declined rapidly after the third day in June. Therefore, a more extended measurement period might not be representative of natural conditions. The amount of water transpired by each plant could be calculated by subtracting the average amount of water evaporated by canned soil from that lost by evapotranspiration from the planted cans on a daily basis.

Soil Analysis

The purpose of the soil analysis was to define the ecological characteristics of the sites inhabited by both plants. It also serves as an indication of the amplitude of variations in the soils and their effect on the distribution of both plants. Those soil characteristics which mainly reflect the fertility and salinity of the sites were studied. Therefore, the analysis was concerned with the following soil constituents: total nitrogen, organic carbon, water soluble salts (total, carbonates, bicarbonates, chlorides), pH, sulphates, phosphates, and the major exchangeable cations (sodium, potassium, calcium and magnesium). Some sulphates and phosphates are water soluble. However, acid sodium acetate solution (pH5) extracts more sulphates and phosphates than extracted in distilled water.

Total nitrogen was determined by the Kjeldahl method and organic carbon by the Walkley and Black rapid titration method described by Piper (1950). Total soluble salts were measured in a 5 to 1 water extract (50 g soil to 250 ml water) by the conductivity meter, carbonates and bicarbonates by titration with 0.01 N hydrochloric acid and chlorides by the volumetric method of precipitation as silver chloride on titration with 0.01 N silver nitrate and using one per cent potassium chromate solution as indicator.

Since any stress in the field is actually the result of both moisture and salinity stresses together, the conductivity data of the samples were converted to osmotic values according to the equation given by Black et al. (1965),

$$\text{O.P. atm.} = 0.36 \times E_c \text{ mmhos/cm.}$$

where E_c is the electrical conductivity. The osmotic pressure of the sample was then converted to actual osmotic values under field conditions by utilizing the moisture content data of the soils for the month of July.

The total soluble salts in the extract was also given as follows:

$$\text{Salt concentration (mg/l)} = 640 \times E_c \text{ (mmhos/cm)}$$

This equation is valid under the assumptions that a mixture of ionized salts exist in the extract and that the ions are predominantly monovalent. The pH was measured in the water extract using a pH meter. Exchangeable cations were extracted in neutral normal ammonium acetate and the individual cations determined on the flame photometer. Procedures for all these, as well as methods of extraction are described in Black et al. (1965). Sulphates and phosphates were extracted in a buffered sodium acetate solution (pH5). Sulphate was determined turbidimetrically by precipitation with barium chloride. The barium sulphate formed remain suspended in solution and could be determined on the colorimeter. Phosphates were determined colorimetrically by treating the extract with one per cent ammonium molybdate and one per cent ammonium metavanadate solutions. The molybdi-vanadio-phosphate complex formed is stable and could be measured colorimetrically.

Johnson (1948) described in detail the extraction and determination procedures for both sulphate and phosphate.

RESULTS

The sites inhabited by saltgrass actually belong to two different major soil types: (1) those having fine textured more or less dark colored soil, i.e. sites 1, 5, 8, and 9, and (2) those representing fine to coarse sandy soil, i.e. sites 2, 3, and 6. This difference is reflected by the plants as their root systems are distinctly different in the two types of soil. In fine textured soil, the roots are fibrous and profusely branching; whereas in sandy soil, roots are coarse and tend to penetrate deeper into the soil (Figures 1 and 2). However, this is not the case with salt cedar. All sites occupied by the latter (sites 3, 4, 6 and 7) are generally sandy soils and the root system does not show obvious variation (Figure 3). Soil fertility seems to correlate with soil texture (Table 1). Sites inhabited by saltgrass are fertile, as indicated by organic carbon and nitrogen content, especially in fine textured soils such as in sites 5, 8, and 9. This is especially apparent in sites 1 and 9 where the salinity is low. Salt cedar sites seem to have no fertility problem. It is quite obvious that fertility decreases with depth in nearly all sites surveyed.

Based on the soil types occupied by both saltgrass and salt cedar, the moisture present (Figure 4) should have been in the upper level of the available range. As expected, fine soil held more moisture than sandy soil. Only site 1 had a low moisture level in July (about 8 per cent along the depth of the profile) due to the elevated nature of

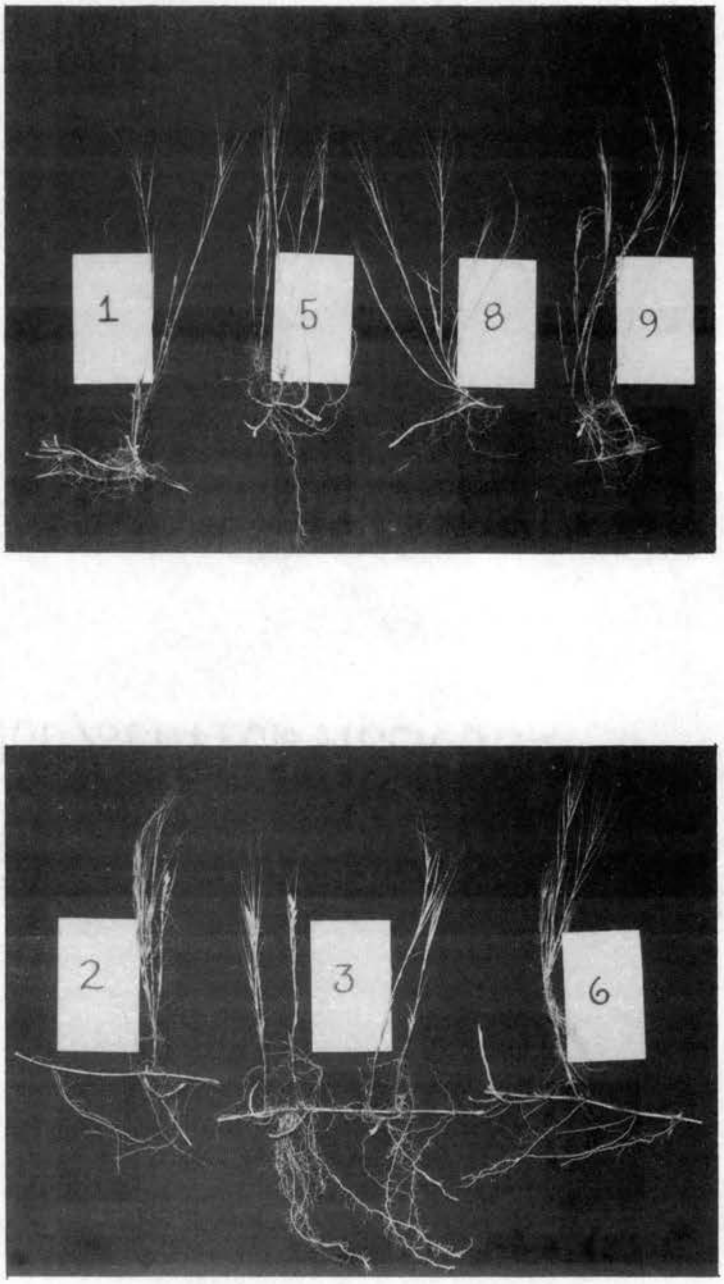

Figure 1. Saltgrass From Sites Having Fine Soil (above) and Sandy Soil (below) Showing Difference in Branching and Extension of the Root System. Numericals Refer to Sites Sampled

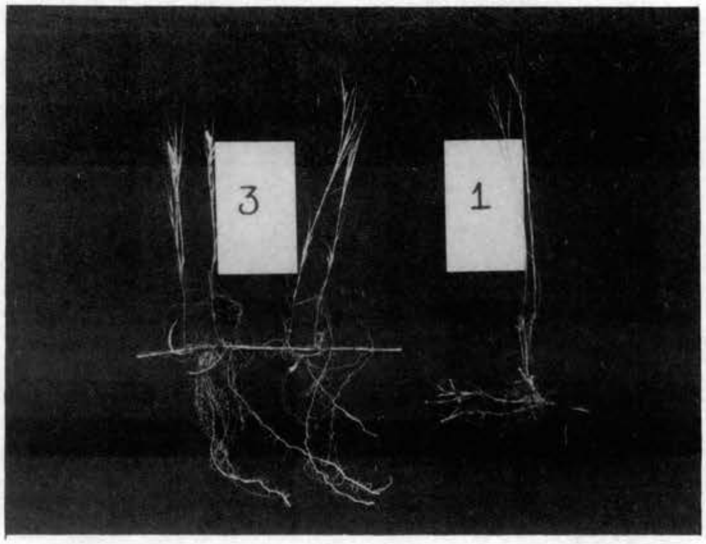

Figure 2. Fibrous and Profusely Branching Root System of Saltgrass from a Typical Fine Soil (Site 1) Compared to a Thick and Deeper Penetrating Root from a Typical Sandy Soil (Site 3)

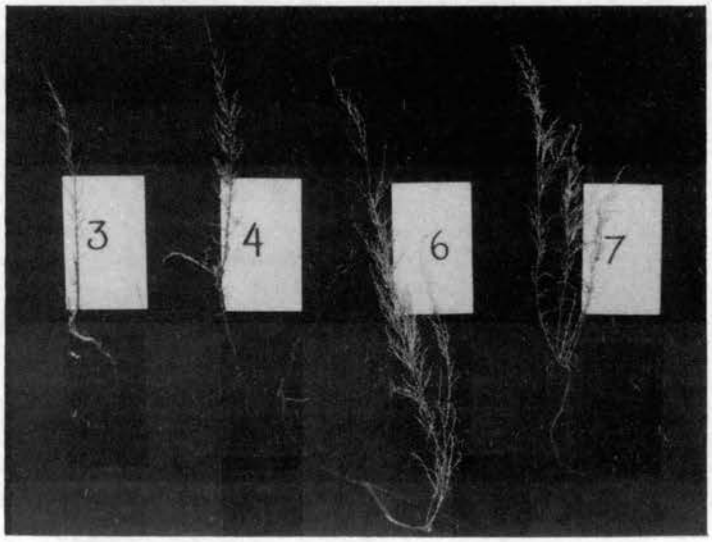

Figure 3. Salt Cedar Seedlings from the Different Sites Studied Showing No Difference in the Root System

TABLE I

AVERAGE VALUES OF PER CENT ORGANIC CARBON AND PPM TOTAL NITROGEN IN THE SOILS OF SITES STUDIED

Site No.	Plant	Depth (Inch)	Per Cent Organic Carbon	Total Nitrogen (ppm)
		0- 2	0.559	413
1	Saltgrass	2- 5	0.798	275
		5-10	0.399	73
		0- 2	0	287
2	Saltgrass	2- 5	0.160	184
		5-10	0.144	80
		0- 2	0.204	160
3	Saltgrass	2- 5	0.136	105
	Salt Cedar	5-10	0.072	43
		0- 2	0.315	233
4	Salt Cedar	2- 5	0.064	254
		5-10	0.048	134
		0- 2	3.192	1170
5	Saltgrass	2- 5	1.037	340
		5-10	0.584	162
		0- 2	0.407	343
6	Saltgrass	2- 5	0.738	475
	Salt Cedar	5-10	0.507	400
		0- 2	0.487	366
7	Salt Cedar	2- 5	0.219	260
		5-10	0.200	234
		0- 2	1.277	781
8	Saltgrass	2- 5	0.399	299
		5-10	0.315	218
		0- 2	2.394	957
9	Saltgrass	2- 5	2.594	849
		5-10	1.546	352

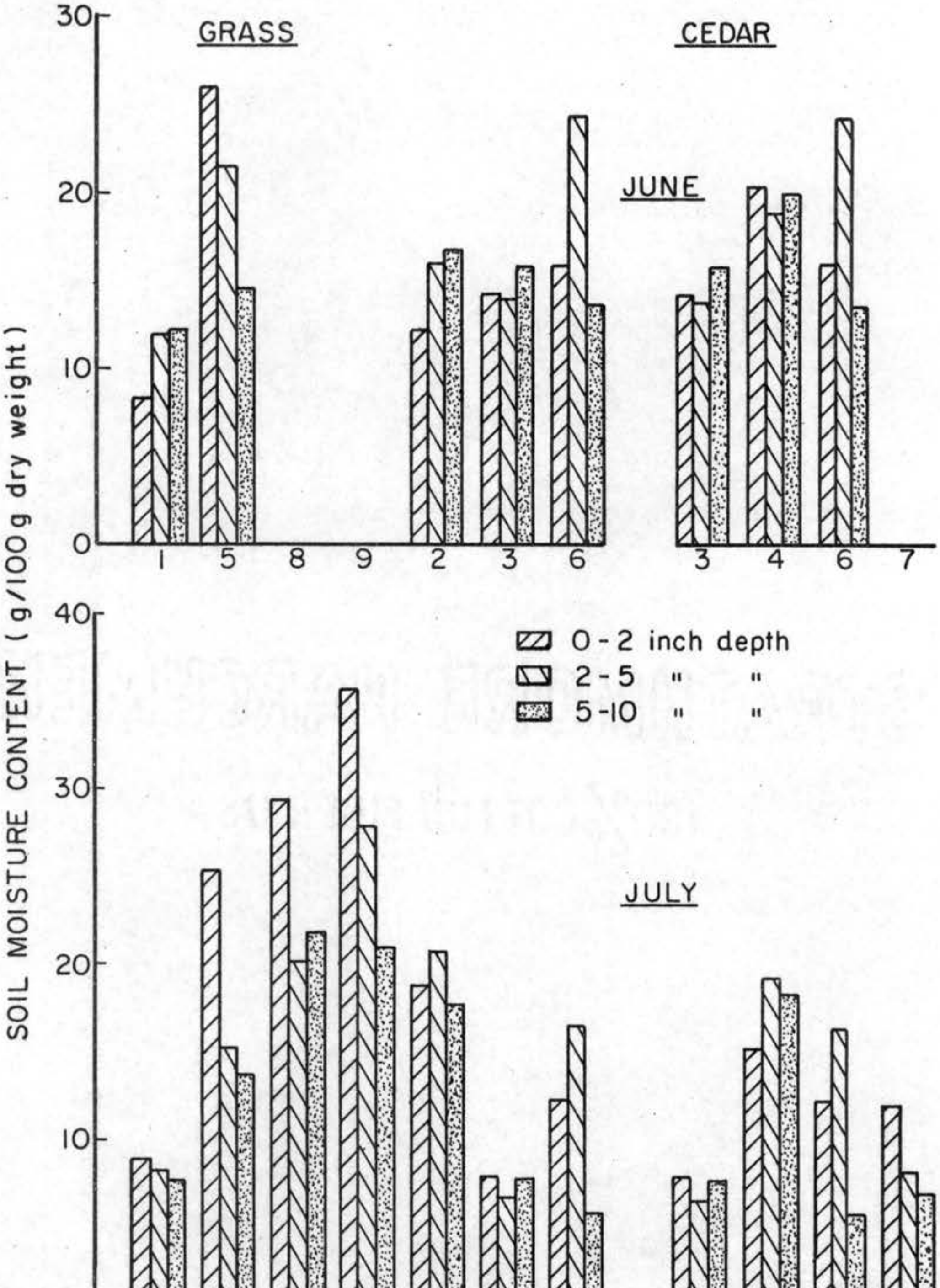

Figure 4. Soil Moisture Content of Sites Inhabited by Saltgrass and Salt Cedar in June (above) and July (below)

the site. The moisture distribution in the soil profile of each site was more or less homogenous; that is, there was little variation in moisture content with varying depth of the profile. This may reflect homogeneity of the soil alongside each profile rather than heterogeneity in particle size distribution at different depths. Also, the moisture status in July was not much different in magnitude and pattern of distribution from that in June, although it showed slightly lower values especially in the sites of salt cedar.

The soil reaction was generally nearly neutral in sites of both plants, running around 7.5 (Appendix B). However, sites 2 and 5 both inhabited by saltgrass show slight alkalinity. The pH in both is 8.0.

Soil salinity in saltgrass areas show a wide variation from as low as about 300 ppm in the subsoil of site 3 to as high as about 25,000 ppm on the surface soil of site 8 (Figure 5). Salt cedar characteristically occupied saline soils (Figure 6) except in site 3. It is quite obvious that salinity in most sites was largely due to chlorides and to a less extent, bicarbonates. Carbonates were practically absent except for traces in site 5, inhabited by saltgrass. In some sites, for example sites 4 to 8, total soluble salts did not correspond to the sum of carbonates, bicarbonates and chlorides. This may indicate the presence of other water soluble ions such as sulphates. However, sulphates and phosphates were determined in the buffered sodium acetate extract since this gives almost total extractable amounts of both ions.

Calculated osmotic values of the soil solutions in sites inhabited by saltgrass and salt cedar are shown in Figures 7 and 8 respectively.

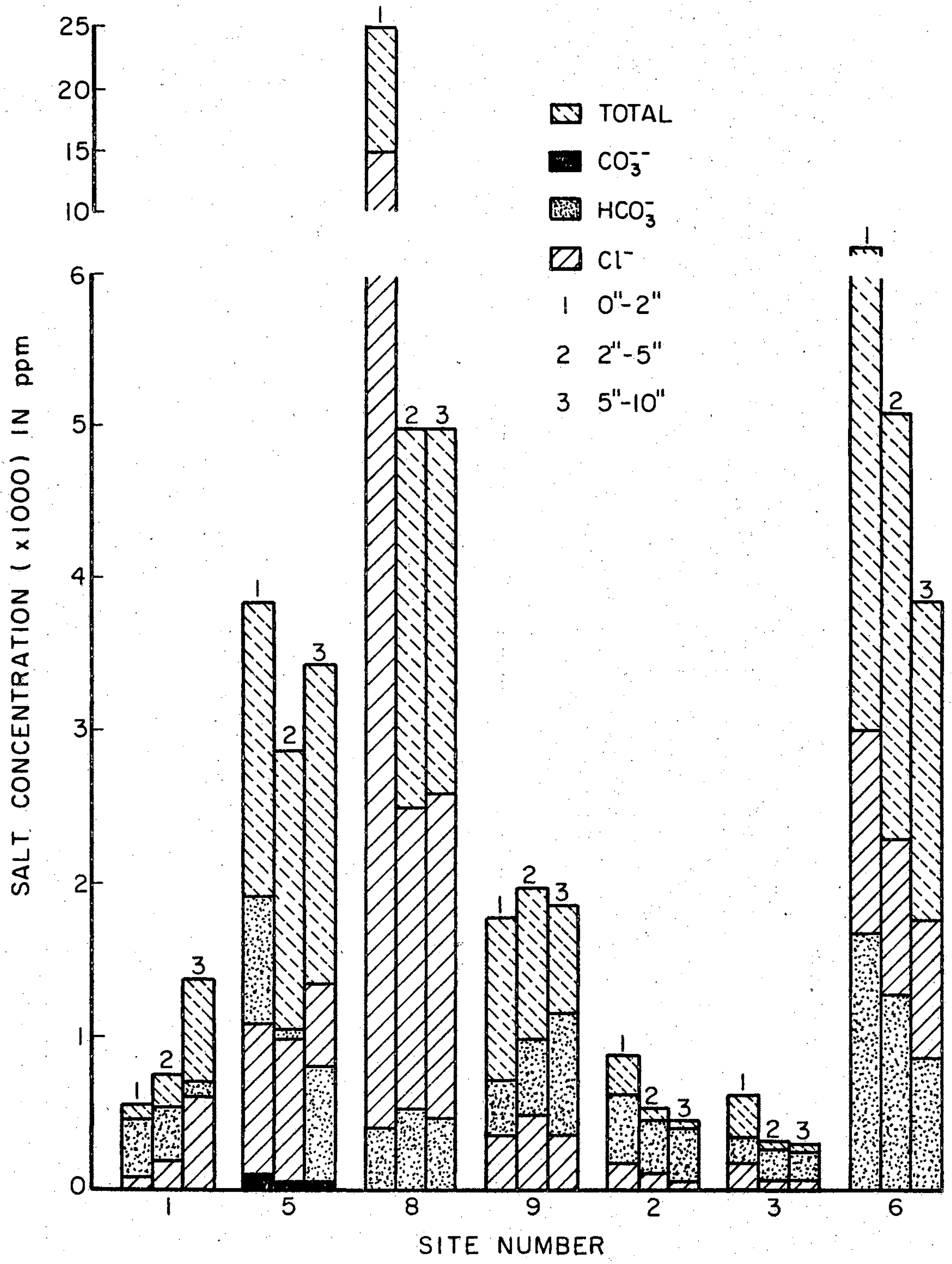

Figure 5. Values of Soluble Salts Measured in the Soils of Sites Inhabited by Saltgrass

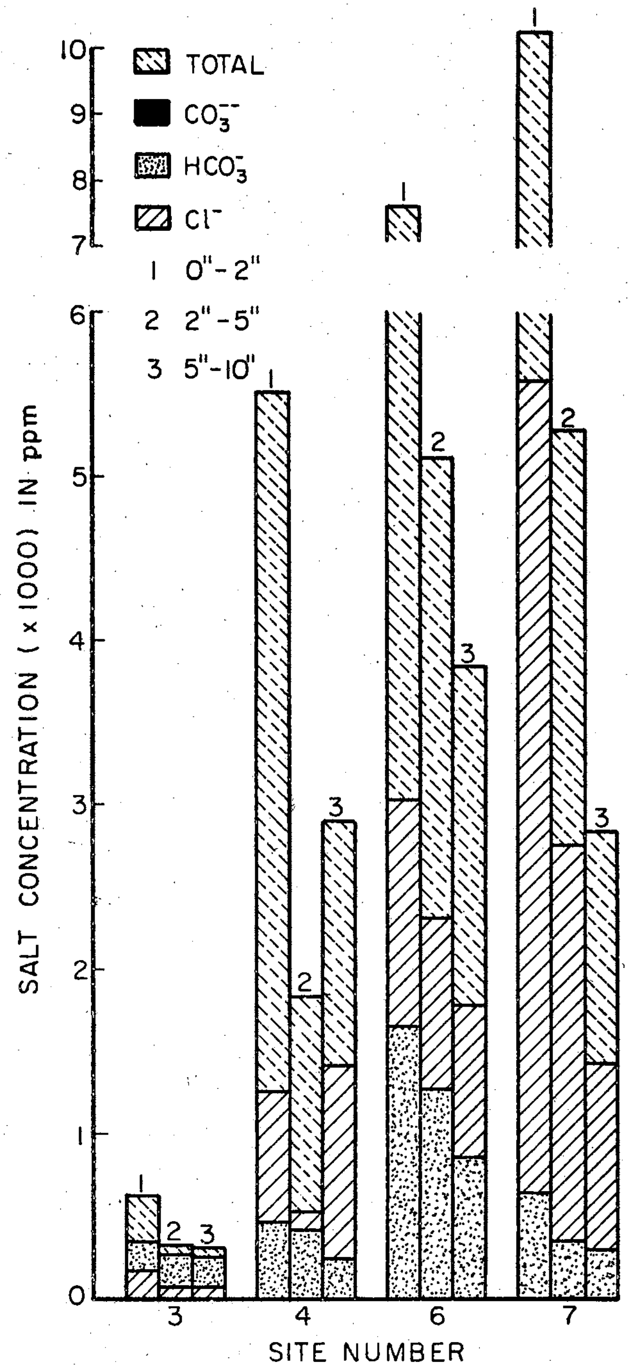

Figure 6. Values of Soluble Salts Measured in the Soils of Sites Inhabited by Salt Cedar

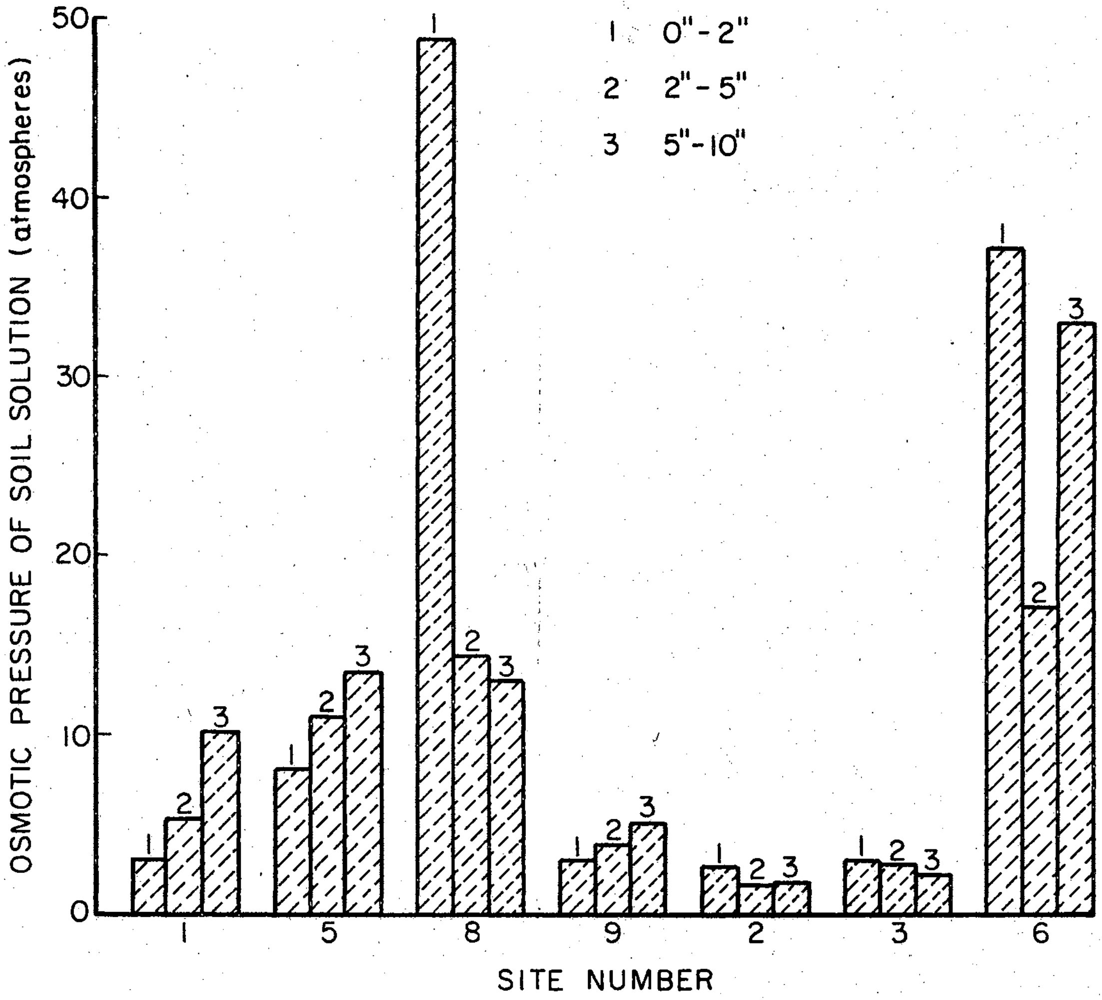

Figure 7. Values of Calculated Osmotic Pressure of Soil Solution in the Sites Inhabited by Saltgrass (Calculations Based on the Moisture Content Measurements for July)

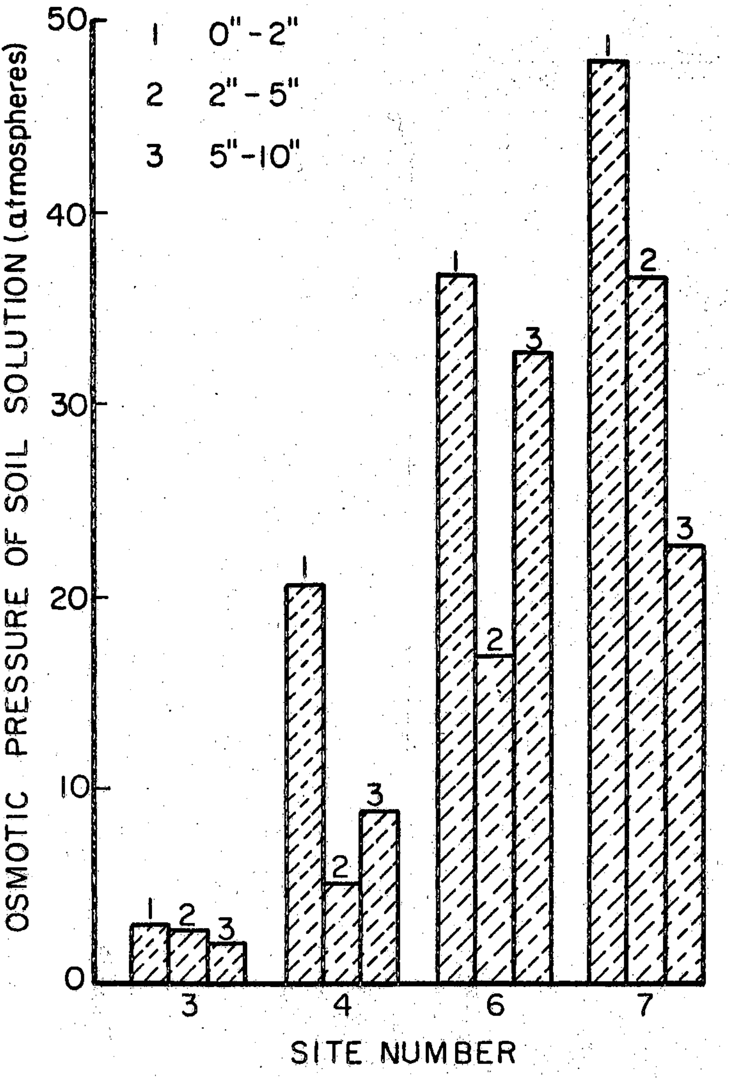

Figure 8. Values of Calculated Osmotic Pressure of Soil Solution in the Sites Inhabited by Salt Cedar (Calculations Based on the Moisture Content Measurements for July)

Osmotic concentrations in sites of saltgrass indicate the same pattern of salinity distribution. Low values were observed in sites 2, 3, and 9; intermediate values in sites 1, 5, and 8; and the highest osmotic concentration occurred in site 6 and the surface soil of site 8. With salt cedar (Figure 8) the same pattern of salinity distribution was reflected in the osmotic values. The osmotic concentration was high in all except site 3.

Distribution of sulphate and phosphate in areas of saltgrass and salt cedar are shown in Table II. Sulphates, similar to soluble salts, vary greatly in areas of saltgrass, whereas they were more or less uniform in all sites of salt cedar. With saltgrass, the amounts varied from nil in sites 1 and 2 to relatively moderate in sites 3, 6, and 8 (in the subsoil) and highest in sites 5 and 9. The same pattern of variation was also observed in phosphate distribution in areas covered by the grass. The phosphate concentration varied from a low of 8 to 10 ppm in sites 2, 3, and 8 to about 30 to 60 ppm or higher in sites 5 and 6. Saltgrass sites apparently had low amounts of phosphate (about 4 to 16 ppm) in all but site 6, where higher concentrations of about 24 to 55 ppm were measured.

At saltgrass sites, exchangeable cations varied widely (Figure 9). Calcium showed the least variation whereas sodium and potassium varied the most. It can be generally observed that in sites where potassium concentration was low, sodium had a high concentration and vice versa. Magnesium showed moderate variation between a low amount of under 100 ppm in site 3 to a high of over 1,000 ppm in site 9. Somewhat similar patterns of variation were found in areas of salt cedar (Figure 10). However, potassium concentration varied less from one site to the other

TABLE II

AVERAGE VALUES OF SULPHATES AND PHOSPHATES MEASURED IN THE SOILS OF SITES STUDIED

Site No.	Plant	Depth (Inch)	SO_4^{--} (ppm)	PO_4^{---} (ppm)
1	Saltgrass	0- 2	0	26
		2- 5	0	25
		5-10	0	15
2	Saltgrass	0- 2	0	19
		2- 5	0	9
		5-10	0	9
3	Saltgrass Salt Cedar	0- 2	84	17
		2- 5	66	10
		5-10	78	11
4	Salt Cedar	0- 2	310	18
		2- 5	49	10
		5-10	66	9
5	Saltgrass	0- 2	137	50
		2- 5	121	69
		5-10	15	38
6	Saltgrass Salt Cedar	0- 2	43	55
		2- 5	55	30
		5-10	33	24
7	Salt Cedar	0- 2	53	17
		2- 5	25	8
		5-10	22	3
8	Saltgrass	0- 2	151	12
		2- 5	24	8
		5-10	23	7
9	Saltgrass	0- 2	61	27
		2- 5	148	27
		5-10	141	21

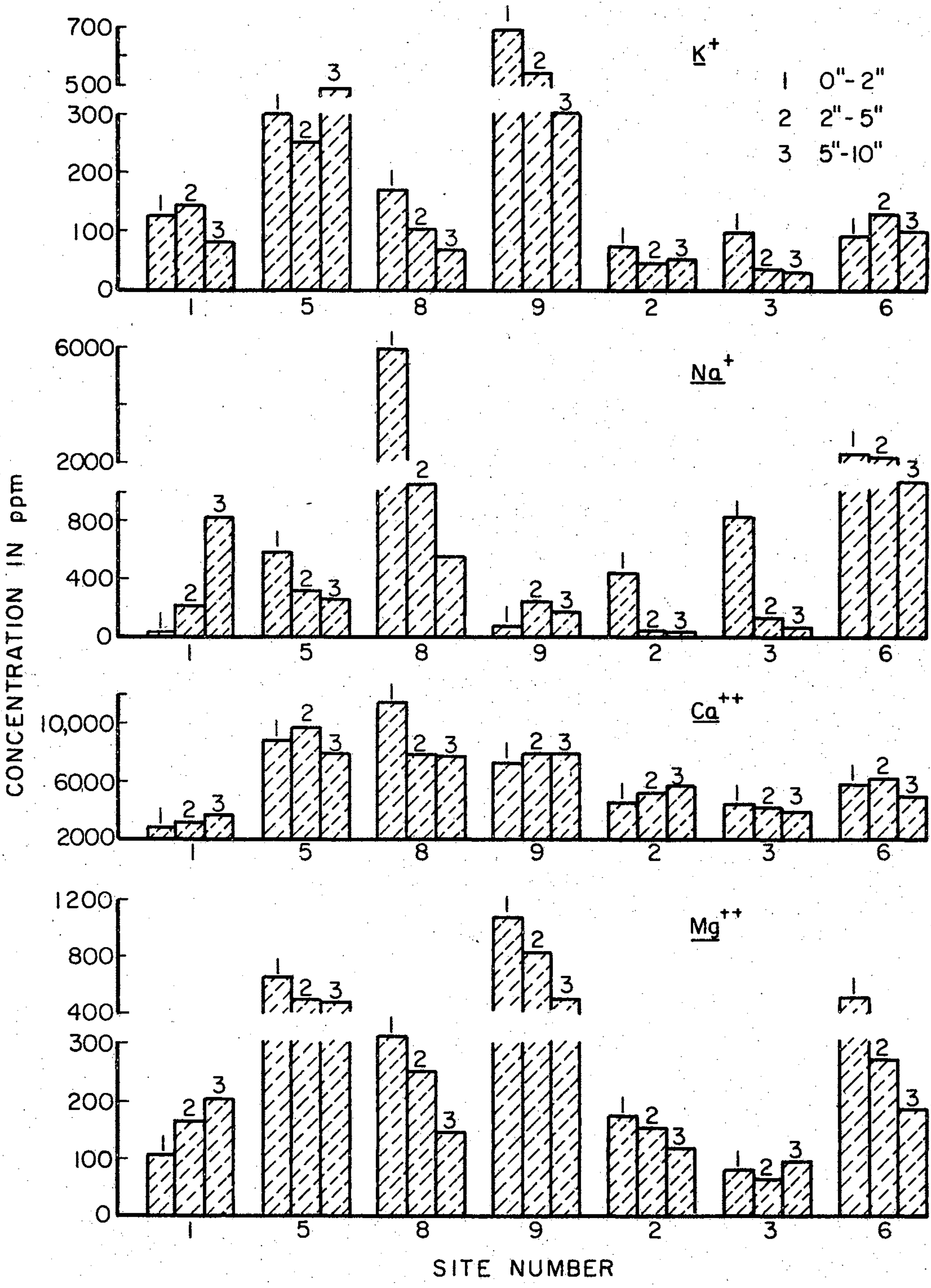

Figure 9. Values of Exchangeable Cations Measured in the Soils of Sites Inhabited by Saltgrass

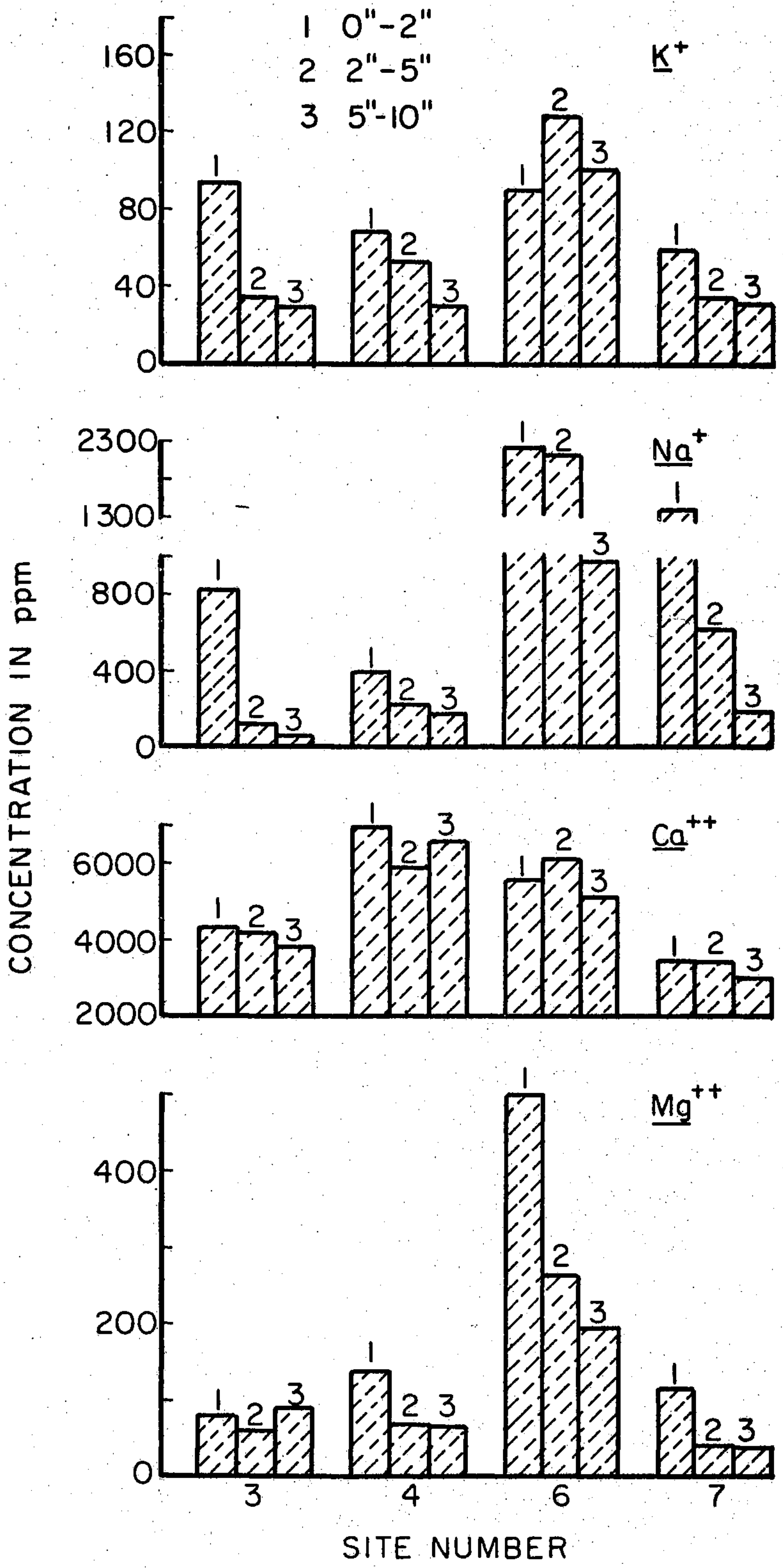

Figure 10. Values of Exchangeable Cations Measured in the Soils of Sites Inhabited by Salt Cedar

than sodium. Magnesium content was fairly uniform in all sites except in site 6, where it was about three times as high as in other sites.

Relative turgidity and osmotic pressure of the plants are generally a reflection of the soil moisture status (Table III). Turgidity of saltgrass did not show wide variation from one site to the other, especially during July, being as high as 90 per cent on the average. Osmotic pressures of saltgrass plants sampled in July show higher values in soils having low available moisture, e.g. site 1, or of high salinity such as sites 6 and 8. Salt cedar showed a more pronounced deficit than saltgrass except in site 3. Relative turgidity of salt cedar stood at about 70 to 80 per cent during both June and July in all sites except in site 3 where plants attained a much higher turgidity of about 90 per cent. This may have been due to low salinity and abundance of water in the sandy soil of this site.

The daily amounts of evaporation from soil and evapotranspiration by potted saltgrass and salt cedar are shown in Table IV. Evapotranspiration data presented in the table could be safely considered as representing the potential rate since the area from which the plants and soil were secured (site 3) had a shallow water table and its sandy soil was nearly saturated. The data clearly indicate a general decreasing trend in evaporation and evapotranspiration from one day to another in both June and July. This, of course, reflects the progressive drying of the soil (with or without the plant) after being separated from the water table; however, the calculated amounts of transpiration by each plant do not show the same trend. Transpiration by plants fluctuated significantly despite progressive drying of the soil. This illustrates the basic difference in the nature of both evaporation and

TABLE III

AVERAGE VALUES OF PER CENT RELATIVE TURGIDITY OF SALTGRASS AND SALT CEDAR IN JUNE AND JULY AND THE OSMOTIC PRESSURE OF SALTGRASS IN JULY AT THE SITES STUDIED

Site No.	Plant	Per Cent Relative Turgidity June	July	Osmotic Pressure (Atm.) July
1	Saltgrass	80.5	86.9	78.32
2	Saltgrass	92.4	83.8	74.40
3	Saltgrass	88.4	95.8	56.78
5	Saltgrass	94.8	89.0	48.57
6	Saltgrass	94.5	94.1	71.65
8	Saltgrass		96.1	87.74
9	Saltgrass		84.7	72.17
3	Salt Cedar	88.5	87.7	
4	Salt Cedar	80.0		
6	Salt Cedar	78.0	69.3	
7	Salt Cedar		68.0	

TABLE IV

AVERAGE VALUES OF DAILY EVAPORATION (E), EVAPOTRANSPIRATION (ET) AND CALCULATED TRANSPIRATION (T) OF SALTGRASS AND SALT CEDAR IN JUNE AND JULY AS MEASURED IN SITE 3

			Saltgrass		Salt Cedar	
Month	Day	E (Inch)	ET (Inch)	T (Inch)	ET (Inch)	T (Inch)
	1	0.228	0.318	0.090	0.238	0.010
	2	0.245	0.325	0.080	0.270	0.025
June	3	0.155	0.183	0.028	0.210	0.055
	4	0.070	0.108	0.038	0.088	0.018
	5	0.048	0.113	0.065	0.060	0.012
	Avg.	0.149	0.209	0.060	0.173	0.024
	1	0.064	0.137	0.073	0.125	0.061
July	2	0.046	0.133	0.087	0.086	0.040
	3	0.015	0.046	0.031	0.023	0.008
	Avg.	0.042	0.105	0.064	0.078	0.036

transpiration and the physical factors that control each of them. Fluctuation in transpiration is more likely to be a reflection of the response of the plants to daily changes in environmental conditions under the unlimiting moisture conditions in this site. The data clearly show that transpirational loss of water by saltgrass is generally far higher than that from salt cedar seedlings when calculated on a land area basis.

DISCUSSION AND CONCLUSIONS

It is clearly indicated by the data on soil chemical characteristics that saltgrass has a wide ecological amplitude. Water supply seems to present no problem for this plant under field conditions. Plants existing in elevated places showed no obvious difference in growth or leaf turgidity from those in areas with a shallow water table. Only the cover is more dense in the former while plants are evenly distributed in the latter. It also seems that saltgrass can tolerate, in addition to salinity, high concentrations of sodium in the soil.

The ecological habitats of salt cedar appears to be more or less uniform. Distribution of seedlings seems to be restricted to sandy soils usually with high salinity. However, one stand, on site 3, had the lowest salinity among the sites studied. Seedlings of salt cedar in this site probably represented a recent invasion in the area which may later be subject to salinization by high rates of evaporation and transpiration lowering of the water table.

Although direct evaporation from the soil appeared to be far greater than transpiration, the data indicate the reverse may hold true when the soil became drier. Fluctuations in transpiration amounts, despite decrease in soil moisture of the weighed cans, substantiate the idea given by Closs (1958) that "under natural conditions, where there is a plentiful water supply in the soil, the transpiration rate is determined by the weather." The moisture in the cans was actually high even after five days of water loss. The apparent decrease in evaporation was the result of the dry crust on the surface soil in the can. The quick formation of this layer is largely controlled by the low capillarity of the sandy soil.

CHAPTER IV

WATER RELATIONS OF SALTGRASS, ALKALI SACATON AND BLUE GRAMA UNDER INCREASING MOISTURE STRESS

Introduction

Soil moisture data taken during the one growing season (Chapter III) indicate that at no site, was there any moisture shortage. However, to find if moisture is a decisive factor in the water relations of saltgrass or if it is of secondary importance, the moisture conditions around the plant roots must be brought to the lower limits of availability. This will show the survival limits of the plants and may manifest more clearly the mechanisms involved in adjusting to moisture stress. Therefore, it was intended to experiment with the plants considered under laboratory controlled moisture levels to test the effects of decreasing availability of soil moisture on transpiration, the relative turgidity and the osmotic pressure in saltgrass, alkali sacaton, and blue grama. The effect of moisture stress in the soil on plant growth has received much attention (Davis, 1942; Scofield, 1945; Gates, 1955 a & b; and Sands and Rutter, 1959) but relatively few investigations regarding its effect on transpiration and water relation of plants have been made.

In connection with studies of this nature, a question may arise about whether or not the results of such investigations are comparable with results obtained from field investigations. The answer to this question is not easy but, within reason, it is felt that they are comparable to the range existing under field conditions.

Materials and Methods

This study was conducted with potted plants. Previously weighed cans (Size No. 5) lined with a double layer of polyethylene bags were filled with equal amounts of sandy loam soil. This soil was previously sterilized in an autoclave, air-dried at room temperature for 24 hours, and then mixed well before filling and the moisture content of the soil was determined. The cans were tapped gently and uniformly on filling to simulate soil density of field conditions. Each can was filled with 2,000 grams of the air-dry soil and the oven-dry weight of this soil was determined. The water availability limits of the soil used, that is the "wilting point" and the "moisture equivalent," were determined. The former was determined by the method described by Briggs and Shantz (1912), following the technique of Furr and Reeve (1945) using sunflower seedlings, and the latter by saturating the soil with distilled water and then centrifuging at 1,000 G as described by Baver (1956). The wilting point for the soil used was found to be 8.19 per cent and the moisture equivalent 13.76 per cent on oven-dry weight basis. Moisture equivalent was chosen for this study instead of the field capacity on the basis that both are more or less equal for most soils (Baver, 1956) but the former is easier to determine in the laboratory. Once these values were determined, the amount of water necessary to bring the soil in each can to the wilting point and to the moisture equivalent was calculated. The amount of water necessary to cover the available range between the field capacity and the wilting point, thus known, was divided into suitable arbitrary levels. These levels were chosen as 10, 25, 40, 55, 70, 85 and 100 per cent of the available range for cans planted with saltgrass and alkali sacaton and 10, 30, 50, 70 and 90 per cent for cans of blue grama. After these amounts were calculated, the total weight of the empty can together with the calculated oven-dry weight of the soil within and the amount of water necessary to bring the soil to a certain available moisture level was computed for every plant to be experimented with. To secure uniform distribution of moisture throughout the soil, irrigation tubes especially made for this purpose were used. These were made of one-half inch diameter glass tubing of a length equal to that of the cans used and were perforated uniformly alongside their walls. One tube inserted in the soil close to the center was used in each can. The weight of the tube was included in the total weight of the can.

A sufficient number of plantings of each plant, usually about 30, were established to provide three replications for each moisture level. The plants were started from seeds in case of alkali sacaton and blue grama and from transplants for saltgrass as seeds of saltgrass are difficult to germinate. The transplants were brought from site 3 described in Chapter III and were carefully chosen to be of nearly equal size. The seeds and transplants were allowed to grow in the greenhouse under soil moisture conditions adjusted daily to near the moisture equivalent. After the germination of alkali sacaton and blue grama seeds, the number of seedlings in each can was reduced to four. Saltgrass transplants gave new sprouts in a week and as soon as these emerged from the soil, the old stems of the transplants were cut down to the soil surface. This insured homogeneity of age and size of the transplants.

At the end of the fourth week, three cans were chosen at random from each plant set and assigned to receive a fixed moisture level maintained by checking the weights at least once daily. The moisture content of the soil in each can was not allowed to drop more than 5 per cent below the assigned level. The plants were kept under the assigned levels for three to four weeks in order to adjust their internal water balance to the soil moisture conditions before transpiration measurements were made.

Transpirational water loss was measured by periodic weighing of the cans. First, each can was brought to the weight of its assigned level. It was then covered by a double layer of polyethylene sheets in such a way that the plant emerged from the center without any possibility of loss of water by direct evaporation from the soil. The cans were weighed immediately and the weights recorded. Usually this process was started in the early morning. The weights of the cans were checked twice daily, at noon and in the evening, in order to insure that transpirational losses did not cause the soil moisture to drop below the desired level. In a twenty-four hour period, the cans showed marked loss of weight as a result of water loss by transpiring plants. At this time, their weights were recorded again and losses were calculated. Then the cans were uncovered, their moisture contents readjusted to the assigned level and the whole processes of weighing and recording repeated for a second twenty-four hour period. This produced records for two days instead of one. The plants in each can were then cut down to the level of the polyethylene cover and immediately weighed. Their relative turgidity was determined immediately by the method described in Chapter III. The plants were then freeze-dried and stored for later grinding and extraction to determine the osmotic pressure of the extract. Conductivity measurements were carried out on the same extracts of alkali sacaton and blue grama which had been used in determining the osmotic pressure of plants. From the conductivity data, another value of the osmotic pressure could be calculated according to the equation given by Black et al. (1965):

$$\text{O.P. (in atm.)} = E_c \text{ (in mmhos)} \times 0.36$$

The osmotic pressure of the sample was then converted back to the actual osmotic pressure in the leaf by taking into consideration the leaf water content of the plants after they have been cut down. The osmotic pressure values calculated from the conductivity measurements represent the ionic fraction in the osmotic material. This may include various cations and anions as well as ionized organic acids. In this case the osmotic pressure values measured by the cryoscopic method are referred to as "total" osmotic pressure whereas those measured by the conductivity method are the "ionic" osmotic pressure.

Results

Transpiration rate of saltgrass (Figure 11) showed a progressive decrease with decreasing available moisture. The decrease started immediately below the moisture equivalent and was more or less linear to about the 40 per cent level of the available range, but below 40 per cent, the decrease followed a hyperbolic relation. Transpiration of saltgrass under greenhouse conditions was relatively high. Plants

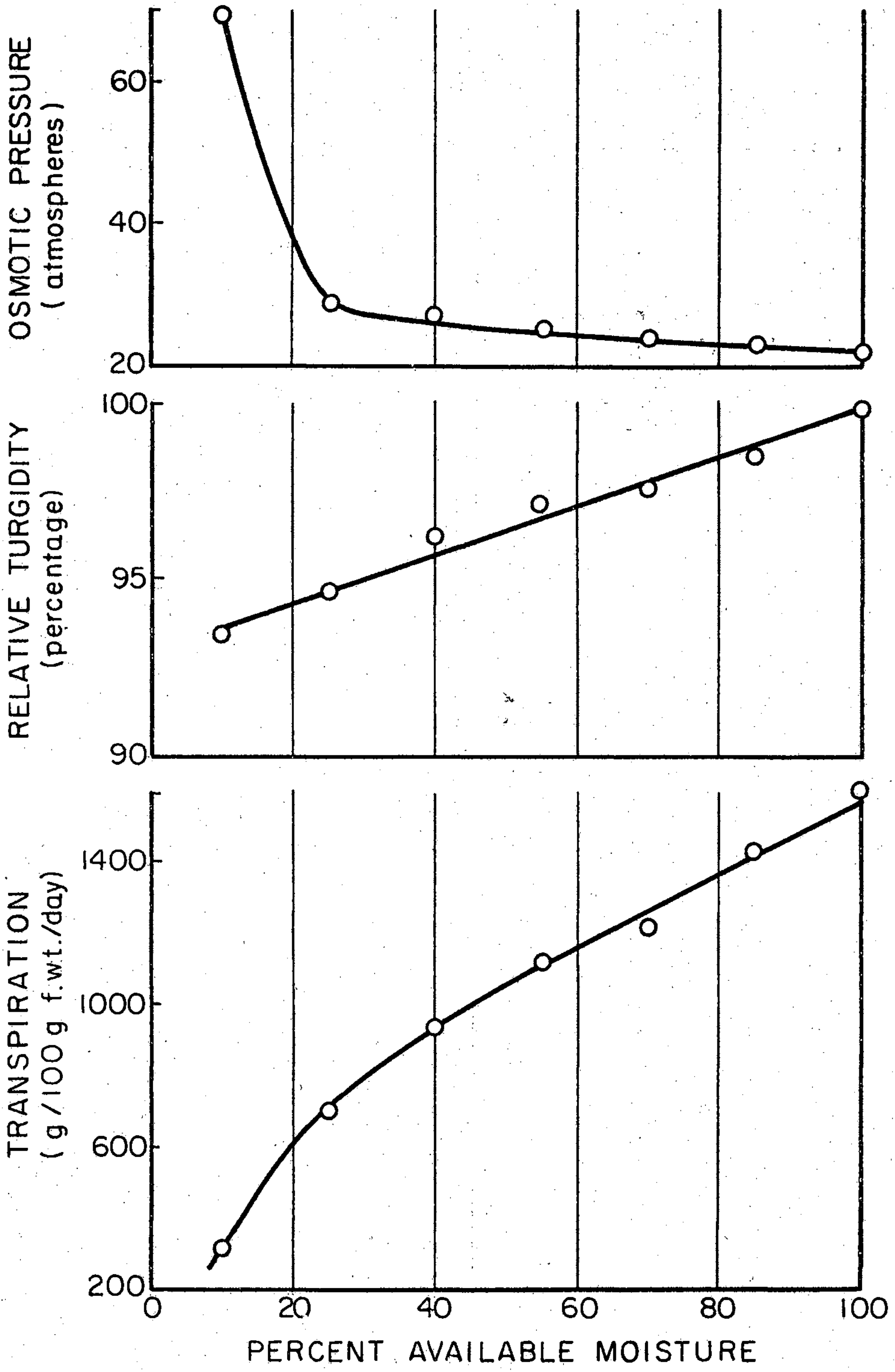

Figure 11. Variation of Average Values of Transpiration, Relative Turgidity and Osmotic Pressure of Saltgrass Under Different Levels of Available Moisture in the Soil

transpired up to about 16 times their weights in moisture (1600 g of water per 100 g leaf fresh weight per day) at the moisture equivalent level. However, transpiration decreased greatly with decreasing availability of moisture to about three times the weights of the plant near the wilting point (310 grams of water per 100 grams plant fresh weight per day). These amounts are sufficiently high enough to substantiate the transpiration data of the plant measured under field conditions although the latter were calculated on an area basis. It also confirms the phreatophytic nature of the plant. Such tremendous water loss by the plant even near the wilting point indicates very little control, if any, by the plant leaves. This is quite clear from changes in the relative turgidity of the plant leaves. Although the latter showed progressive decrease with decreasing available soil moisture in a nearly linear fashion, the decrease over the entire available range was relatively small (from 99.8 per cent at the moisture equivalent to 93.4 per cent at the 10 per cent level of the available range). This is a pronounced indication that the plants probably did not suffer from any serious water deficit in their leaves. In this case, higher rates of water loss by transpiration should have been immediately followed by rapid absorption from the soil. Even the osmotic pressure of the plants showed this slight response to decreasing available moisture in the soil. Increase in osmotic pressure progressed from 21.36 atmospheres at the moisture equivalent to only 28.80 atmospheres at the 25 per cent level of the available range; however, an abrupt increase below that level to 68.97 atmospheres was observed. This may be the only mechanism to counter high moisture tension in the soil and to oppose the excessive transpirational water loss which seems to be unchecked by any regulatory mechanism in the leaves. In this manner, the plants could keep a constant water flow into the leaves from other parts of the plant, and hence relatively high turgidity, by maintenance of an osmotic gradient. The relatively greater decrease in transpiration rate below the 25 per cent level of the available range may be a reflection of this abrupt increase in osmotic pressure as a result of a higher retention of water in the leaves by osmotic forces.

In alkali sacaton (Figure 12) the transpirational behavior is similar to that of saltgrass. However, the magnitude of transpiration in alkali sacaton is much less than in saltgrass. A comparison may not be accurate in this respect, since measurements were not made under controlled climatic conditions, particularly temperature and humidity. Also, the measurements in both plants were not made simultaneously. Despite this, variations due to probable differences in climatic conditions at times of measurements in both plants cannot account for the much lower transpiration in alkali sacaton. Transpiration of alkali sacaton amounted to 325.6 grams per 100 grams leaf fresh weight per day (three times as much as its weight) at the moisture equivalent level. This dropped to only 105.1 grams per 100 grams leaf weight per day at the 10 per cent level of the availability scale. The decrease in transpiration was in a curvilinear manner. This may indicate some sort of tendency to resist excessive water loss on the part of the plant. The relative turgidity response to decreasing moisture availability also suggests this. There was a tendency by the plant to maintain a high relative turgidity as the available moisture dropped from the moisture equivalent to the 55 per cent level of the availability

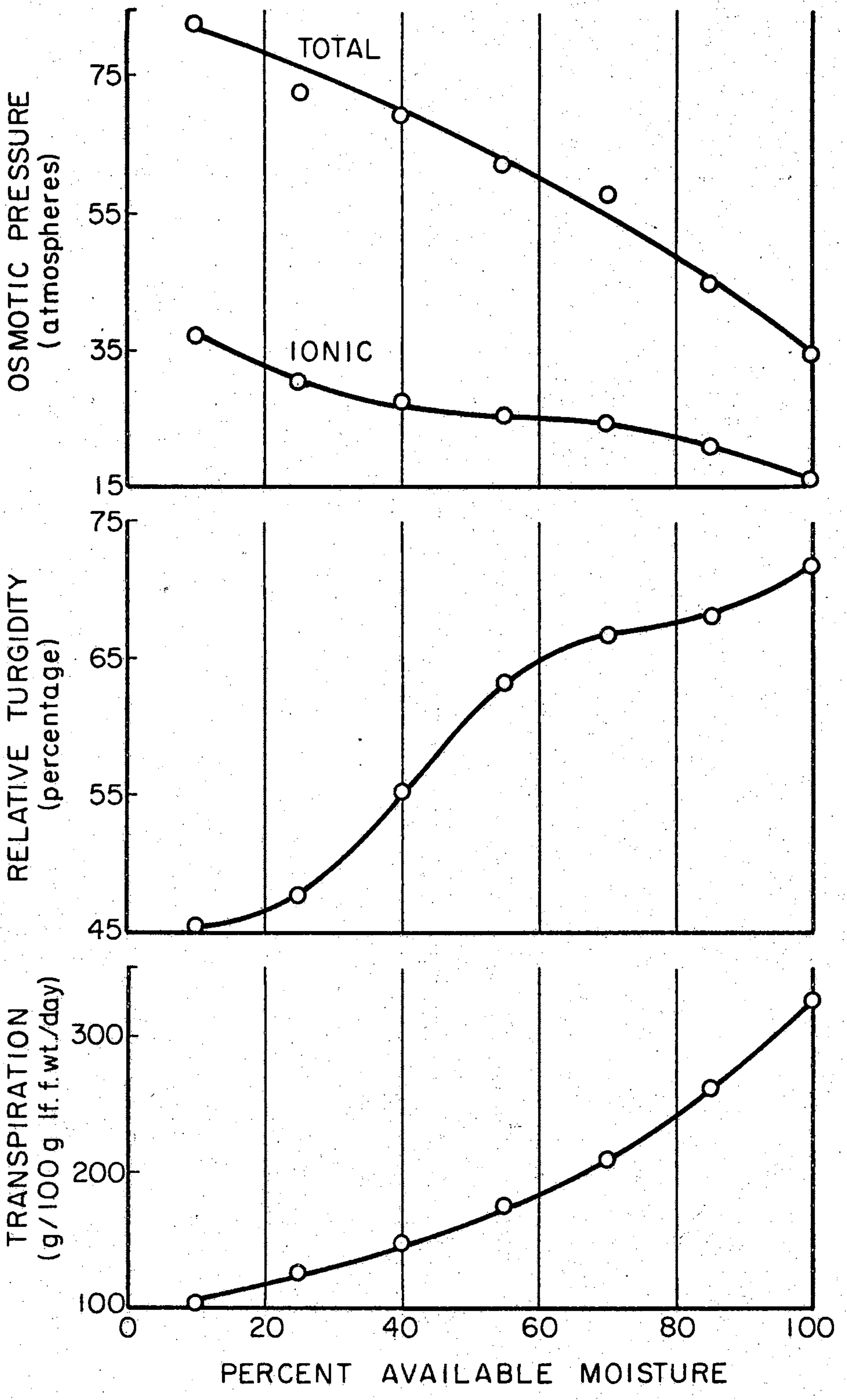

Figure 12. Variation of Average Values of Transpiration, Relative Turgidity and Osmotic Pressure of Alkali Sacaton Under Different Levels of Available Moisture in the Soil

scale. Below 55 per cent, decrease in turgidity (that is, increase of water deficit in plants) was quite sharp. The saturation deficit of 28.3 per cent which existed at the top of the availability scale did increase to 54.4 per cent at the 10 per cent level of available moisture. It was only 36.7 per cent at the middle of the range (the 55 per cent availability level) which is not much different from that at the moisture equivalent. The total osmotic pressure of the plant increased substantially with decreasing available moisture in a curvilinear fashion from 34.31 atmospheres at the uppermost point of the available range to 82.39 atmospheres at the 10 per cent level. The ionic fraction showed more or less the same trend of behavior with a slight tendency to level off near the middle of the availability range. However, the osmotic pressure of this fraction remained far below that of the total osmotic material over the entire available range. The difference between both is more pronounced near the wilting point (about 45 atmospheres at the 10 per cent level of availability compared to only about 18 at the highest point of availability).

Transpiration of blue grama (Figure 13) showed an early decline with decreasing available moisture. The decline was approximately linear. A leveling off of the transpiration rate is noticeable at the mid-range of soil moisture availability. The transpiration rate of blue grama was fairly high as indicated by its magnitude of 711 grams per 100 grams leaf fresh weight per day at the 90 per cent level of the available range. Despite the early sharp decline, the transpiration rate was reduced by only slightly less than half at the 10 per cent level of moisture availability. Relative turgidity stayed fairly high (97.3 to 98.2 per cent) down to the upper third of the available range

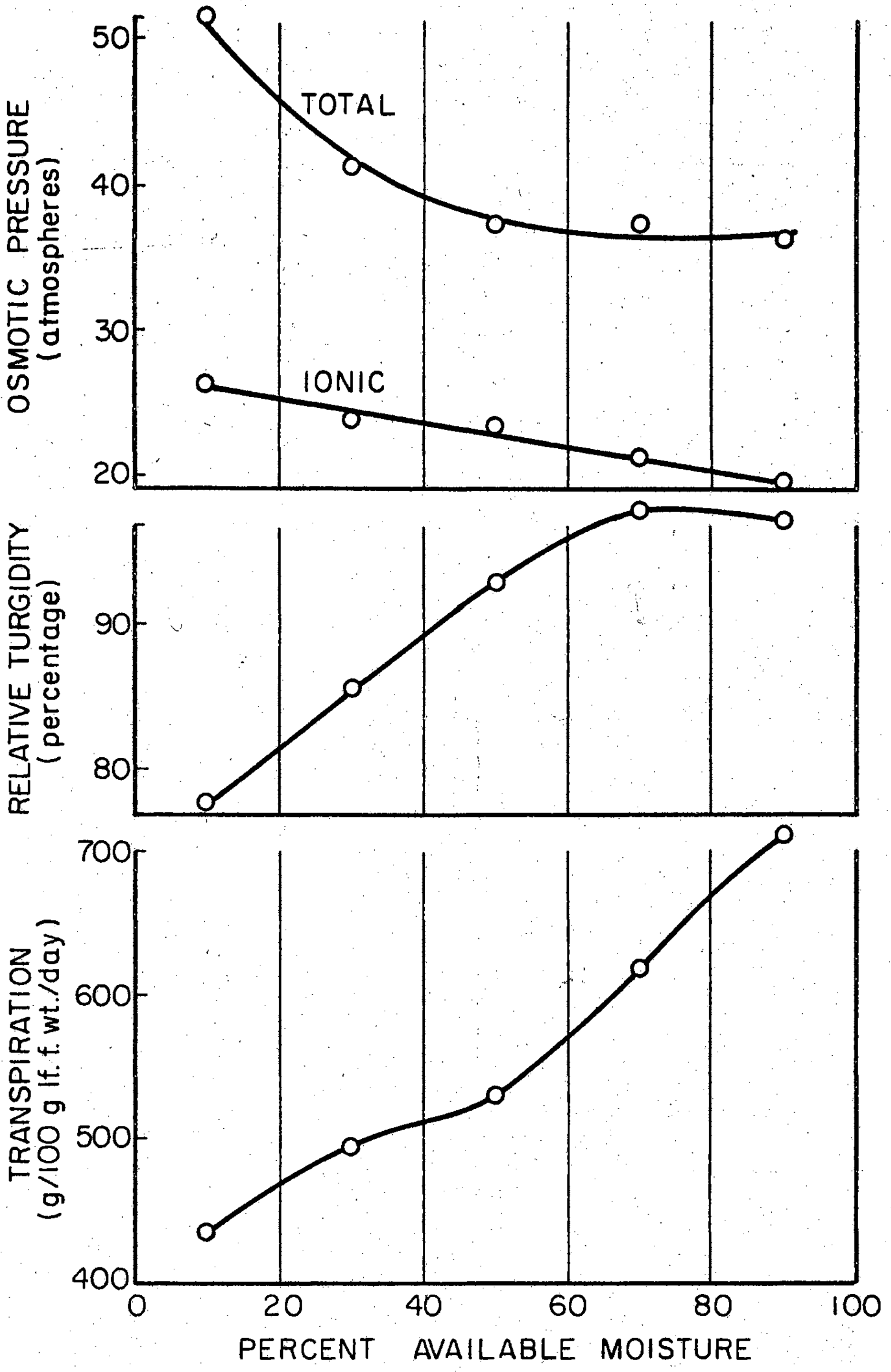

Figure 13. Variation of Average Values of Transpiration, Relative Turgidity and Osmotic Pressure (Total and Ionic) of Blue Grama Under Different Levels of Available Moisture in the Soil

but it then declined linearly to a low of 77.7 per cent. The total osmotic pressure of the leaves remained relatively stable (about 37 atmospheres) in the upper half of the available range but then increased to a high of 51.66 atmospheres at the 10 per cent level of availability. The ionic fraction increased only slightly, in a linear fashion, from a low of 19.51 atmospheres at the 90 per cent level to 26.34 atmospheres at the 10 per cent level of the available range. As with alkali sacaton, the difference between the ionic fraction and the total osmotic material was greater at the lower levels of availability (about 25 atmospheres at the 10 per cent level) than at the upper levels of the scale (only about 16 atmospheres at the 90 per cent level).

Discussion and Conclusions

Transpiration curves for the plants under consideration varied considerably in their mode of change in relation to changing water availability in the soil. Although a linear relationship between transpiration and the level of soil available moisture in both saltgrass and blue grama was observed, a tendency toward a logarithmic relation at lower levels of moisture availability existed in the transpiration curve of saltgrass and a tendency to level off at the mid-range in that of blue grama was observed. The logarithmic relation was clearly manifested in the case of alkali sacaton. It is likely that a linear relationship between transpiration and the change in soil moisture availability indicates that water was equally available to the plant at all levels of stress. If this is true, it indicates that the plant plays no significant role in counter-balancing the stress exerted at its root surface by increasing moisture stress at the lower levels of availability. The reverse is true in a logarithmic type of relationship, which indicates unequal availability along the range of available soil moisture. In this case, a leveling off in the decreasing trend of transpiration with increasing soil moisture stress as the wilting point is approached indicates that the plant tends to counter this stress by maintaining a high transpiration rate. This phenomenon is substantiated by a progressive increase in the osmotic concentration (both total and, to a less extent, the ionic fraction).

A logarithmic relation between transpiration and soil moisture status was also shown by Closs (1958) with mustard plants. Similar trends were also shown in the transpiration curves of Denmead and Shaw (1962) in their investigation on corn. All these investigators indicated that the logarithmic behavior of transpiration curves suggest possible unequal moisture availability over the entire range of available moisture. The unequal availability described here is different from that concluded by Veihmeyer and Hendrickson (1955) who indicated that transpiration does not start to decrease until the moisture content of the soil approaches some stage near the wilting point. The results presented in this paper indicate that transpiration started to decrease immediately below the moisture equivalent and this decrease tended to become progressively less as the moisture decreased toward the wilting point.

The change in the relative turgidity of leaves with decreasing available moisture was found to be generally linear in the plants considered, although there was some tendency in alkali sacaton and blue grama to retain higher turgidities in their leaves in the upper third of the available range. This tendency in both sacaton and grama, despite an obvious decrease in transpiration rate, can be explained by the increase in osmotic concentration in the leaves which would tend to retain water. In this case, transpirational pull is not expected to contribute significantly to water movement into the leaves, as indicated by the declining rate immediately below the moisture equivalent. Reports by other investigators show no definite relationship between soil moisture availability and the moisture status in the leaf tissues. Sands and Rutter (1958) showed that in Pinus sylvestris L. a leaf water deficit of 8 per cent at field capacity developed to only 17 per cent when the soil moisture was reduced to the permanent wilting point. Watanabe (1959) pointed out that the water content of Acacia mollisima leaves was not affected by the soil moisture content until it was reduced nearly to the permanent wilting point.

The role of osmotic pressure in the adjustment of the plants' internal water relations to increasing moisture stress of the soil seems to vary from one plant to another. In saltgrass and blue grama, obvious increase in osmotic concentration occured only when the wilting point was approached. In alkali sacaton, the increase in osmotic concentration started immediately below the moisture equivalent and increased progressively toward the wilting point. The increase in osmotic concentration could be attributed to several factors among which the photosynthetic and respiration rates may be the most significant. Also drastic changes in the relative turgidity might play a role in this respect. Detailed discussion of the physiology of mechanisms involved is beyond the scope of this study. The role of the ionic fraction in osmotic adjustment seems to be less significant than the role of the non-ionic fraction. Differences between the total osmotic concentration and the ionic osmotic concentration was shown to be much higher near the wilting point than at the moisture equivalent in both alkali sacaton and blue grama.

CHAPTER V

WATER RELATIONS OF SALTGRASS, ALKALI SACATON AND BLUE GRAMA UNDER SALINITY STRESS

Introduction

In none of the field sites inhabited by saltgrass did the calculated values of osmotic pressure of the soil solution exceed 32.9 atmospheres below the top two inch surface layer of the soil. Actually, in most of the sites studied, the calculated osmotic pressure centered around 10 atmospheres or less. This indicates that saltgrass did not suffer from high salinity stress under field conditions. Only in site 6 did the osmotic pressure reach the maximum of 32.9 atmospheres and this was at the 5 to 10 inch depth where maximum penetration of saltgrass roots could be found.

Laboratory studies on the effect of salinity on the water relations of the three grasses under consideration was intended also to define the tolerance limits of these grasses. Experimentation with healthy plants growing under optimum moisture conditions was necessary to separate the effect of salinity stress from that of stress resulting from moisture shortage in the soil. Increasing salinity stress in the soil was tested at a fixed level of soil moisture. The level selected was the moisture equivalent (that is, field capacity).

Some workers distinguish between effects due to salinity and those due to the sodium adsorption ratio, SAR (Ayers et al., 1951). Others used sodium chloride and calcium chloride, in solution, in amounts related by a value of the sodium adsorption ratio which was sufficiently small to exclude the possibility of ionic composition effects of a growth depressing nature (Gauch and Wadleigh, 1943, 1945; Bolt, 1955; Bower and Copper, 1956; and Bower, 1959).

In the study presented in this chapter, the emphasis is centered on the osmotic effect of the soil solution. It was found necessary to have a fixed sodium adsorption ratio while using different osmotic concentrations in the solutions. An SAR value of 1/8 (12.5 per cent) was decided as low enough to avoid sodium toxicity as frequently reported by workers in this area.

Materials and Methods

Cans were filled with soil and planted, following the detailed procedure previously discussed in Chapter IV. The plants were allowed to grow with the moisture content in the cans periodically adjusted to the moisture equivalent level as previously described. Initially, 51 cans were planted with each species. When the seedlings were four weeks old, their soils were treated with especially prepared saline solutions having determined osmotic concentrations. Treatments were carried out with solutions having osmotic values ranging from 0 to 170 atmospheres. These solutions contained both sodium chloride and calcium chloride in amounts calculated to give certain osmotic values when dissolved in a certain volume of distilled water. Three cans, chosen at random from the set of 51, were treated at each osmotic concentration. Each can was treated with the assigned saline solution by adding a volume of the solution exactly equal to the amount of water necessary to bring the soil moisture to the level of field capacity. In doing this, care was taken to add the solution in fractions on successive days so that the initial water content of the soil would remain at field capacity. Treatment in this way required three to five days to complete. After treatment, the plants were allowed to adjust to the new stress in the soil. Care was taken to keep the moisture content of the soil always at field capacity. This necessitated checking the weights of the cans twice daily as described in Chapter IV. Loss of water, as indicated by decrease in weight of the cans, was controlled by adding the necessary amount of distilled water.

In calculating the amounts of both sodium chloride and calcium chloride which, when dissolved in one liter gives a solution of a particular osmotic pressure, the equation followed by Lagerwerff and Holland (1960) was used:

The sodium adsorption ratio (SAR) = $\mathrm{Na^+/(Mg^{++} + Ca^{++})}$ $\mathrm{mmoles^{\frac{1}{2}}}$. $\mathrm{liter^{-\frac{1}{2}}}$

Since the amount of magnesium in the soils studied was shown to be negligible compared to calcium (usual in soils with high calcium content,) the equation can be written as:

$$\mathrm{SAR} = \mathrm{Na^+/(Ca^{++})^{\frac{1}{2}}\ mmoles^{\frac{1}{2}}\ .\ liter^{-\frac{1}{2}}}$$

To calculate the amount of sodium chloride and calcium chloride for a solution of one atmosphere at SAR of 1/8, for example, it follows that, $\mathrm{SAR} = \mathrm{Na^+/(Ca^{++})^{\frac{1}{2}}} = 1/8$, therefore, $8\ \mathrm{Na^+} = \mathrm{(Ca^{++})^{\frac{1}{2}}}$, or

$$64\ (\mathrm{Na^+})^2 = \mathrm{Ca^{++}}\ \text{in mmoles. liter}^{-1} \quad . . . . (1)$$

And, since we have:

24 me NaCl per liter constitute a solution of one atmosphere osmotic pressure, and, 32 me $CaCl_2$ per liter constitute a solution of one atmosphere osmotic pressure, therefore, we need to adjust:

$$\text{me NaCl}/24 + \text{me CaCl}_2/32 = 1 \text{ atm.} \; . \; . \; . \; . \; . \; . \; . \; . \; (2)$$

Thus, substituting for Ca in equation (2) by its value in equation (1), we get:

$$\text{NaCl} + 48\ (\text{NaCl})^2 = 24 \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; (3)$$

Equation (3) is a quadratic equation of the form:

$$Ax^2 + Bx = C\ ,$$

where x is the variable, and it can be determined from the solution of the equation which gives:

$$x = \frac{-B \pm (B^2 + 4AC)^{\frac{1}{2}}}{2A}$$

In this manner, we can solve for the amount of NaCl as follows:

$$\text{NaCl} = \frac{-1 \pm (1-4 \times 48 \times -24)^{\frac{1}{2}}}{2 \times 48} = \frac{-1 \pm (4609)^{\frac{1}{2}}}{96} = \frac{66.89}{96}\ \text{me. liter}^{-1} \quad \text{or,}$$

$$\text{CaCl}_2 = 64 \times \left(\frac{66.89}{96}\right)^2 \text{me. liter}^{-1} \quad \text{or,}$$

$$\text{CaCl}_2 = 64 \times \left(\frac{66.89}{96}\right) \times 55.49 = 1723.83\ \text{mg. liter}^{-1}$$

The amounts of sodium chloride and calcium chloride to be dissolved in one liter to give osmotic pressures of 5, 10, 15, 20, 25, 30, 40, 50, 60, 90, 130 and 170 atmospheres, at a fixed SAR value of 1/8, were calculated. The calculated amounts, together with the corresponding values of total salinity in each solution in ppm are shown in Table V.

The treated plants were left for three to four weeks to adjust to the levels of salinity stress. Plants which could not tolerate high salinities showed signs of wilting, yellowing and then died two to three days after completing the treatment. Various degrees of slight yellowing or wilting occured at higher levels of salinity in plants which survived.

Result

The tolerance limits to soil salinity, as expected, varied considerably among the species. Saltgrass survived salinities of up to 90 atmospheres; alkali sacaton up to 50 atmospheres; and blue grama to only 40 atmospheres.

Transpiration of saltgrass (Figure 14) showed a sharp decline with increasing osmotic concentration of the soil solution. The decrease seemed to be logarithmic and its rate tended to level off at concentrations of 40 atmospheres and above. The transpiration rate at 90 atmospheres was reduced to about half the potential rate. Nevertheless, the rate of loss at this high salinity stress reflects the phreatophytic nature of the plant. The water loss at this upper limit of tolerance was seven times the weight of the plant (700 gm per 100 gm leaf fresh weight per day). Relative turgidity decreased progressively in the same manner, but tended to level off at the higher potential of 60 atmospheres. Also, reduction in the relative turgidity was clearly great (from 92.29 per cent in the control plants to 50.40 per cent at

TABLE V

CALCULATED AMOUNTS OF NaCl AND $CaCl_2$ PER LITER WHICH GIVE DIFFERENT VALUES OF OSMOTIC PRESSURE IN SOLUTION AT A FIXED SAR OF 1/8

Osmotic Pressure (Atm.)	Salt Amount in g/l NaCl	Salt Amount in g/l $CaCl_2$	Total in Solution ppm
5	0.0918	8.76	8852
10	0.1300	17.58	17710
15	0.1592	26.35	26509
20	0.1842	35.28	35464
25	0.2060	43.81	44016
30	0.2257	52.98	53206
40	0.2607	70.69	70951
50	0.2619	87.35	87612
60	0.3195	99.75	100069
90	0.3914	159.31	159701
130	0.4708	250.24	250711
170	0.5382	301.19	301728

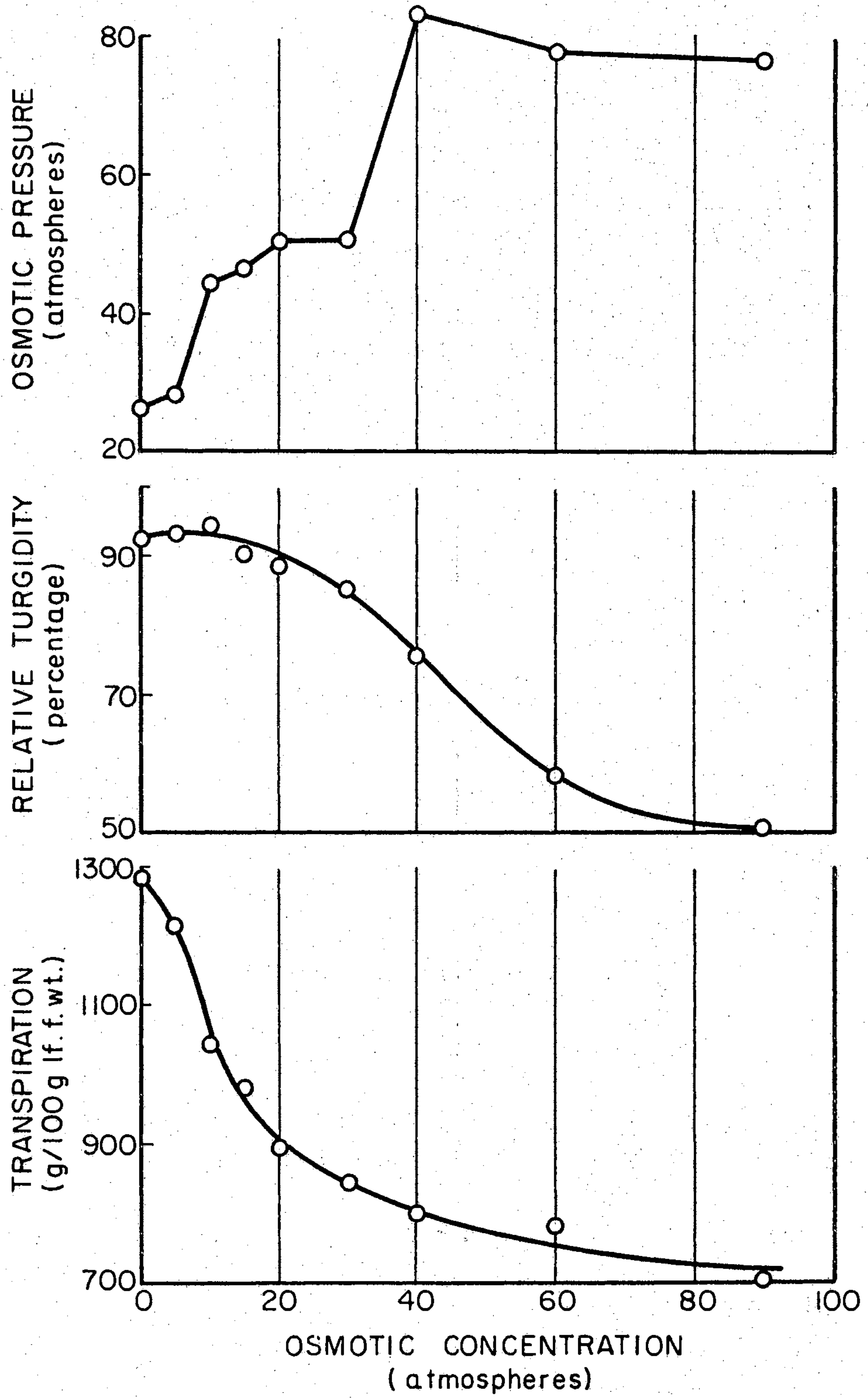

Figure 14. Variation of Average Values of Transpiration, Relative Turgidity and Osmotic Pressure of Saltgrass Under Different Levels of Osmotic Concentrations of the Soil Solution

90 atmospheres soil salinity). The osmotic pressure of plants increased non-linearly up to the 40 atmosphere soil solution concentration. Beyond the 40 atmospheres concentration of the soil solution, the osmotic pressure of saltgrass remained nearly constant.

In alkali sacaton (Figure 15), decrease in the transpiration rate was sharp initially up to the level of 10 atmospheres osmotic pressure in the soil solution. Above that concentration, transpiration decreased almost linearly with increasing soil salinity. The magnitude of transpiration of alkali sacaton was, however, low compared to that of saltgrass. Reduction in the transpiration rate with increasing salinity was relatively great. Transpiration at 30 atmospheres soil salinity was approximately one-third of the potential rate. Response of relative turgidity to increasing osmotic potential in the soil was slight up to the 20 atmospheres level. Decline in relative turgidity was sharper thereafter. Although the control plants (plants which did not receive a salinity treatment) started with a relative turgidity of 91.4 per cent, yet a 30 atmospheres osmotic potential in the soil decreased the turgidity to only 76.3 per cent. The osmotic pressure of plants increased sharply up to the 25 atmospheres osmotic potential in the soil to a maximum of 61.50. This is slightly less than three times the value attained by the control plants. At concentrations higher than 25 atmospheres in the soil solution, the osmotic pressure of the plants showed a marked decrease which was sharp at first and then slight thereafter. The ionic fraction of the plants' osmotic material did not show the same maximum as the total osmotic material. This fraction showed a progressive gradual increase with increasing soil salinity up to the 40 atmospheres level. The increase was sharper at higher

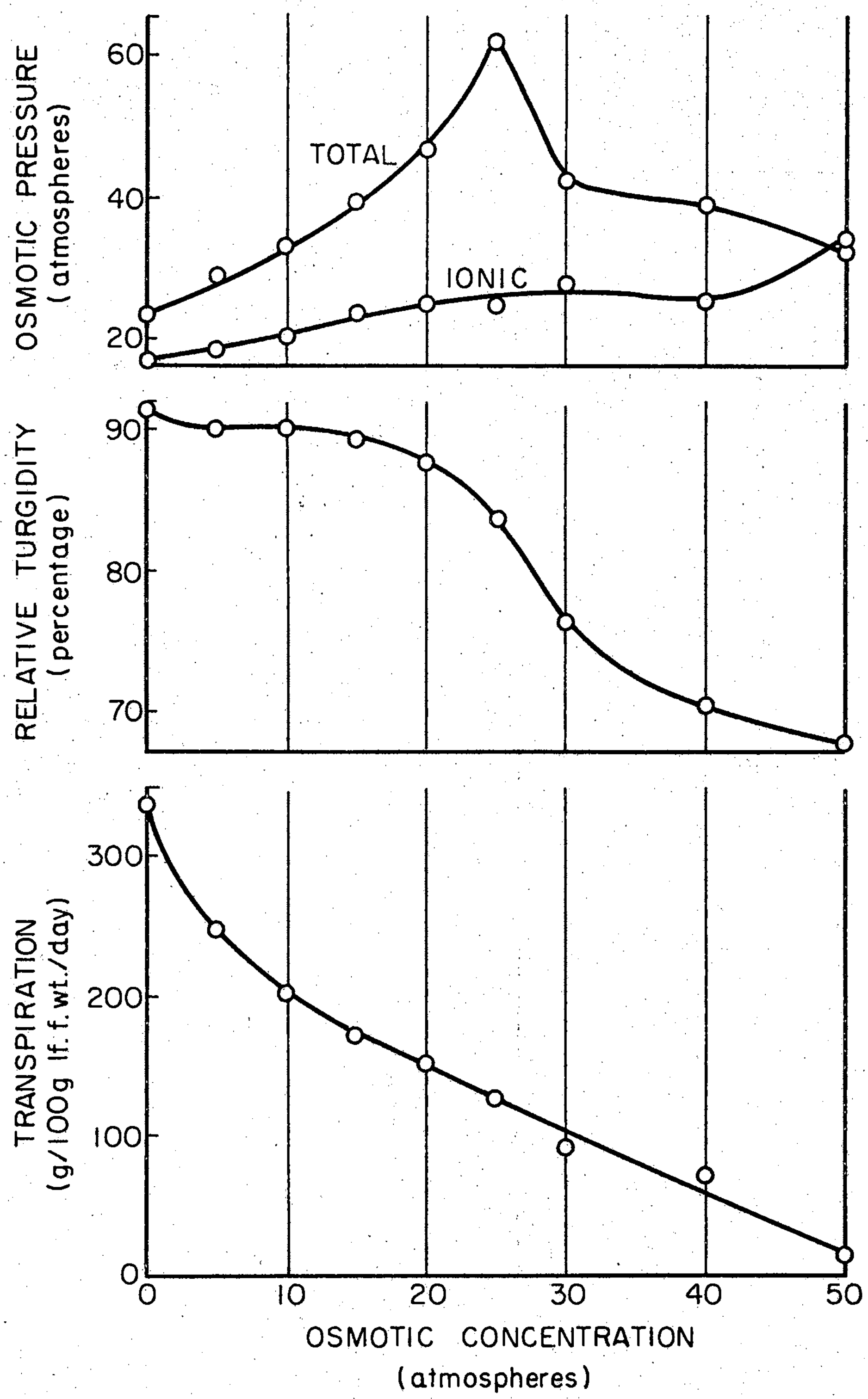

Figure 15. Variations of Average Values of Transpiration, Relative Turgidity and Osmotic Pressure of Alkali Sacaton Under Different Osmotic Concentrations of the Soil Solution

salinity stress. It is quite obvious that accumulation of ionic material in the plants is independent from that of the non-ionic substances. The difference of about seven atmospheres between the ionic fraction and total osmotic material in the control plants is much less than that of about 37 atmospheres in plants under 25 atmospheres stress. This big difference in stressed plants reflects either a higher photosynthetic rate or more hydrolysis of reserve carbohydrates as a result of stress. It is safe to assume that the tolerance limit of this plant is not the 50 atmospheres level of soil salinity but actually the 25 atmospheres. The maximum adjustment that the plant could reasonably sustain was attained at this level of stress. This is also indicated by the sharp decrease in turgidity of plants at 20 atmospheres stress. Although decrease in total osmotic material followed the maximum attained at 25 atmospheres stress, there was a tendency to level off at stresses of 30 atmospheres and above. It is clear that the osmotic potential of plants at higher salinity stress is largely due to the ionic fraction. It became actually an expression of the ionic fraction alone at the 50 atmospheres osmotic pressure of the soil solution.

In blue grama (Figure 16), transpiration rate decreased more or less linearly with increasing osmotic potential in the soil. The rate of transpiration at 40 atmospheres stress was almost reduced by half its value in comparison to the control plants. Relative turgidity decreased logarithmically with increasing stress above the 10 atmospheres stress level in the soil. The osmotic pressure of plants showed a progressive increase with increasing stress up to the 20 atmospheres level where a maximum of 46.48 atmospheres was reached (compared to 36.28 atmospheres in the control plants). The osmotic pressure dropped

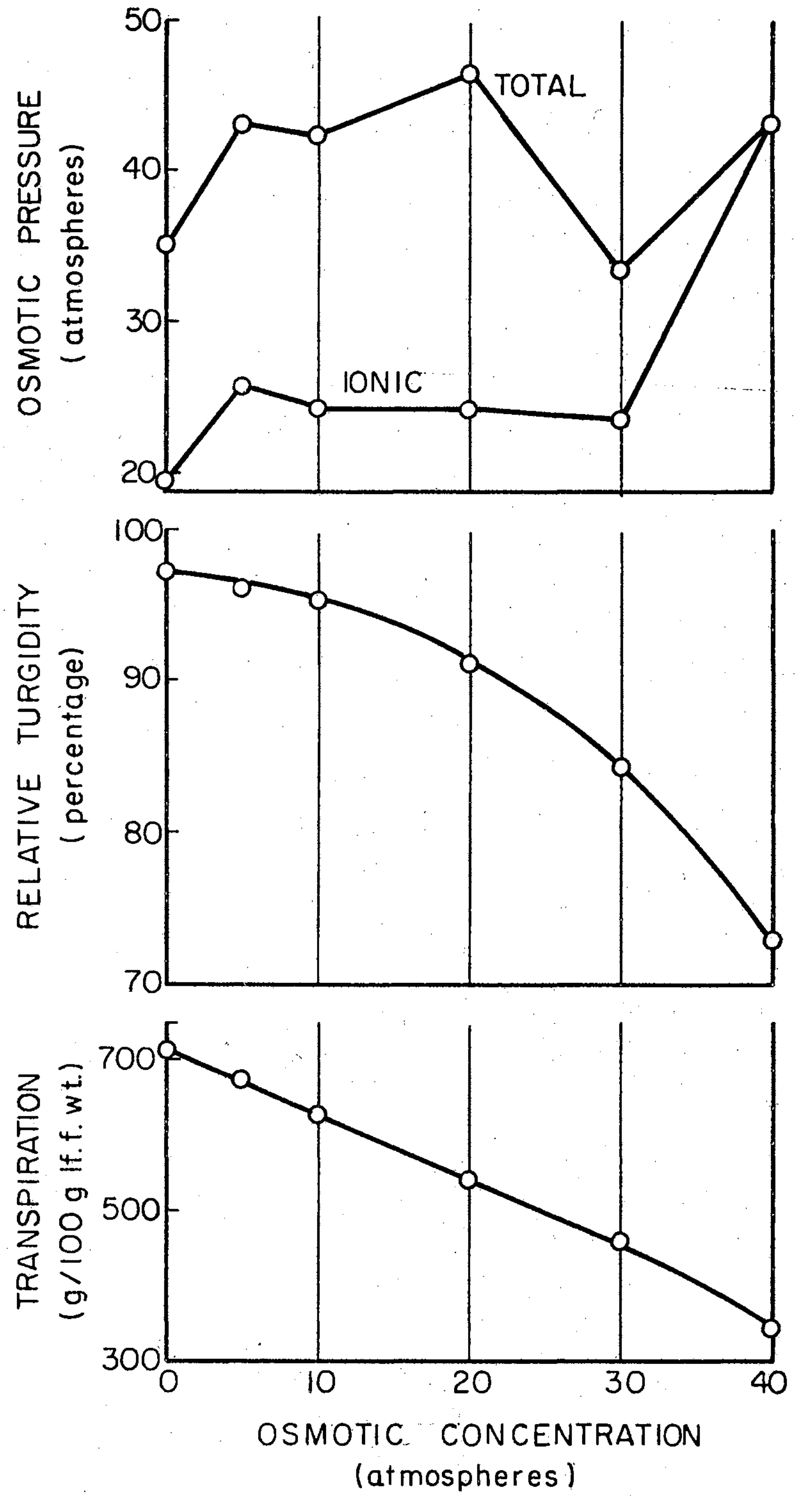

Figure 16. Variation of Average Values of Transpiration, Relative Turgidity and Osmotic Pressure of Blue Grama Under Different Levels of Osmotic Concentrations of the Soil Solution

sharply at higher salinity stress. The ionic fraction of osmotic material increased slightly in the first five atmospheres salinity stress, then tended to remain more or less constant at higher stresses until the 30 atmospheres stress level. It then showed a sharp increase with increasing salinity stress in the soil from 30 to 40 atmospheres. The osmotic potential of the plant at this level of stress was due solely to the ionic fraction.

Discussion and Conclusions

The results presented show a drastic reduction in the transpiration rate of the plants studied as the soil osmotic potential increased. The transpirational behavior seems to be a response to increasing salinity stress rather than a regulatory mechanism to counteract the stress. It is more likely to be the osmotic pressure of the plant that plays the largest role in counteracting the stress. The observed increase in the osmotic pressure of plants with increasing soil salinity up to a maximum, followed by a decrease and leveling off, throws some light on osmotic adjustment as the possible mechanism involved. We find a consistent occurrence of a maximum osmotic value in the three plants studied at a concentration far below the highest which the plant can survive. This maximum may be the actual physiological limit of tolerance that the plant can sustain without an impairment to the water balance or the metabolism of the plant. However, it may not be accurate to refer to this increase in osmotic pressure as an indication of increased synthesis of osmotic material stimulated by stress. Other possibilities may include increased hydrolysis of insoluble carbohydrates and proteins (Eaton et al., 1948; Wadleigh et al., 1945;

Woodhams et al., 1954; and Mothes, 1956); also the decrease in osmotic pressure of plants after the maximum could be attributed to a higher respiration rate rather than to a slower synthesis (Woodhams et al., 1954). The possibility that there may be a maximum physiological adjustment by the plant at some level of salinity stress far below the highest stress the plant can tolerate is somewhat supported by these data. Maximum osmotic potential in saltgrass was attained at 40 atmospheres osmotic potential in the soil, although the plants' tolerance limit was 90 atmospheres. In sacaton, the maximum was at 25 atmospheres although it could tolerate stresses of up to 50 atmospheres in the soil solution. Blue grama had its maximum at 20 atmospheres whereas its tolerance limit was 40 atmospheres. It is rather evident that this maximum is attained near the midrange of the highest stress which the plant could survive. Comparison between the magnitude of these maxima and the potential of the stress at which they take place is equally important. In saltgrass, the maximum of 83.23 atmospheres was attained at 40 atmospheres stress. In sacaton, it was 61.50 atmospheres and attained at 25 atmospheres stress. Blue grama had a maximum of 46.48 atmospheres attained at 20 atmospheres stress. This indicates that the magnitude of this maximum is about twice the amount of stress at which it is attained, and about equal to or slightly greater than the highest stress that the plant can survive.

The ionic fraction of the osmotic material seems to play a slight role in enabling the plant to adjust to salinity stress. The increase in this fraction in both blue grama and saltgrass was not as obvious as changes in the total osmotic material. The sudden and sharp increase of the ionic fraction in blue grama and sacaton just at the highest salinity stress the plants could tolerate may indicate no active uptake of ionic material from the soil by the plant roots. This is supported by the data since all the osmotic material in the plant at the highest level of stress could be accounted for by the ionic fraction. It is quite probable that root damage takes place at these high concentrations, thus making it possible for substantial passive uptake of the ionic material and its rapid translocation through the transpiration stream.

Relative turgidity seems to have no role, or plays only an indirect role, in offering the plant a means of adjustment to stress. Its role may be stimulated by the increase in osmotic material. This is especially true at the lower levels of stress where the relative turgidity retained its high magnitude with relatively slight change as the salinity stress in the soil increased.

CHAPTER VI

SUMMARY

Saltgrass and salt cedar, reported as phreatophytes, were surveyed in the Great Salt Plains of Oklahoma. No water stress problem faced either plant under field conditions during the season this study was made. Transpirational water loss from both plants, though it seemed to be less than loss by evaporation, was substantial. Salt cedar occupies fairly uniform soil types, mostly sandy to sandy loam, with high salinity equally common to the areas studied. Saltgrass occupies a diversity of habitats with variations in salinity, soil texture and fertility. Stresses of salinity in areas inhabited by saltgrass, calculated as the osmotic potential of the soil solution, show that saltgrass has fairly favorable conditions for growth and physiological adjustment. Osmotic stresses average about ten atmospheres in most places.

Laboratory studies of the water relations of saltgrass, alkali sacaton and blue grama under moisture or salinity stress were conducted. The studies confirmed the phreatophytic nature of saltgrass even under stress conditions in the soil resulting from a decreased moisture availability or increased salinity. A criterion common to the plants studied was a decreased transpiration rate under stress conditions whether due to salinity or deficient moisture. The type of relation between transpiration and moisture stress varied according to the species involved. With saltgrass and blue grama, the decrease in transpiration was linear, with a tendency of blue grama to retain a high transpiration rate at medium stress. Alkali sacaton showed a logarithmic decrease in transpiration with increasing moisture stress. Plants adjusted to moisture stress by a combination of a tendency to maintain a high transpiration rate, high relative turgidity, and progressive increase in osmotic pressure, especially at low magnitudes of stress.

Adjustment to salinity appears to be different in mechanism than adjustment to moisture stress. The osmotic potential of the plants seems to play a greater role in adjustment to salinity. Saltgrass could tolerate stresses up to 90 atmospheres under summer greenhouse conditions. Alkali sacaton survived 50 atmospheres salinity whereas blue grama died at stresses higher than 40 atmospheres.

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APPENDIX A

AVERAGE VALUES OF PER CENT SOIL MOISTURE CONTENT IN THE SITES STUDIED IN JUNE AND JULY

Site No.	Plant	Depth (Inch)	Per Cent Moisture Content (g/100 g dry wt.) June	July
1	Saltgrass	0- 2	8.4	9.0
		2- 5	12.0	8.3
		5-10	12.2	7.8
2	Saltgrass	0- 2	12.1	18.5
		2- 5	15.9	20.7
		5-10	16.8	17.6
3	Saltgrass Salt Cedar	0- 2	14.3	7.9
		2- 5	13.9	6.7
		5-10	15.8	7.7
4	Salt Cedar	0- 2	20.4	15.2
		2- 5	19.1	19.2
		5-10	20.0	18.3
5	Saltgrass	0- 2	26.0	25.5
		2- 5	21.4	15.4
		5-10	14.6	13.7
6	Saltgrass Salt Cedar	0- 2	15.8	12.2
		2- 5	24.4	16.4
		5-10	13.4	5.7
7	Salt Cedar	0- 2		12.0
		2- 5		8.2
		5-10		6.9
8	Saltgrass	0- 2		29.3
		2- 5		20.1
		5-10		21.7
9	Saltgrass	0- 2		35.6
		2- 5		27.9
		5-10		20.8

APPENDIX B

AVERAGE VALUES OF SOLUBLE SALTS, pH, AND CALCULATED OSMOTIC PRESSURE OF SOILS IN THE SITES STUDIED

Site No.	Depth (Inch)	pH	ppm Soluble Salts				Osmotic Pressure (Atm.)
			Total	CO_3^{--}	HCO_3^-	Cl^-	
1	0- 2	7.3	550	0	460	89	3.1
	2- 5	7.4	746	0	518	178	5.3
	5-10	7.4	1386	0	690	621	10.3
2	0- 2	8.1	880	0	633	178	2.6
	2- 5	8.0	541	0	460	89	1.5
	5-10	7.8	464	0	403	48	1.6
3	0- 2	7.5	624	0	345	178	2.9
	2- 5	7.5	333	0	284	41	2.8
	5-10	7.6	310	0	272	41	2.2
4	0- 2	7.5	5504	0	460	1243	20.7
	2- 5	7.5	1824	0	430	533	5.2
	5-10	7.5	2912	0	230	1420	9.1
5	0- 2	8.1	3840	113	1898	1065	8.1
	2- 5	8.2	2880	57	1035	976	11.1
	5-10	8.3	3456	57	805	1331	13.5
6	0- 2	8.2	7616	0	1668	3018	37.2
	2- 5	8.0	5120	0	1266	2308	17.1
	5-10	7.5	3840	0	863	1775	32.9
7	0- 2	7.5	10240	0	633	5591	48.0
	2- 5	7.6	5280	0	345	2751	36.6
	5-10	7.5	2832	0	288	1420	22.6
8	0- 2	7.3	25280	0	403	14999	48.7
	2- 5	7.4	4960	0	518	2485	14.4
	5-10	7.6	4960	0	460	2574	13.0
9	0- 2	7.3	1792	0	690	355	2.9
	2- 5	7.8	1984	0	978	444	3.8
	5-10	7.7	1856	0	1150	355	5.1

APPENDIX C

AVERAGE VALUES OF EXCHANGEABLE CATIONS MEASURED IN THE SOILS OF SITES STUDIED

Site No.	Depth (Inch)	Exchangeable Cations (ppm)			
		Na^+	K^+	Ca^{++}	Mg^{++}
1	0- 2	25	125	2800	105
	2- 5	220	145	3100	176
	5-10	828	80	3550	205
2	0- 2	442	71	4500	173
	2- 5	37	44	5300	152
	5-10	33	48	5525	116
3	0- 2	820	94	4350	79
	2- 5	125	35	4200	60
	5-10	50	29	3850	93
4	0- 2	400	70	6950	140
	2- 5	227	54	5850	69
	5-10	170	31	6600	66
5	0- 2	580	299	8900	660
	2- 5	337	248	9600	495
	5-10	268	336	7900	478
6	0- 2	275	90	5600	499
	2- 5	150	128	6100	265
	5-10	960	101	5100	195
7	0- 2	1400	59	3450	117
	2- 5	605	35	3425	42
	5-10	185	33	3025	40
8	0- 2	6000	170	11500	314
	2- 5	951	104	7850	249
	5-10	545	66	7600	142
9	0- 2	56	690	7400	1065
	2- 5	230	543	7900	824
	5-10	148	300	7900	519

APPENDIX D

AVERAGE VALUES OF TRANSPIRATION, RELATIVE TURGIDITY AND OSMOTIC PRESSURE OF SALTGRASS AT DIFFERENT LEVELS OF AVAILABLE MOISTURE IN THE SOIL

Availability Percent	Transpiration[1] (g/100 g lf. f. wt./day)	Relative Turgidity Percent	Osmotic Pressure (Atm.)
5- 10	310	93.4	68.97
20- 25	705	94.6	28.80
35- 40	939	96.2	26.95
50- 55	1120	97.1	25.26
65- 70	1222	97.5	23.79
80- 85	1435	98.4	22.85
95-100	1606	99.8	21.36

[1] Entries on a common vertical line indicate no significant difference among levels of stress at the 5 per cent level of confidence.

APPENDIX E

AVERAGE VALUES OF TRANSPIRATION, RELATIVE TURGIDITY AND OSMOTIC PRESSURE OF ALKALI SACATON UNDER DIFFERENT LEVELS OF AVAILABLE MOISTURE IN THE SOIL

Availability Percent	Transpiration[1] (g/100 g lf. f. wt./day)	Relative Turgidity Percent	Osmotic Pressure (Atm.) Total	Osmotic Pressure (Atm.) Ionic
5- 10	105.1	45.6	82.39	37.11
20- 25	126.5	47.7	72.76	30.64
35- 40	149.4	55.3	69.11	27.64
50- 55	176.4	63.3	62.40	25.78
65- 70	209.6	66.7	57.83	24.43
80- 85	260.0	68.0	44.97	21.20
95-100	325.6	71.7	34.31	16.26

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[1] Entries on a common vertical line indicate no significant difference among levels of stress at the 5 per cent level of confidence.

APPENDIX F

AVERAGE VALUES OF TRANSPIRATION, RELATIVE TURGIDITY AND OSMOTIC PRESSURE OF BLUE GRAMA UNDER DIFFERENT LEVELS OF AVAILABLE MOISTURE IN THE SOIL

Availability Percent	Transpiration[1] (g/100 g lf. f. wt./day)	Relative Turgidity Percent	Osmotic Pressure (Atm.)	
			Total	Ionic
0- 20	435	77.7	51.66	26.34
20- 40	495	85.7	41.26	23.81
40- 60	529	92.9	37.25	23.32
60- 80	617	98.2	37.32	21.16
80-100	711	97.3	36.28	19.51

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[1] Entries on a common vertical line indicate no significant difference among levels of stress at the 5 per cent level of confidence.

APPENDIX G

AVERAGE VALUES OF TRANSPIRATION, RELATIVE TURGIDITY AND OSMOTIC PRESSURE OF SALTGRASS UNDER DIFFERENT OSMOTIC CONCENTRATIONS OF THE SOIL SOLUTION

Osmotic Pressure of Soil Solution (Atm.)	Transpiration[1] (g/100 g lf. f. wt./day)	Relative Turgidity Percent	Osmotic Pressure (Atm.)
0	1284	92.29	26.15
5	1216	92.85	28.19
10	1044	94.45	44.58
15	981	90.23	46.52
20	895	88.60	50.79
30	844	85.16	50.93
40	799	75.45	83.23
60	779	58.16	77.97
90	700	50.40	76.61

[1] Entries on a common vertical line indicate no significant difference among levels of stress at the 5 per cent level of confidence.

APPENDIX H

AVERAGE VALUES OF TRANSPIRATION, RELATIVE TURGIDITY AND OSMOTIC PRESSURE OF ALKALI SACATON UNDER DIFFERENT OSMOTIC CONCENTRATIONS OF THE SOIL SOLUTION

Osmotic Pressure of Soil Solution	Transpiration[1] (g/100 g lf. f. wt./day)	Relative Turgidity Percent	Osmotic Pressure (Atm.) Total	Osmotic Pressure (Atm.) Ionic
0	335.7	91.4	23.76	16.43
5	249.2	90.1	28.93	18.52
10	201.7	90.0	33.32	20.17
15	174.5	89.4	39.76	23.65
20	154.0	87.7	47.15	25.06
25	127.5	83.6	61.50	24.52
30	94.3	76.3	43.57	27.69
40	72.9	70.2	39.28	25.08
50	14.7	67.6	32.14	34.35

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[1] Entries on a common vertical line indicate no significant difference among levels of stress at the 5 per cent level of confidence.

APPENDIX I

AVERAGE VALUES OF TRANSPIRATION, RELATIVE TURGIDITY AND OSMOTIC PRESSURE OF BLUE GRAMA UNDER DIFFERENT OSMOTIC CONCENTRATIONS OF THE SOIL SOLUTION

Osmotic Pressure of Soil Solution	Transpiration[1] (g/100 g lf. f. wt./day)	Relative Turgidity Percent	Osmotic Pressure (Atm.)	
			Total	Ionic
0	711	97.3	36.28	19.51
5	674	96.0	43.24	25.84
10	630	95.2	42.47	24.56
20	540	91.1	46.48	24.39
30	461	84.3	33.67	23.82
40	340	72.8	43.28	43.05

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[1] Entries on a common vertical line indicate no significant difference among levels of stress at the 5 per cent level of confidence.

VITA

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