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RESPONSE PATTERNS OF BOUTELOUA GRACILIS

LEAF WATER POTENTIAL, MEASURED WITH

THE THERMOCOUPLE PSYCHROMETER

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## ABSTRACT

The leaf water balance of Bouteloua gracilis (H.B.K.) Lag. was studied during the summer of 1971 on the Pawnee Grassland, a semiarid shortgrass prairie in northeastern Colorado. A multi-chamber sample holder with Spanner thermocouple psychrometers was constructed to allow field measurements of the diurnal and seasonal trends of leaf water potential ( $\Psi_{\text{leaf}}$ ). The potential decreased each day from a morning high which became lower as the season progressed, reaching a minimum of about -70 bars in August. The diurnal data show how rapidly the potential responds at certain times of the year to change in vapor pressure deficit. The early morning level of  $\Psi_{\text{leaf}}$  appears to be determined by soil water potential, but diurnal responses are a function of soil water potential, vapor pressure deficit (VPD), and leaf condition. Early in the growing season soil water was more available and the magnitude of diurnal response was low, despite considerable change in VPD. As soil water is depleted, the magnitude of  $\Psi_{\text{leaf}}$  change during the day increased, probably due to a greater absorption lag. As soil water became extremely limiting and leaf condition declined, the diurnal change was less. It seems apparent that VPD is less important for control of  $\Psi_{\text{leaf}}$  when soil water is readily available or when plant water stress is sufficiently severe to prevent stomatal opening during the day.

Response patterns of B. gracilis  $\Psi_{\text{leaf}}$  were about the same on three different Pawnee soils, an observation which may simplify the development of a spatial model.

Experiments were conducted to determine the effect of simulated rainfall totaling 13.0 mm. Blue grama  $\Psi_{\text{leaf}}$  responded rapidly with an increase from -60 bars to -30 bars in 12 hr. However, 9 days after watering, the  $\Psi_{\text{leaf}}$  was the same as the control. Limited data are presented which show

the effect of increased water stress on photosynthesis. Leaf water stress increased more rapidly on plots with more leaf area. The results are discussed with regard to the adaptations that have evolved in B. gracilis for the shortgrass prairie environment.

## INTRODUCTION

The functioning of vegetation in an arid environment is controlled to a large extent by water availability. Since water stress affects nearly every aspect of plant growth, modifying anatomy, morphology and physiology (Kramer, 1969), it is of interest to measure the water stress of plants adapted to areas of low rainfall and high evapotranspiration and to observe how the stress varies under different conditions. The objective of this study was to examine the response patterns of leaf water potential of Bouteloua gracilis (H.B.K.) Lag., a common species in the shortgrass prairie of North America, and to determine which environmental factors exercise the greatest control over this potential. Leaf water potential is a sensitive indicator of plant water balance, and B. gracilis was studied because it is a drought tolerant species that comprises about 80 percent by weight of the gramineous vegetation of many shortgrass ecosystems (Albertson, et al., 1966).

The degree of plant water stress depends on the relative rates of water absorption and transpiration, both of which are affected by a combination of soil, plant and atmospheric conditions. Transpiration rate is determined by leaf structure, stomatal resistance, vapor pressure deficit and wind. The rates of water absorption are controlled by the rate of water loss, structure of the root system, soil aeration, soil temperature and soil water potential (Kramer, 1963). These environmental factors influence plant growth by affecting the internal water balance of a plant and hence the physiological factors which control growth. For example, water stress has been shown to affect

rates of photosynthesis (Boyer, 1970b), RNA metabolism (Gates and Bonner, 1959), leaf enlargement and metabolic rates (Boyer, 1970a), and translocation and mineral absorption (Kramer, 1963).

Water potential is a rather new term in plant-water relations. It is numerically equal to the negative value of diffusion pressure deficit, being the difference between the free energy or chemical potential per unit molal volume of pure water and that of water in solution at the same temperature and pressure. The potential of pure water is arbitrarily set at zero, and therefore the potential of water in cells and solution is less than zero, or negative (Kramer, Knippling and Miller, 1966). Several authors (Slatyer and Taylor, 1960; Kramer, Knippling and Miller, 1966; and Slatyer, 1967) have suggested using the term water potential rather than diffusion pressure deficit because it is more consistent with thermodynamic concepts.

Total plant water potential is composed of various component potentials as shown by the following equation from Brown (1970),

$$\Psi = \Psi_{\pi} + \Psi_m + \Psi_p \quad (1)$$

where  $\Psi$  is total water potential,  $\Psi_{\pi}$  is the osmotic component,  $\Psi_m$  is the matric component and  $\Psi_p$  is the pressure potential. In the plant  $\Psi$  is negative or rarely zero in a fully turgid cell. The relationship between water potential and relative vapor pressure is

$$\Psi = \frac{RT}{V} \ln \frac{e}{e_o} \quad (2)$$

where  $\Psi$  is water potential in bars,  $R$  is the universal gas constant,

$T$  is absolute temperature in  $^{\circ}\text{K}$ ,  $\bar{V}$  is the partial molal volume of water,  $e$  is the actual vapor pressure of water in the system, and  $e_0$  is the vapor pressure of pure free water. Equation (2) shows that vapor pressure of water in a system is a sensitive indicator of water potential; the psychrometer actually measures the vapor pressure.

Spanner (1951) was the first to use small thermocouple psychrometers to measure water potential, but since that time numerous investigators have used them for both soil water potential and plant water potential (Richards and Ogata, 1958; Ehlig, 1962; Boyer, 1966; Hoffman and Splinter, 1968; Lang, 1968; Rawlins, Gardner and Dalton, 1968; and, Wiebe, Brown, Daniel and Campbell, 1970). Due to strict temperature requirements of thermocouple psychrometry, measurements of plant water potential have, for the most part, been restricted to the laboratory. For this study a sample chamber with thermocouple psychrometers was designed that allows field measurements of leaf water potential. With this instrument it was possible to observe the seasonal and diurnal response patterns of B. gracilis (blue grama) leaf water potential, as well as the response to natural and simulated rainfall. The research was conducted on the Pawnee Grassland, the intensive study area of the Grassland Biome phase of the International Biological Program.

## DESCRIPTION OF STUDY AREA

The Pawnee Grassland is about seven miles north of Nunn, Colorado, and is located on the Central Plains Experimental Range, operated by the Agricultural Research Service of the U.S.D.A. Clear, warm days and cool nights characterize the climate during the growing season. During a 15 year period the annual precipitation averaged 304 mm, 72 percent of which fell during the growing season (Klippel and Costello, 1960). Most of the precipitation was received in thunderstorms of short duration. Winds with velocities of 48 to 56 kilometers per hour are frequent, and winds of gale velocity are experienced at some time during most years. Daily high temperatures during the growing season average 27° C, but a high of 40° C and a low of -23° C have been recorded in a 15 year period from 1939 through 1953.

The vegetation on the Pawnee Grassland is characterized by blue grama (Bouteloua gracilis) and buffalo grass (Buchloe dactyloides [Nutt.] Engelm.) which produce 65 to 90 percent of the forage taken by cattle (Klippel and Costello, 1960). Taller grasses such as western wheatgrass (Agropyron smithii Rydb.) and needle and thread (Stipa comata Trin. & Rupr.) are conspicuous on areas of better range condition. Short sedges such as threadleaf (Carex filifolia Nutt.) and sun sedge (Carex heliophila [= pennsylvanica] Mackenz.) are generally present throughout the vegetation cover. Several perennial forbs are common, including scarlet gaura (Gaura coccinea Nutt. ex Pursh), slimflower scurfpea (Psoralea tenuiflora Pursh), scarlet globemallow (Sphaeralcea coccinea [Pursh] Rydb.), pricklepoppy (Argemone polyanthemus Ownb.) and



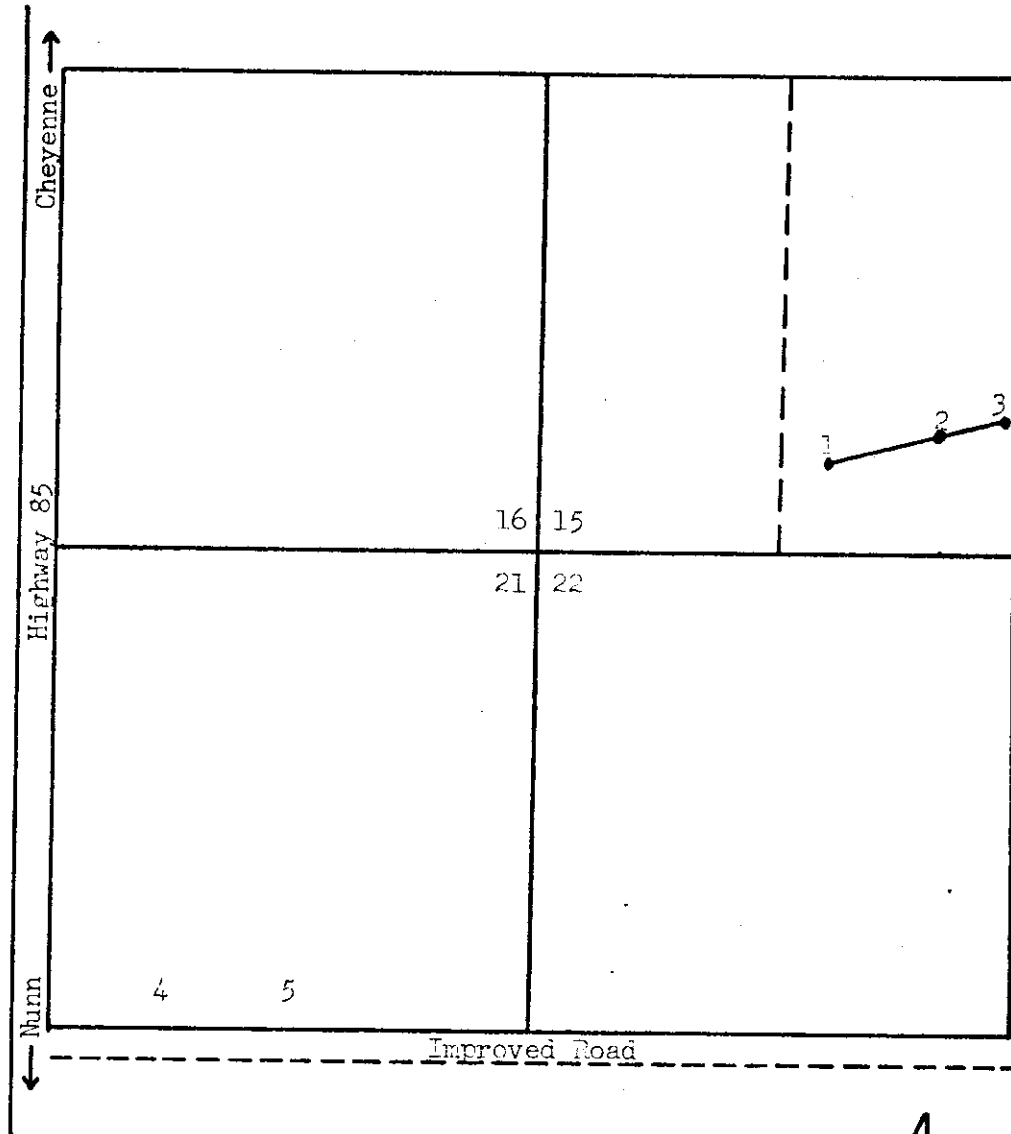
wavyleaf thistle (Cirsium undulatum (Nutt.) Spreng.). Annual forbs include Russian thistle (Salsola kali tenuifolia Tausch.), lambsquarter (Chenopodium album L.), mountain evening primrose (Oenothera latifolia [Rud.] Munz), and woolly Indianwheat (Plantago purshii Roem. & Schult.). Common shrubs include rubber rabbitbrush (Chrysothamnus nauseosus [Pall.] Gritt.), broom snakeweed (Gutierrezia sarothrae [Fursh] Britt. & Rusby) and fringed sagewort (Artemisia frigida Willd.). Plains pricklypear (Opuntia polyacantha Haw.) is also common.

The soils of the Pawnee Grassland are representative of the dark brown and brown soils of the cool and semiarid grasslands of the Central Great Plains region (Klipple and Costello 1960). The major soil series include the Ascalon fine sandy loam, Renohill clay loam, Shingle clay loam and Vona fine sandy loam. In addition, there are areas of undifferentiated soils.

## METHODS

Two approaches were used to evaluate the response patterns of Bouteloua gracilis leaf water potential and to determine what factors were most critical for controlling leaf water stress. The first approach was designed to evaluate diurnal and seasonal patterns on different soil types. Accordingly, a transect was selected that traversed the Ascalon, Renohill and Shingle-Renohill soil series. Van Haveren (1972) had established neutron access tubes and soil thermocouple psychrometers (at 2, 10, 20, 40, and 60 cm depths) along this same transect, making it a logical choice for a leaf water potential study. Three study areas were selected along the transect, each near a stack of Van Haveren's soil psychrometers and one on each soil type. The transect was located on a moderately summer-grazed (ca. 1 ha per yearling month) pasture in the east half of section 15 (T 10N, R 66W), Fig. 1.

The second approach was experimental in nature, involving simulated rainfall and sites with different leaf areas. The objective was to evaluate the possible significance of short summer showers by determining how rapidly leaf water stress subsided following a pulse of moisture, how rapidly the pre-treatment stress was reattained, and whether the response was influenced by a greater amount of leaf area. Some of my measurements were coordinated with the CO<sub>2</sub> uptake studies of A. J. Dye and Joe Trlica, and the infiltration and soil respiration studies of Freeman Smith, Bruce Van Haveren and David Coleman, all of Colorado State University. The location and method for each experiment will be described later in this report.



#### Legend

- 1 Ascalon soil series
- 2 Renohill soil series
- 3 Shingle-Renohill soil series
- 4 Stress plots
- 5 BFP Headquarters



Sections 15, 16, 21, 22  
T 10N R 66W

#### Scale

1 mile =  $2\frac{1}{2}$  inches

Fig. 1. Map of a portion of the Pawnee Grassland showing the location of the soil transect (1, 2, and 3) and the experimental plots (4).

### Measurement of Leaf Water Potential

Chromel-constantan thermocouple psychrometers were used to measure water potential. The interested reader is referred to Spanner (1951), Korven and Taylor (1959), Boyer and Knipling (1965), Lambert and van Schlifgaarole (1965), Boyer (1966), Campbell, Zollinger and Taylor (1966), Dalton and Rawlins (1968), Hoffman and Herkelrath (1968), Brown (1970) and Wiebe, Campbell, Gardner, Rawlins, Cary and Brown (1971). Peck (1968), 1969) gives the complete theory for the Spanner thermocouple psychrometer.

Each psychrometer was calibrated over solutions of KCl of known water potential (0.1m, 0.3m, 0.5m, 0.7m, 1.0m, 1.2m, 1.4m, and 1.6m). From the calibration curve of known water potential versus microvolt output, the water potential of any material can be determined in a range from 0 to -70 bars. A typical calibration curve for one of the psychrometers is shown in Fig. 2.

One restriction in the use of Spanner psychrometers is strict temperature control during the short time that measurements are made; ambient temperature fluctuations result in an error of about 1 bar per 0.01 °C. To provide adequate insulation of the psychrometers and reduce temperature fluctuations, a multi-chamber sample holder with thermocouple psychrometers was constructed of machineable nylon to allow the field measurement of leaf water potential of 14 samples. Instrument design is shown in Fig. 3, 4, 5, and 6. A minimum of two inches of nylon separated each psychrometer from the exterior. In addition, the entire apparatus was placed in a styrofoam insulated box to further reduce temperature fluctuations.

Two excised leaves were used for each determination of blue grama leaf water potential. A two inch segment of one leaf lined the walls

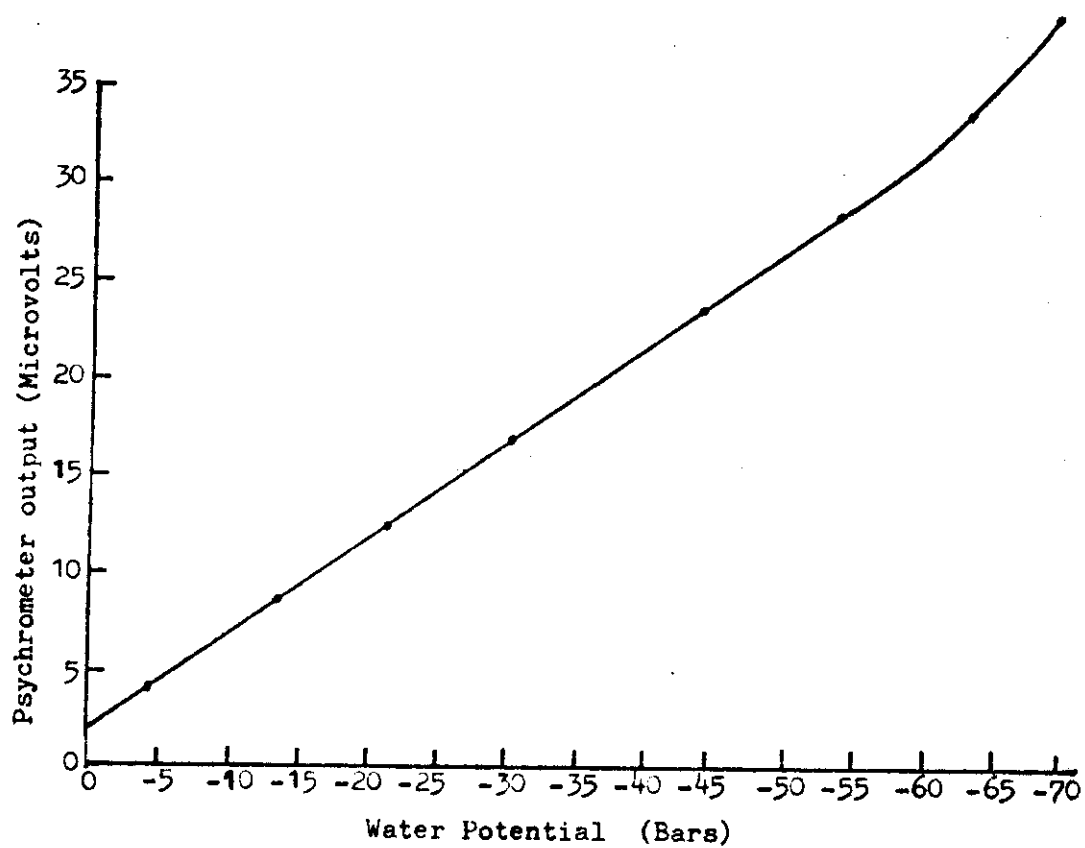


Fig. 2. Calibration curve for Spanner thermocouple psychrometer No. 5B3.

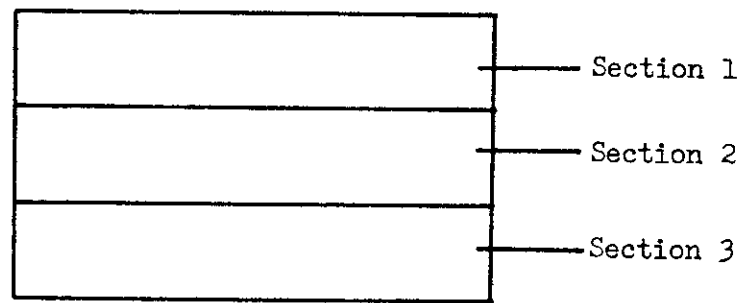


Fig. 3. Side view of multi-chamber sample holder ( $\frac{1}{4}$  scale).

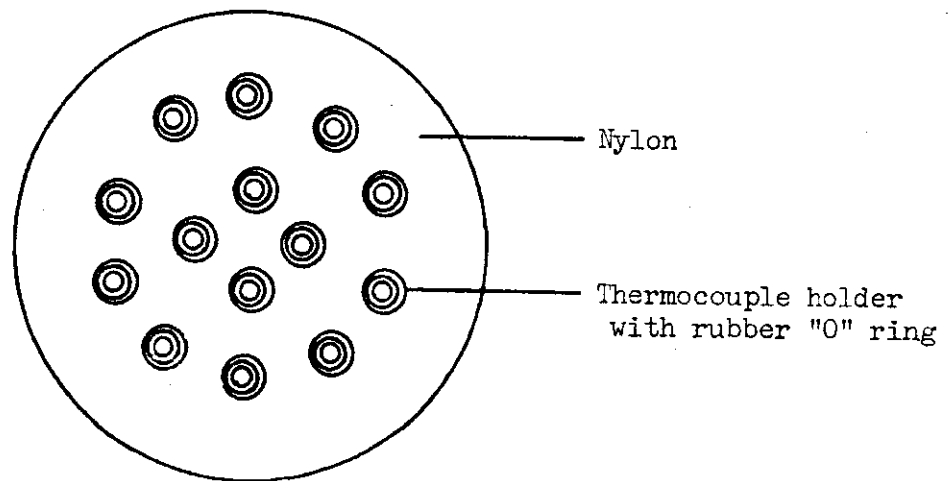


Fig. 4. Bottom view of Section 2 ( $\frac{1}{4}$  scale).

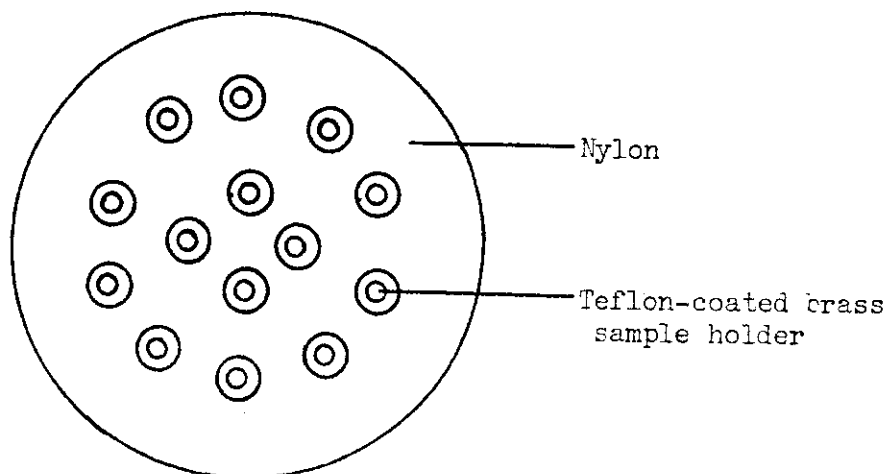


Fig. 5. Top view of Section 3 ( $\frac{1}{4}$  scale).

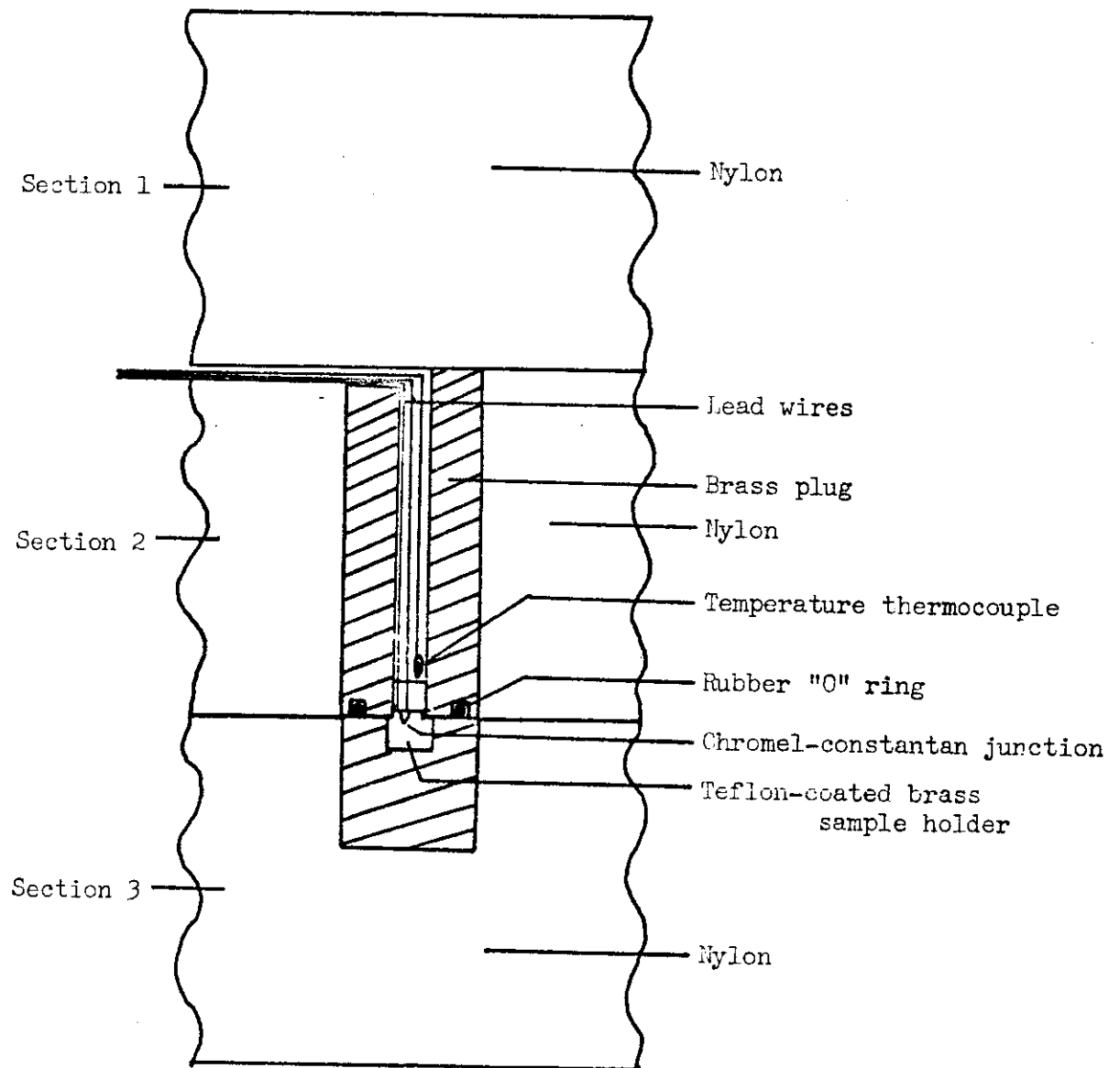


Fig. 6. Cut-away section view of one thermocouple psychrometer sample chamber (actual size).

of the sample chamber and a two inch segment of the second leaf was cut into approximately  $1/8$  inch pieces to fill the remainder of the chamber. When all 14 of the chambers were filled with leaf material, the sample holder was sealed by bolting the instrument together with hex head bolts. Rubber "O" rings permitted a tight seal around the chambers and prevented the loss of water vapor. The time required to fill all 14 chambers was 3 to 4 minutes, and it was determined that no significant drying of leaf material occurred during this time. After a predetermined equilibration time of one hour (see Fig. 7), leaf water potential was measured.

The copper lead wire from the chromel wire was attached to the positive terminal of a switch box and the lead wire from the constantan wire was attached to the negative terminal of the switch box (Construction details in Brown 1970), which was in turn connected to a Kiethley Model 155 microvoltmeter. The switch box contains circuitry which can impose a cooling or heating current to the thermocouple junction. An electromotive force (EMF) generated at the thermocouple junction before cooling is proportional to the dry bulb temperature of the sample chamber. The junction can be cooled by imposing a 5 milliamp current in a direction opposite to the normal flow of current for 25 seconds. This is known as the Peltier effect. When the chromel-constantan junction is cooled below the dew point of the atmosphere of the sealed chamber, condensation of water on the junction will occur. The EMF generated at the junction after cooling is due to the evaporation of the condensate and is proportional to the wet bulb temperature of the atmosphere in the chamber. The difference between the two EMF readings



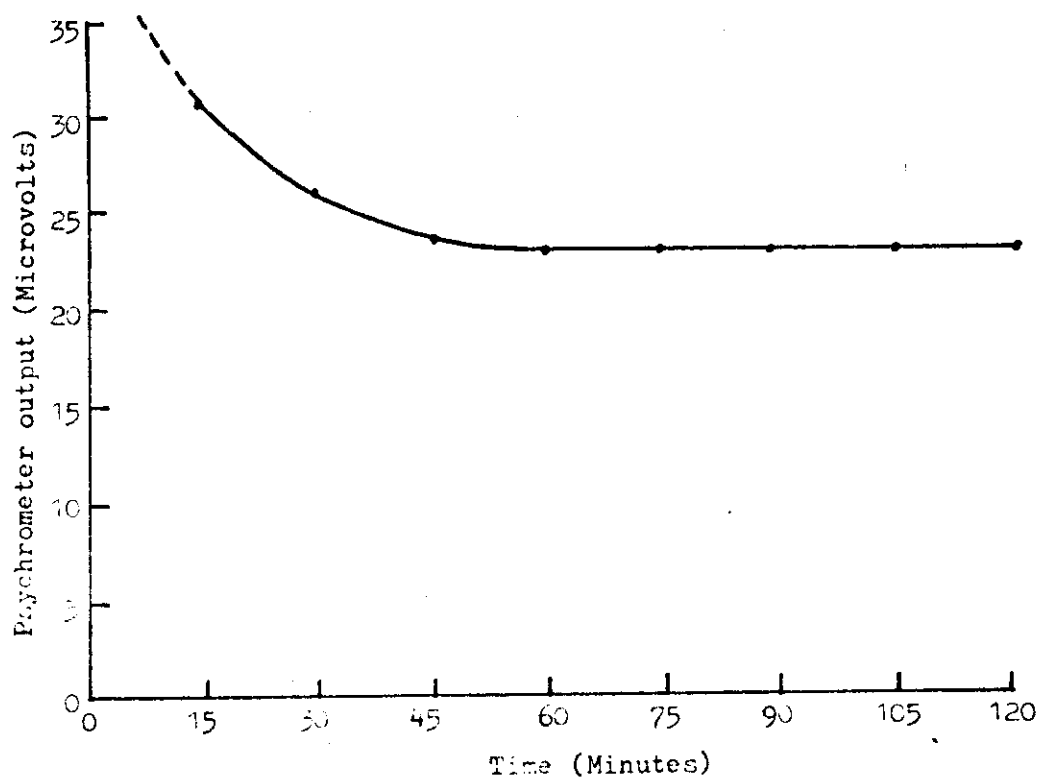


Fig. 7. Equilibration curve for *B. gracilis* leaf material.

is the wet bulb depression. The temperature of each individual chamber is determined from a thermocouple located behind the chromel-constantan junction.

The step-by-step procedure is as follows:

1. The lead wires are attached as previously described.
2. The switch box is turned to the "read" position.
3. The microvoltmeter is set to zero output.
4. The switch box is then set on the cooling position for 25 seconds.
5. The switch box is then turned to the read position and deflection of the needle on the microvoltmeter is read.
6. The above procedure is repeated two or three times or until reproducible readings are obtained.
7. The microvolt output is converted to leaf water potential using the calibration curve for the appropriate thermocouple.

Leaf water potential was also determined by the Shardokov dye method as outlined by Knipling (1966). Twenty to twenty-five leaves of blue grama were placed into 15 x 100 mm test tubes containing 10 ml. of graded sucrose solutions of known water potential. Four hours equilibration time was required for the dye method.

Leaf water potential was measured along the soil type transect weekly from June 11 to August 11, 1971, four times a day (0430, 1000, 1500 and 1930 hours Mountain Standard Time). The periodicity of measurements for each of the experiments will be described later. Leaf area data were available from Knight (in press).

### Measurement of Environmental Factors

Air temperature and relative humidity were determined with an aspirated psychrometer at the midpoint height of blue grama leaves each time leaf material was sampled for water potential. These readings were later converted to vapor pressure deficit. Precipitation and soil water potential data were available from Van Haveren (1972).

### Data Analysis

In addition to simple graphical analysis to determine patterns of leaf water potential, the data were analyzed by linear regression, and by stepwise and multiple regression and correlation (Steel and Torrie 1960), the dependent variable being leaf water potential and the independent variables being vapor pressure deficit and soil water potential at five depths.

## RESULTS

### Comparison of Psychrometry and Dye Techniques

The Shardokov dye method gave consistently higher potential measurements than the psychrometer, Fig. 8. Although Knipling and Kramer (1967) reported close agreement between the two methods for a variety of species (Cornus florida L., Quercus alba L., Pinus strobus L., Helianthus annuus L., and Nicotiana tabacum L.), they did not examine any grasses. Goode and Hagerty (1965) caution that solute uptake by plant tissue leads to apparent higher water potentials than actually exist, and this may be one reason for the results obtained with B. gracilis. Despite the discrepancy, Fig. 8 shows that both methods resulted in similar relative changes during the day.

The question arises about which method is measuring the actual water potential. The psychrometric readings are probably more accurate because the measurements obtained were more consistent with the soil water potential data and because the technique is less subject to error (Spanner 1951, Box 1965, and Rawlins and Dalton 1967).

### Soil Transect Study - Diurnal Patterns

The maximum leaf water potential for each of the three soil types was measured consistently at 0430 hours MST. These early morning maximum values, however, declined steadily during the summer from about -25 bars in mid-June to about -65 bars in mid-August, with no major differences noted between soil types, Fig. 9, 10, and 11. Even the higher mid-June values of -25 bars are very low for a morning "recovery" reading; leaf area in fact has been observed to decline after mid-June (Knight, in press).

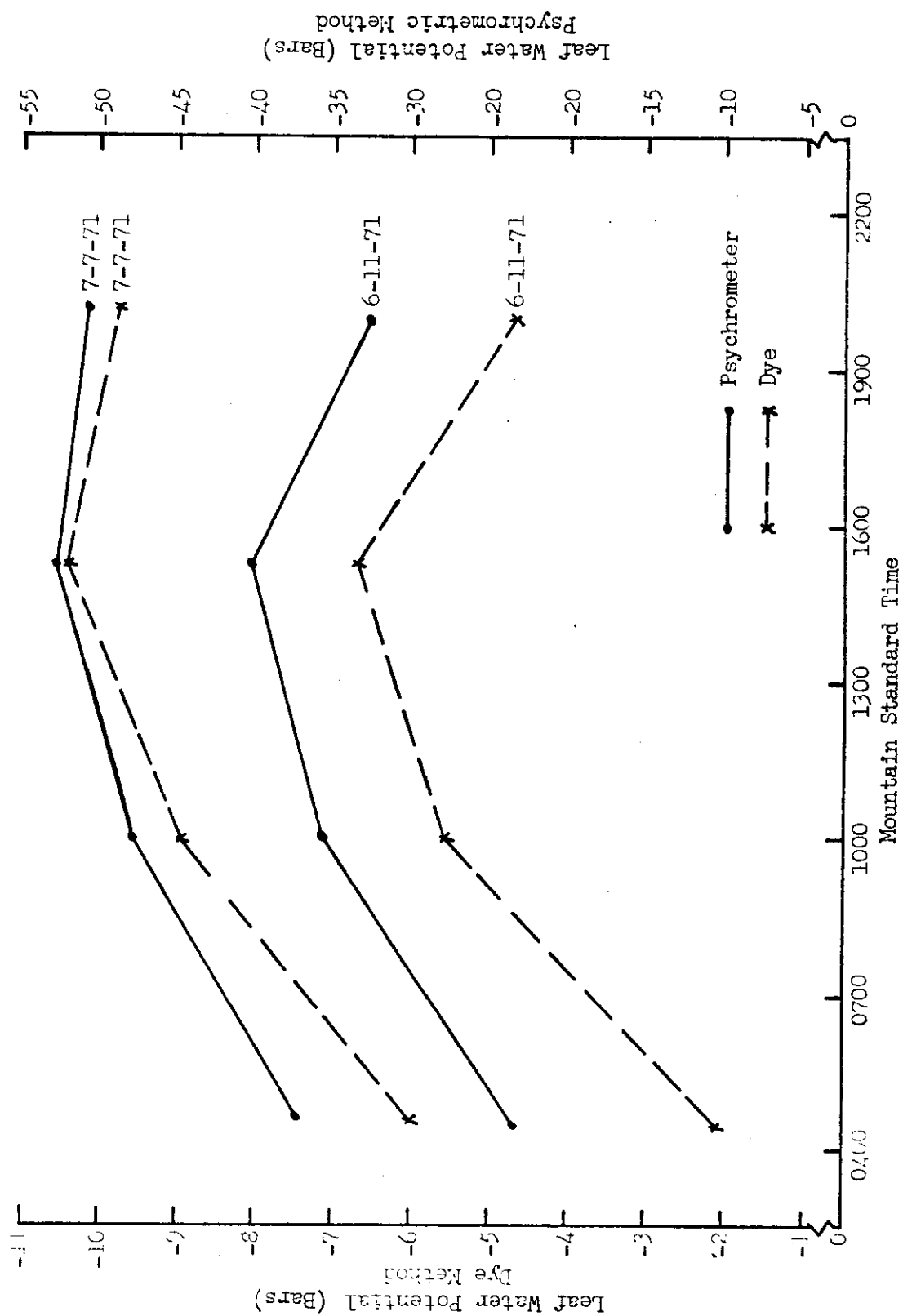


Fig. 8. Comparison of dye and psychrometric methods (Ascalon Soil Series).

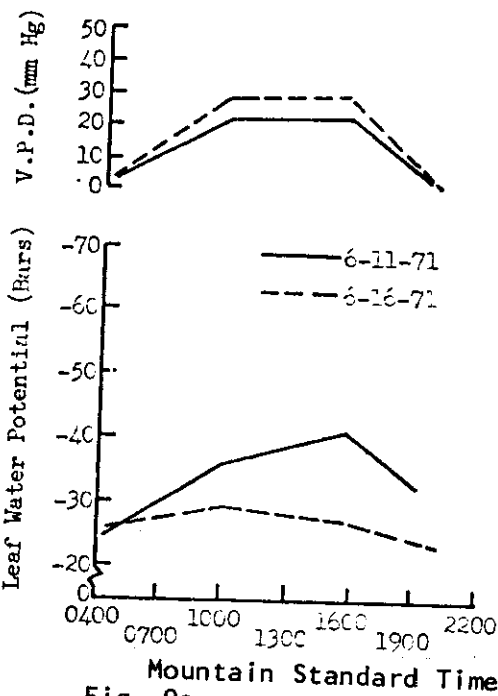


Fig. 9a.

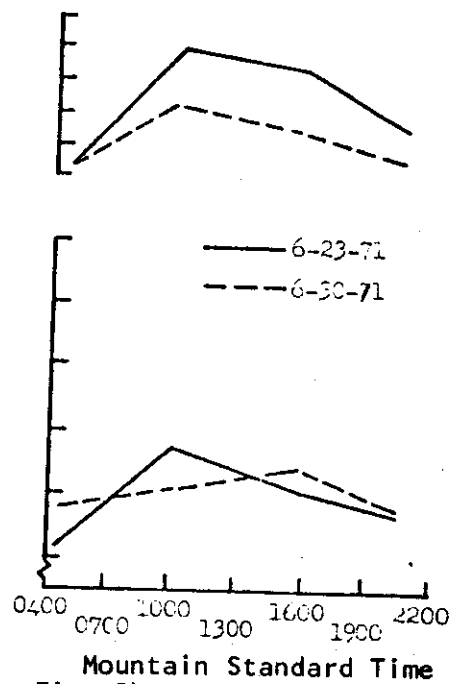


Fig. 9b.

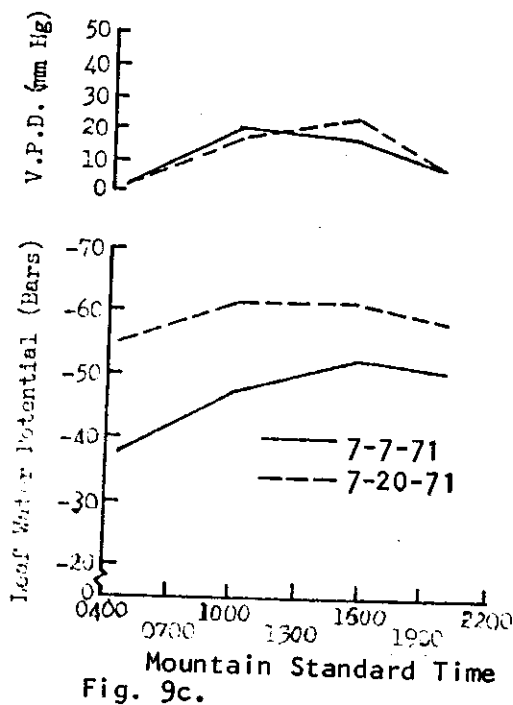


Fig. 9c.

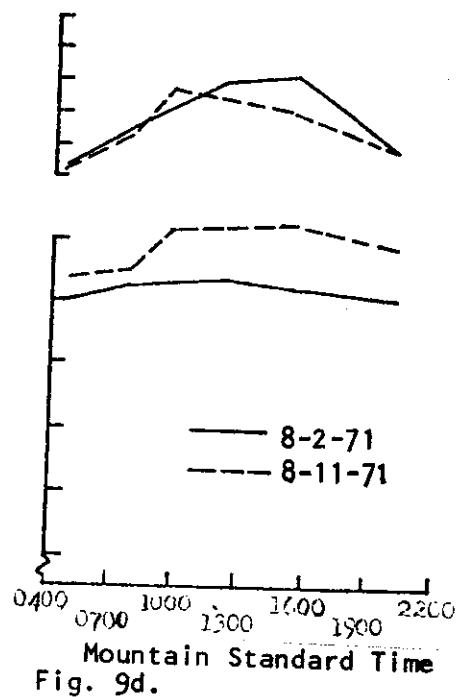


Fig. 9d.

Fig. 9a, b, c and d. Diurnal and seasonal trends of leaf water potential and vapor pressure deficit on the Ascalon site of the soil transect.

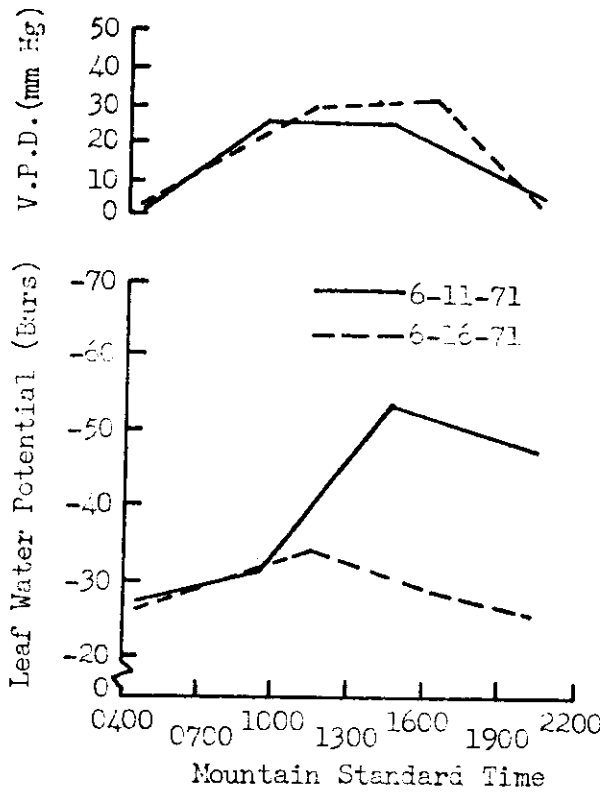


Fig. 10a.

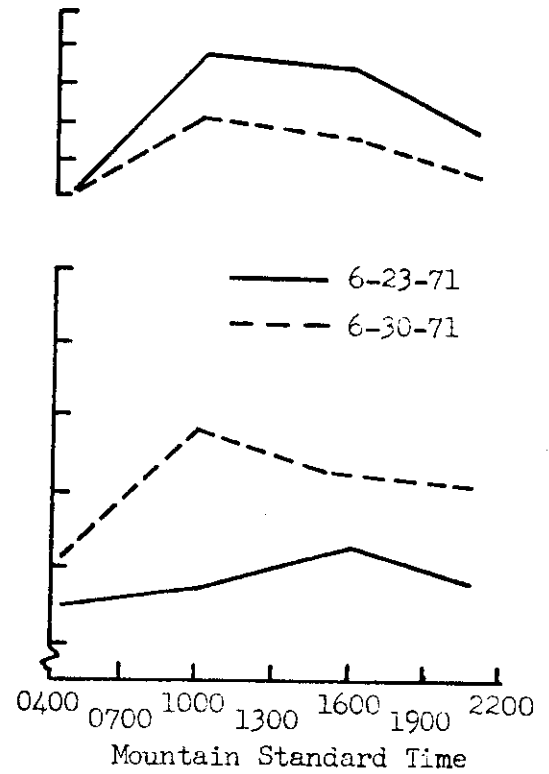


Fig. 10b.

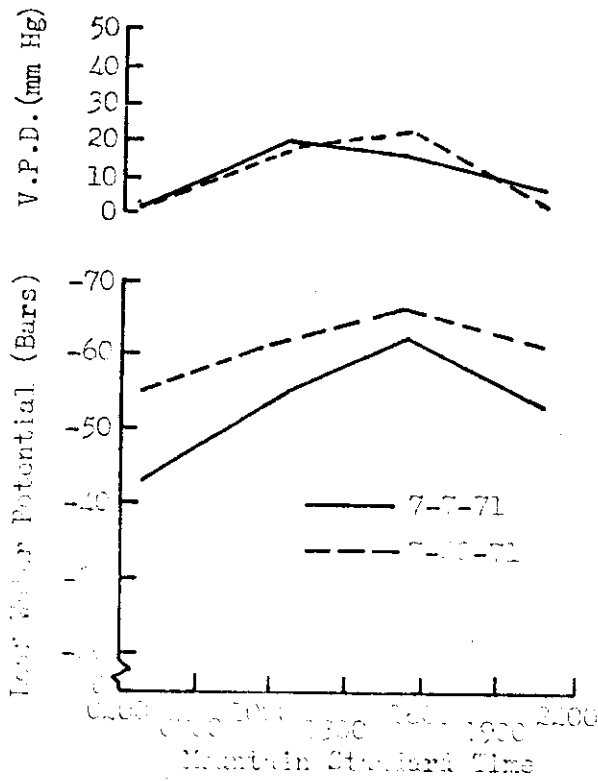


Fig. 10c.

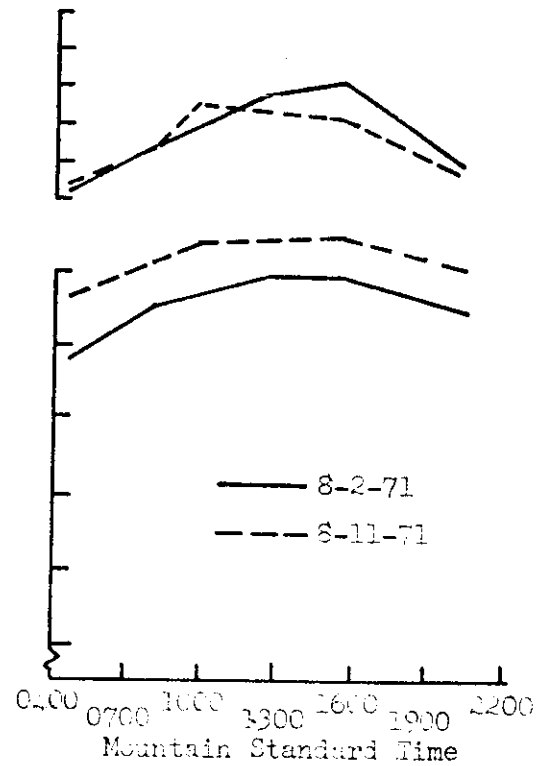


Fig. 10d.

Fig. 10a, b, c and d. Diurnal and seasonal trends of leaf water potential and vapor pressure deficit on the Renohill site of the soil transect.

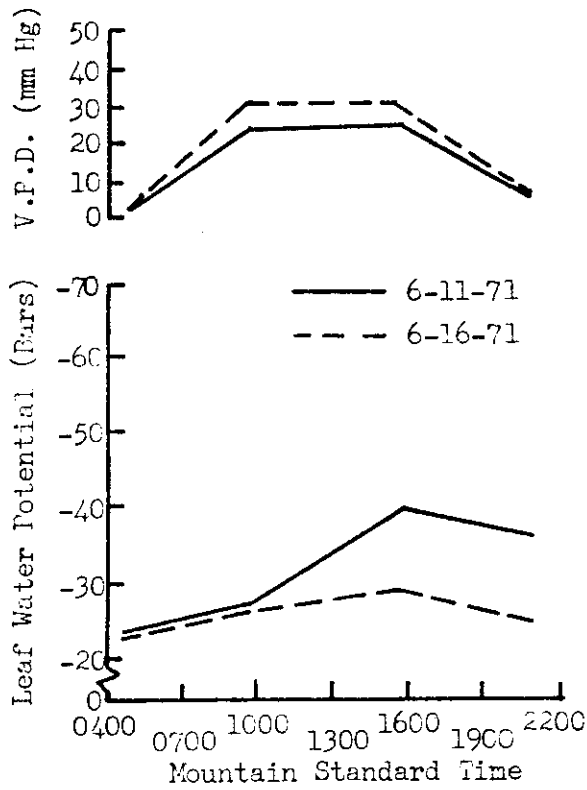


Fig. 11a.

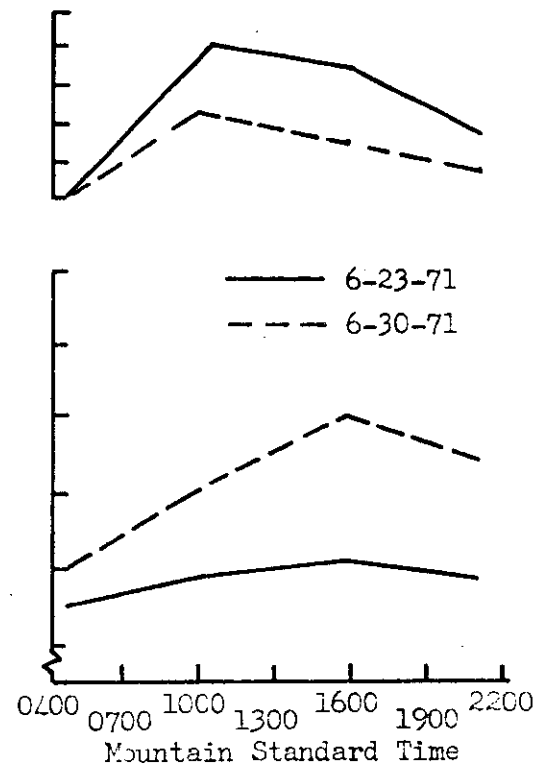


Fig. 11b.

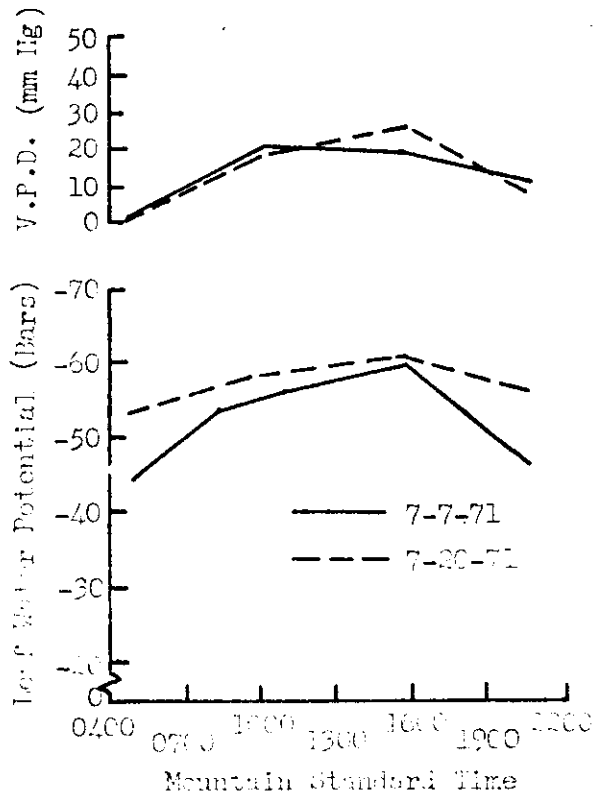


Fig. 11c.

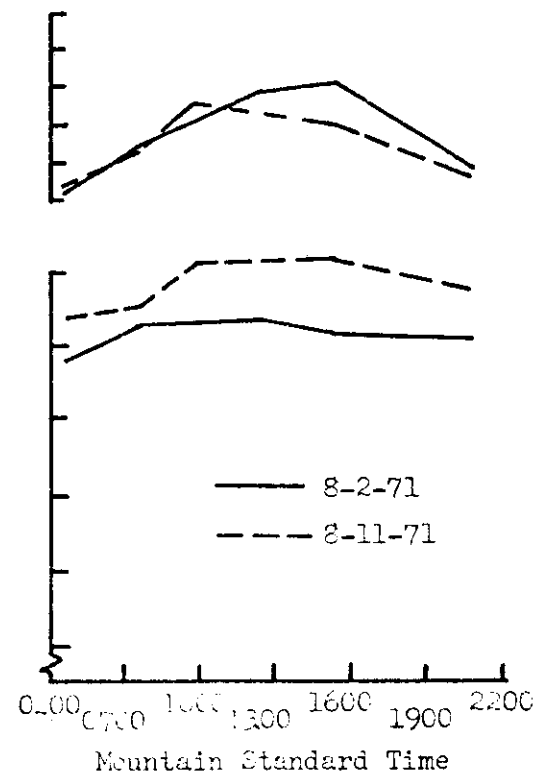


Fig. 11d.

Fig. 11a, b, c and d. Diurnal and seasonal trends of leaf water potential and vapor pressure deficit on the Shingle-Renohill site of the soil transect.



As expected, the  $\psi_{\text{leaf}}$  declined steadily until late morning or early afternoon. Minimum  $\psi_{\text{leaf}}$  was measured usually at about the same time as maximum VPD, and ranged from -40 to -50 bars in mid-June to about -70 bars in mid-August, Fig. 9, 10, and 11. As temperature and VPD decrease in the afternoon and evening, absorption of water approaches or exceeds transpiration with a gradual increase in  $\psi_{\text{leaf}}$ . The same trends were observed on all three soil types throughout the study period.

An examination of Fig. 12, 13, and 14 shows that on some days the diurnal change in  $\psi_{\text{leaf}}$  is negligible, whereas on other days there is considerable change. A possible explanation for this difference in response pattern is based on soil water availability and stage of plant growth. For example, on June 11 there was a considerable change during the day; the soil was very dry at this time (-40 to -50 bars at 2 cm). Just before June 16, the next sampling date, a light shower occurred which allowed the  $\psi_{\text{leaf}}$  to increase considerably. The magnitude of  $\psi_{\text{leaf}}$  change on the 16th was much reduced from the previous week, most likely because there was less of a lag in water absorption with the larger amount of soil water. As soil water decreased in the following weeks, the magnitude of  $\psi_{\text{leaf}}$  change during the day increases, until July 20 when diurnal fluctuations were again reduced. This final damping of diurnal fluctuations is probably due to unavailability of soil water, the onset of senescence and the closure of stomata throughout the day. It seems apparent that VPD is thus not as important a factor affecting  $\psi_{\text{leaf}}$  when soil water is readily available or when plant water stress is sufficiently severe to prevent stomatal opening during the day.

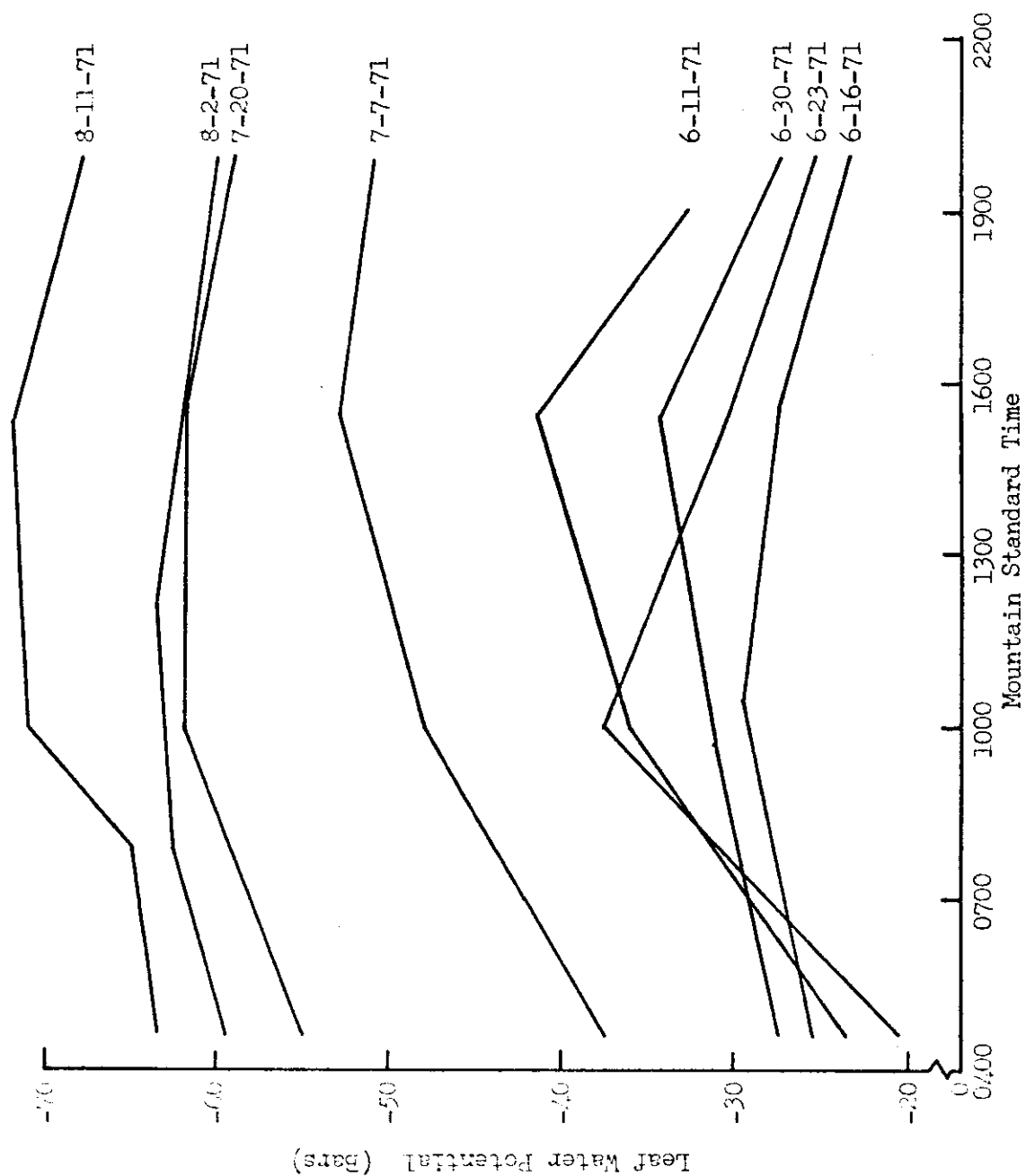


Fig. 12. Diurnal and seasonal trends of leaf water potential on the Ascalon site of the soil transect.

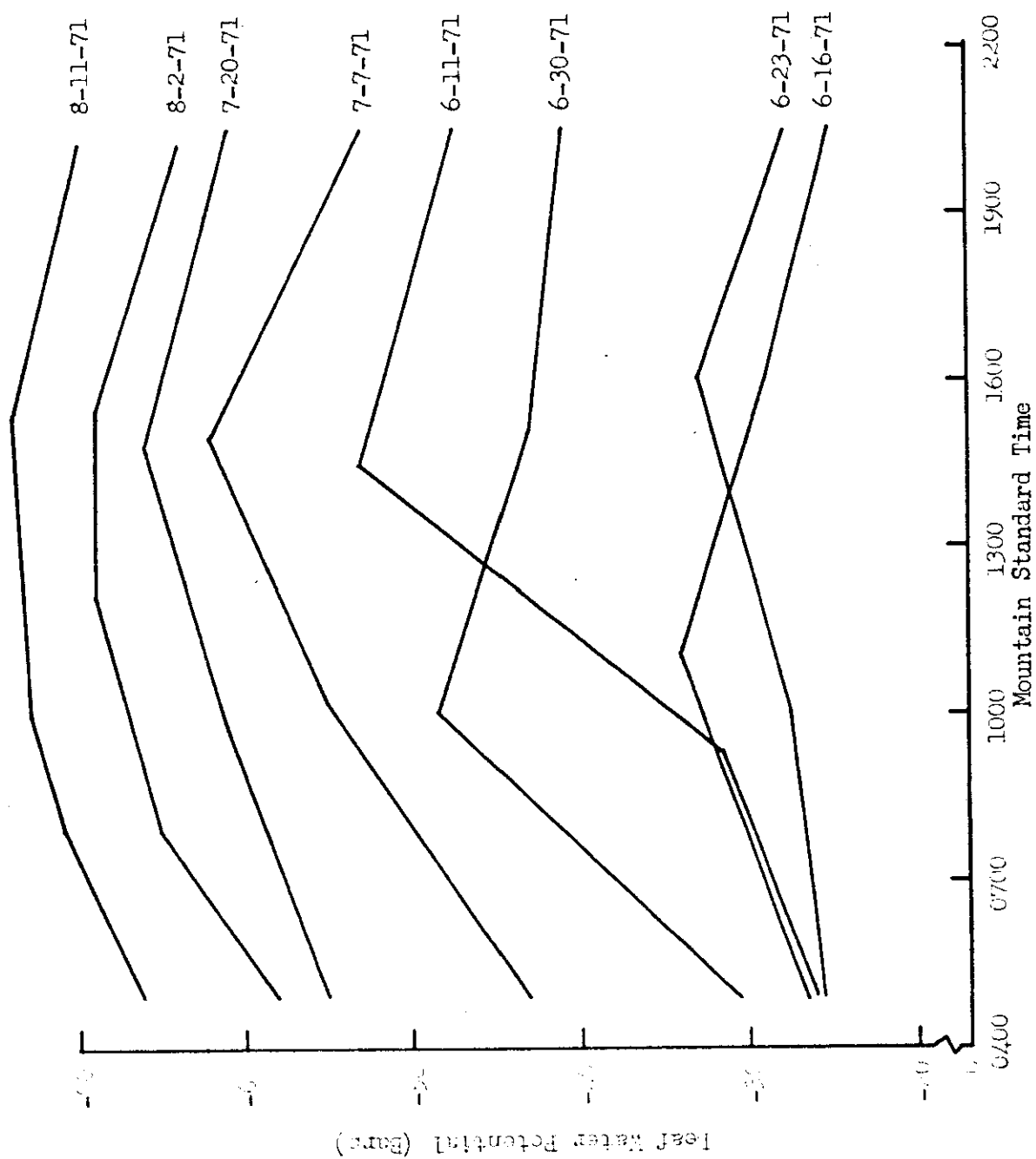


Fig. 13. Diurnal and seasonal trends of leaf water potential on the Renohill site of the soil transect.

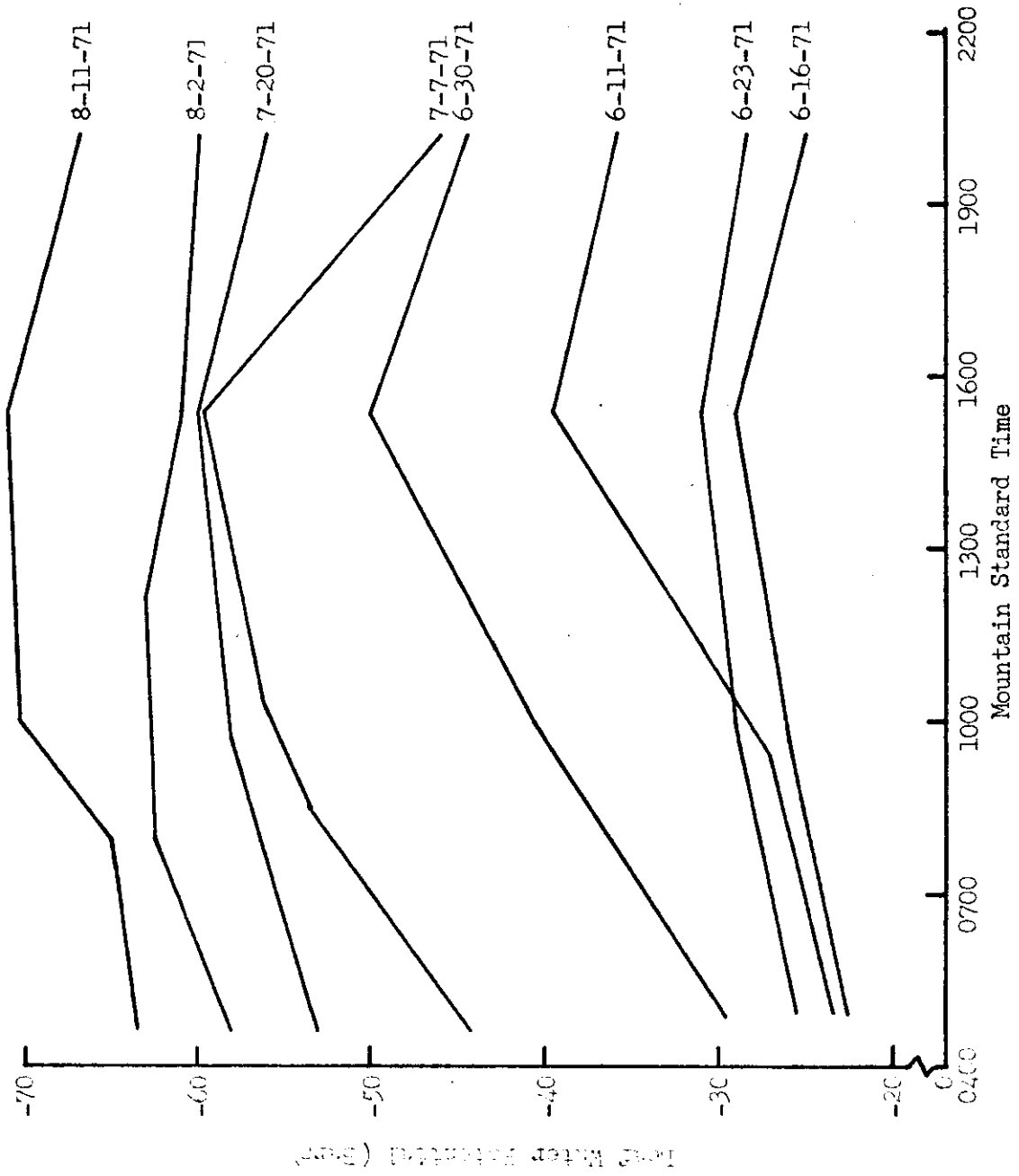


Fig. 14. Diurnal and seasonal trends of leaf water potential on the Shingle-Renohill site of the soil transect.

### Soil Transect Study - Seasonal Patterns

While diurnal fluctuations in  $\Psi_{\text{leaf}}$  appear to be governed mainly by VPD, seasonal trends are influenced by soil water. Soil water potential for the Ascalon, Renohill and Shingle-Renohill soil sites is shown in Fig. 15, 16, and 17 for May through July. Soil water potential for the 2, 10, and 20 cm depths is nearly the same for all three soils, but major differences occur at the 40 and 60 cm depths. Below 20 cm the Ascalon soil appears to be the driest, the Renohill soil next, and the Shingle-Renohill the least dry. Despite these differences below 20 cm, the seasonal trends of leaf water potential (Fig. 9--14) are very similar for the three soil types, suggesting that most of the plant root system is in the upper 20 cm (a fact which is known from other research on the Pawnee Grassland, Sims et al. 1971).

### Soil Transect Study - Conclusions

Although no field studies on the relationship of leaf water potential, soil water potential and vapor pressure deficit of native grasses have been reported, the results for B. gracilis compare favorably (qualitatively) with the schematic representation of Slatyer (1967) and the observed results of Gardner and Nieman (1964) on pepper plants. The early morning level of leaf water potential is determined by soil water potential, but diurnal responses are a function of vapor pressure deficit and leaf condition. When water is readily available, the magnitude of diurnal response to VPD is low. As soil water is depleted, the early morning  $\Psi_{\text{leaf}}$  decreases and the magnitude of plant water stress increases during

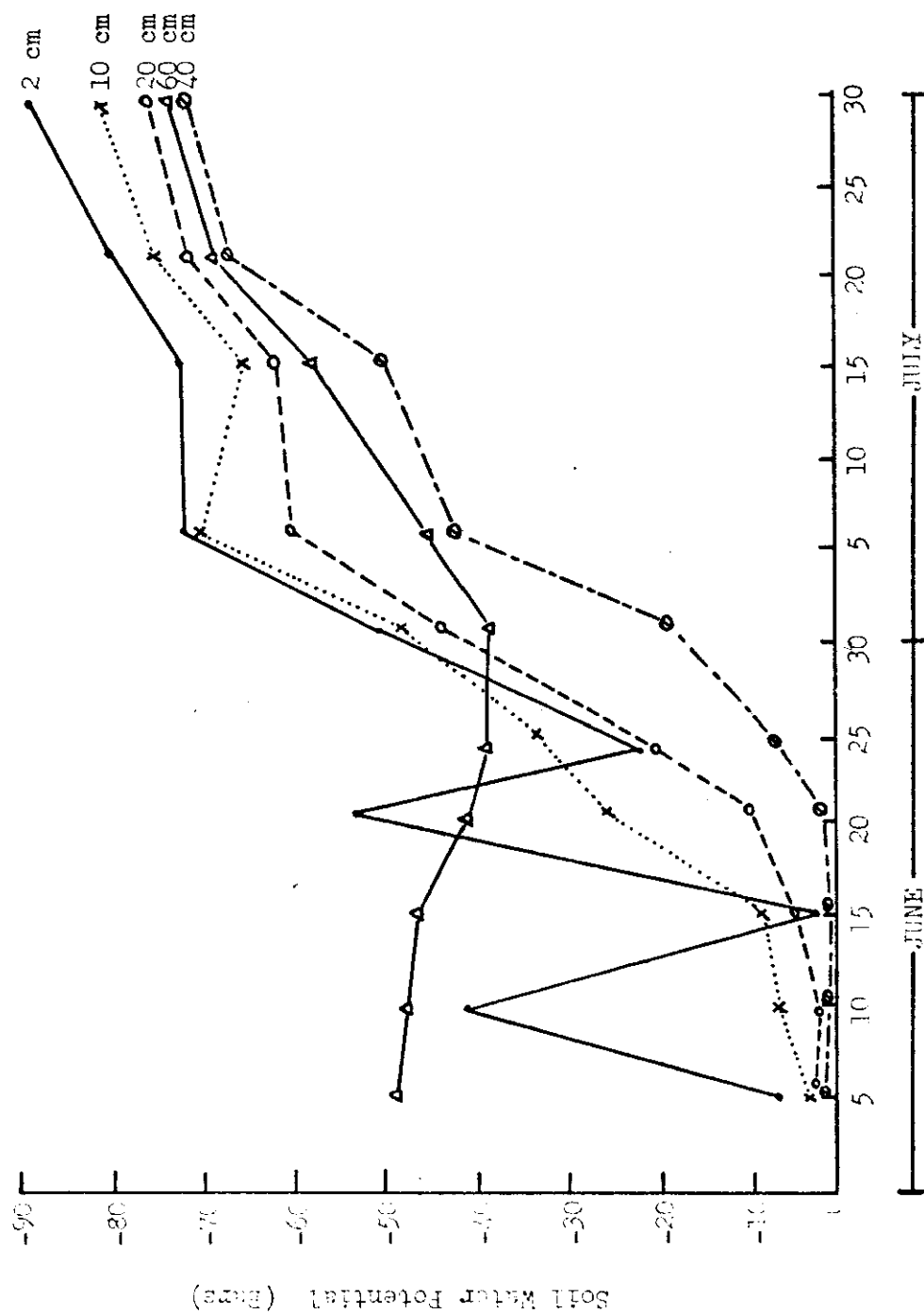


Fig. 15. Seasonal course of soil water potential of the Ascalon site of the soil transect (from Van Haveren, 1972).

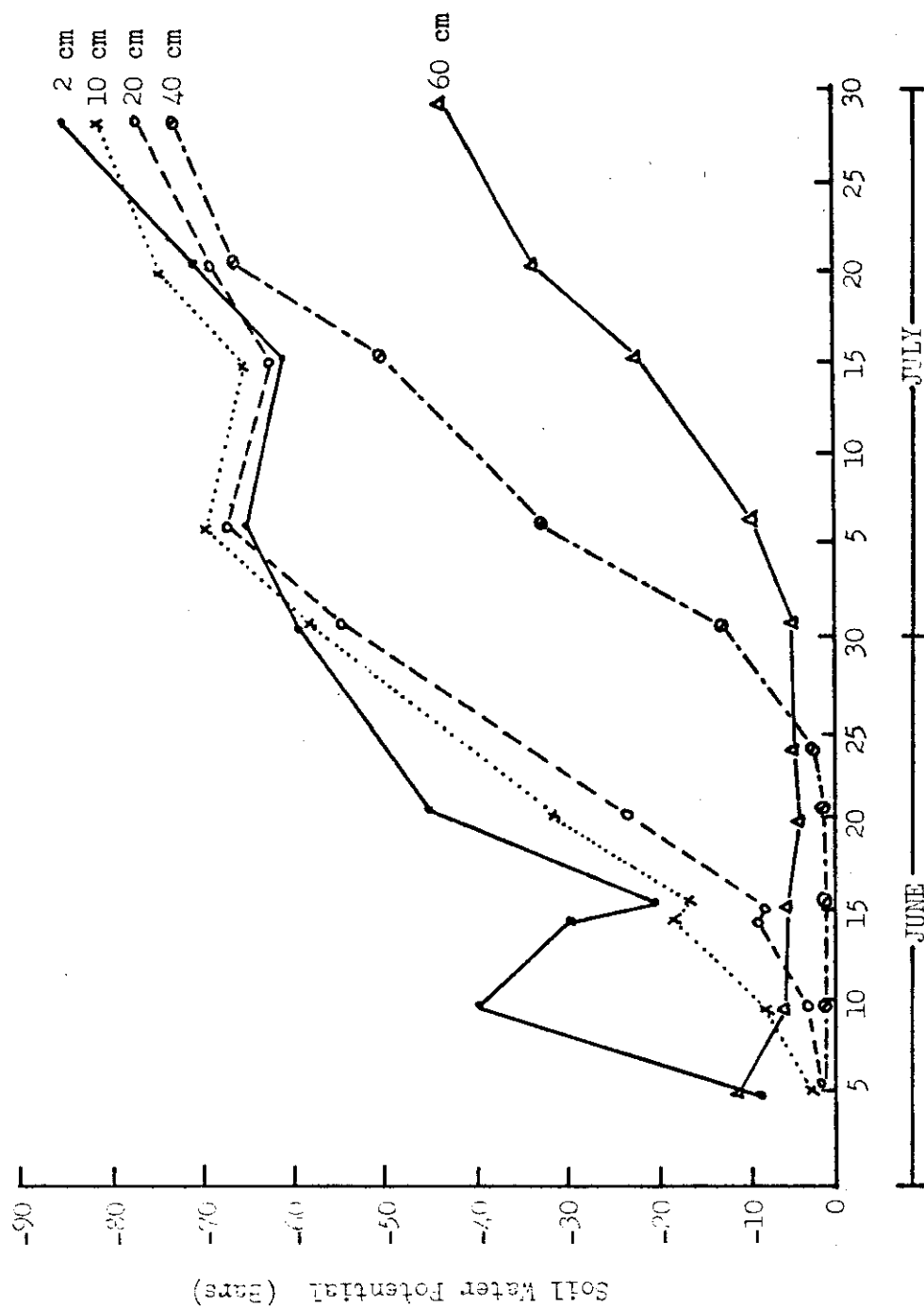


Fig. 16. Seasonal course of soil water potential of the Renchill site of the soil transect (from Van Haveren, 1972).

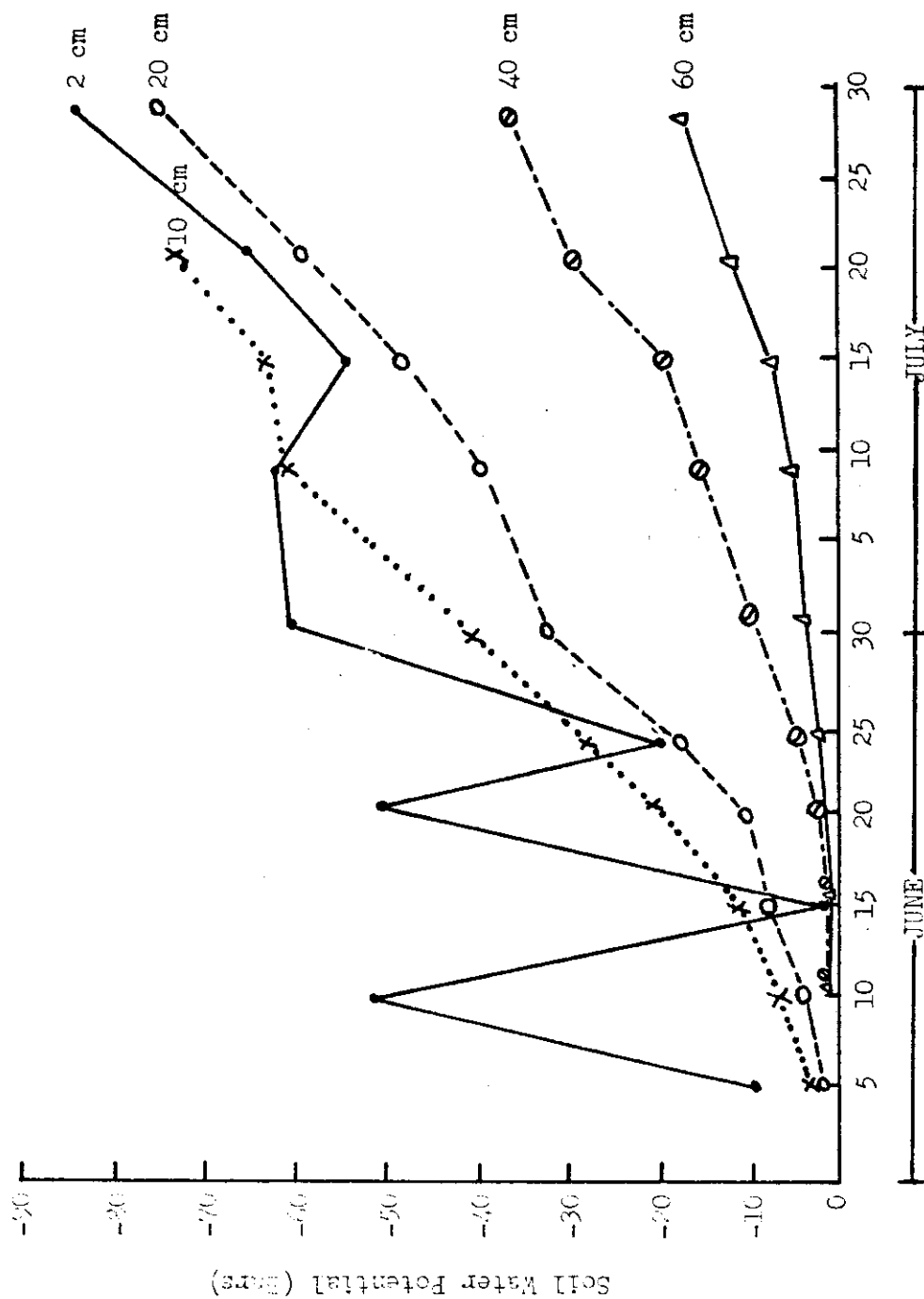


Fig. 17. Seasonal course of soil water potential of the Shingle-Renohill site of the soil transect (from Van Haveren, 1972).



midday due to a greater absorption lag, with a gradual recovery in the evening. As water becomes extremely limited and leaf condition declines, the diurnal changes become less.

Although 80 percent of the root biomass is found in the top 20 cm of soil (Sims et al. 1971), functional blue grama roots must go fairly deep since the soil water potential for all measured depths on the Ascalon and Renohill soils in July and August was lower than blue grama  $\Psi_{\text{leaf}}$ . This is somewhat of an anomaly, since theory suggests that there is a gradient from higher  $\Psi_{\text{soil}}$  to lower  $\Psi_{\text{plant}}$  to still lower  $\Psi_{\text{air}}$  when the plant is transpiring. A non-transpiring plant should have a  $\Psi$  about equal to the  $\Psi_{\text{soil}}$  after equilibrium is reached. It cannot be expected, however, that all roots of a plant or all portions of the soil would have the same  $\Psi$ . The anomaly seems best explained by the observation that B. gracilis roots extend deeper than 60 cm, the maximum depth of  $\Psi_{\text{soil}}$  measurement. Weaver (1954) reports a dense mat of blue grama roots from 46 to 91 cm, depending on the soil type, with the longest roots found at depths of 152 and 182 centimeters.

Water deficit affects primary productivity by reducing photosynthetic rates and leaf enlargement. Reduction of photosynthesis is related to increases in leaf diffusive resistance (Boyer 1970b) and to transport of photosynthate from active sites (Slatyer 1967). Comparing photosynthetic rates for blue grama sod on an Ascalon soil similar to that on the soil transect, but from a different area on the Pawnee Grassland, one finds a marked reduction in  $\text{CO}_2$  uptake with a decrease in  $\Psi_{\text{leaf}}$ . On June 16 at 1000 hours MST, the photosynthetic rate was  $43.9 \text{ mg CO}_2/\text{dm}^2 \text{ leaf}$

area/hr. with a  $\Psi_{\text{leaf}}$  of -29.5 bars. By June 23 at the same hour, the  $\Psi_{\text{leaf}}$  had dropped to -37.5 bars and the  $\text{CO}_2$  uptake rate had declined by about 73 percent (Dye 1972). Both days were clear, so it seems reasonable to assume that  $\Psi_{\text{leaf}}$  was the controlling factor, at least indirectly.

Although not measured, the maximum  $\Psi_{\text{leaf}}$  of blue grama probably occurs in late April or May when much of the total leaf growth occurs. Boyer (1968, 1970a) reports decreased leaf enlargement with reduced turgor pressure. As leaf water potential decreased in late June on the Pawnee, there was also a reduction in green leaf area of blue grama; maximum leaf area index for blue grama was recorded on June 15 in 1970 and 1971 (Knight, in press).

Modeling of a heterogeneous system, such as the Pawnee Grassland, is at best difficult. The reason for studying three different soil types was to determine if any spatial variation existed in leaf water potential of B. gracilis. The results show very little difference in blue grama leaf water potential on the three soil types during the study period, a fact that may be helpful in the development of a spatial model.

## EXPERIMENTAL STUDIES

### Simulated Rainfall Study

The objective of the simulated rainfall study was to examine the effect of a pulse of water on  $\Psi_{\text{leaf}}$ . The study sites were on the soil transect previously described. Leaf water potential was measured on the Ascalon and Shingle-Renohill soil prior to and periodically following watering with a large Soil Conservation Service infiltrometer (courtesy of Dr. Frank Rauzi and Freeman Smith). At 0900 hours MST on August 1, 12.2 mm of water were applied to the Ascalon soil in 10 minutes with 10.3 mm infiltrating. At 0925

hours MST on August 2, 13.0 mm of water was applied in 11 minutes to the Shingle-Renohill soil with 11.3 mm infiltrating. The response of soil water potential for the two sites is shown in Fig. 18 and 19.

The  $\Psi_{\text{leaf}}$  for blue grama on the Ascalon soil was not measured until two days after the start of the infiltration experiment. There is a 30 bar difference between the treatment and control at 0700 hour MST on August 3, two days after watering (Fig. 20, Appendix C). As expected, the diurnal responses of the experimental plot are greater than those of the control plot due to the availability of soil water at this late date in the growing season. The control and experimental plots had nearly the same  $\Psi_{\text{leaf}}$  and diurnal patterns 10 days after the initiation of the experiment, Fig. 20d and 21d.

Blue grama on the Shingle-Renohill soil had a similar response. Figure 21 and Appendix C show that leaf water potential responded within 30 minutes to the simulated rainfall, and continued to increase throughout the day to a maximum of -30.0 bars at 2000 hours MST. On the following morning, an even higher water potential was measured indicating further response during the night. Sampling on subsequent days shows the leaf material of the experimental plot to dry out rapidly (as did the soil) until on August 11, nine days after watering, when the control and experimental plots had the same leaf water potential.

In assessing the effect of simulated rainfall on blue grama at a time when the soil was very dry and vegetation visibly stressed,

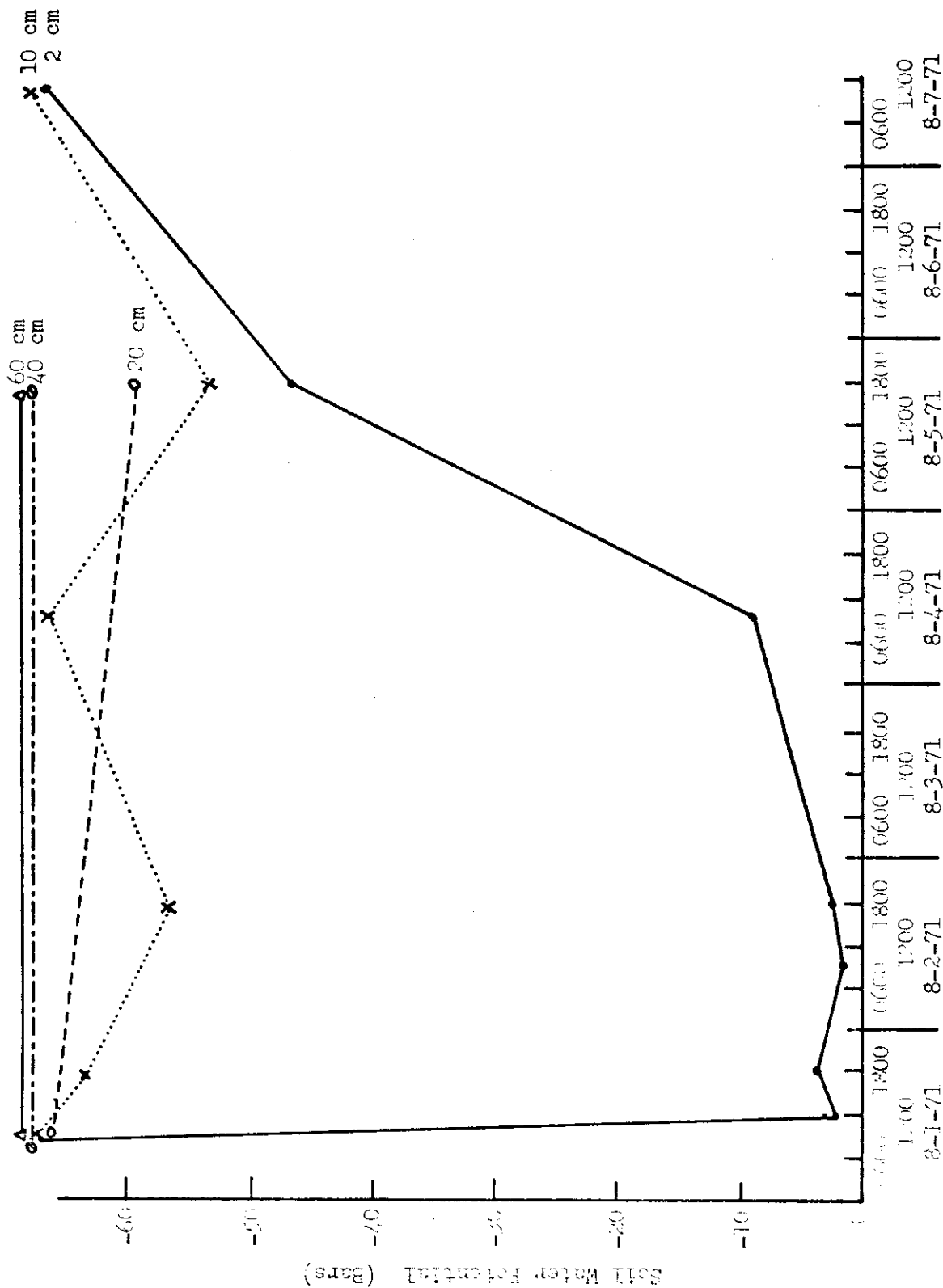
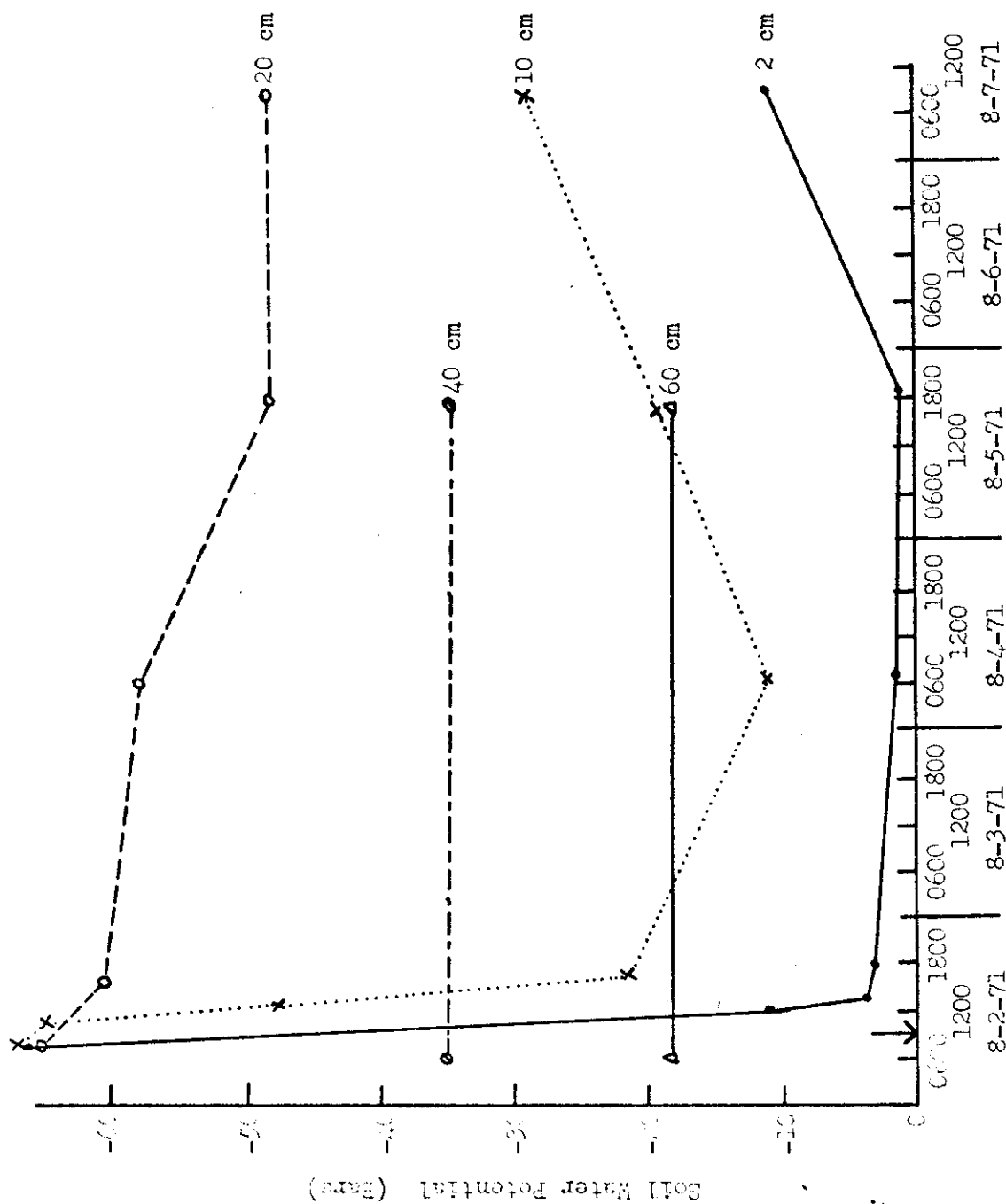


Fig. 18. The response of  $\psi$  soil of the Ascalon soil on the soil transect to 12.2 mm of water applied at 0900 hours MST on August 1 (from Van Haveren, 1972).



**Fig. 19.** The response of  $\psi$  soil of the Shingle-Renchill soil on the soil transect to 13.0 mm of water applied at 0925 hours MST on August 2 (from Van Haveren, 1972).

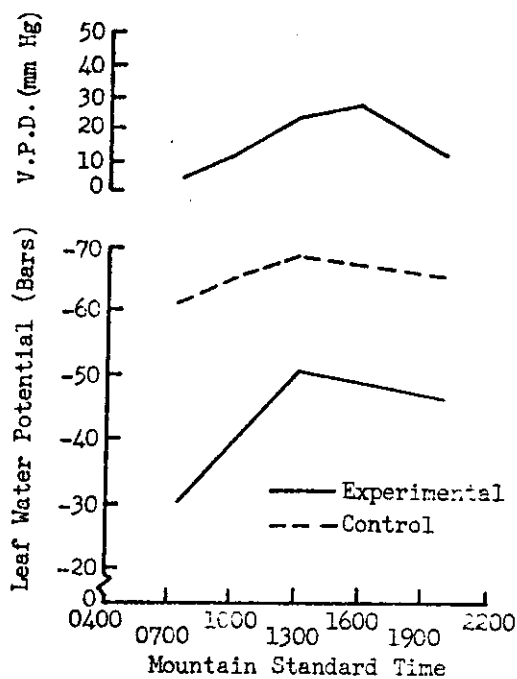


Figure 20a. August 3.

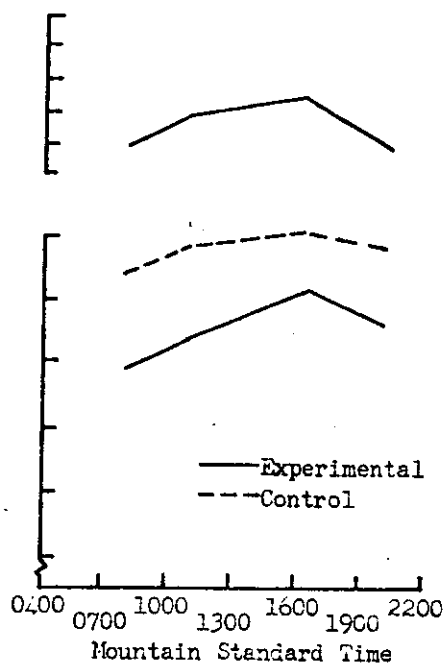


Figure 20b. August 6.

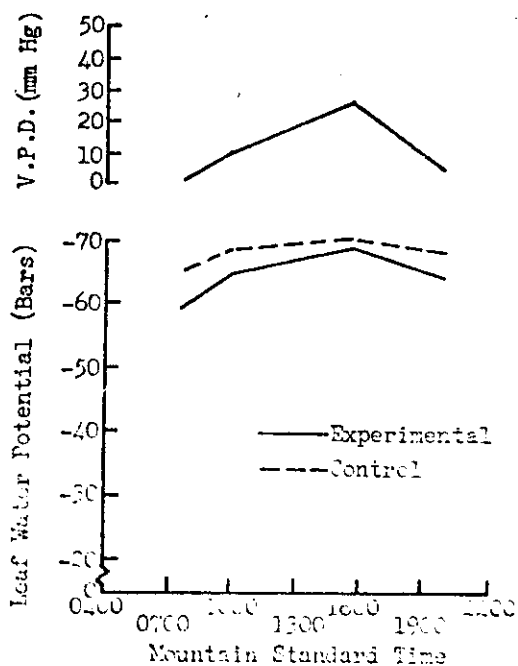


Figure 20c. August 9.

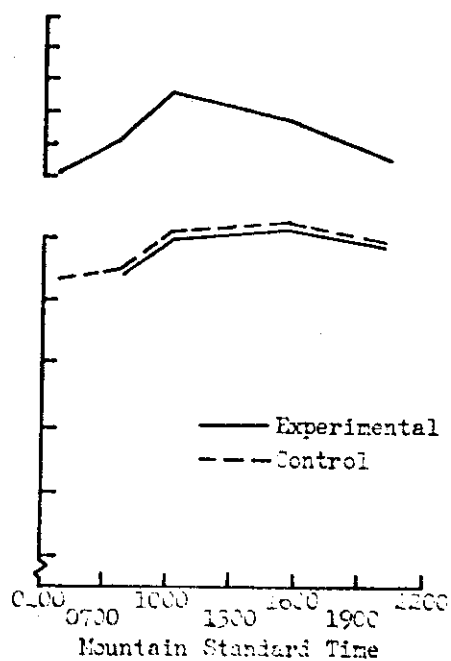


Figure 20d. August 11.

Fig. 20a, b, c and d. The response of *B. gracilis* on Ascalon soil to a pulse of 12.2 mm of water applied at 0900 hours MST on August 1.

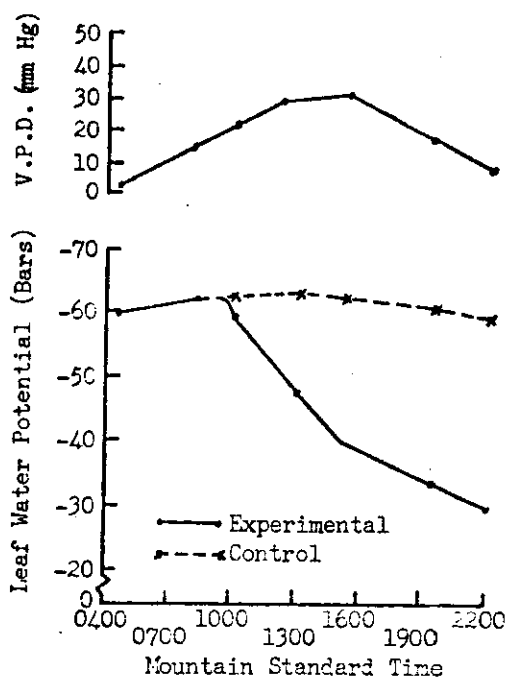


Figure 21a. August 2.

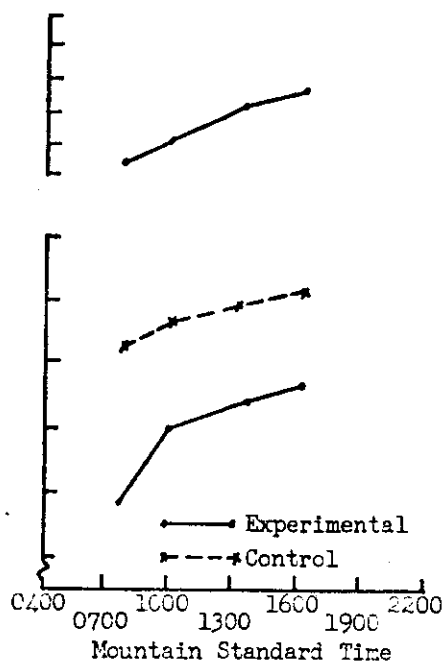


Figure 21b. August 3.

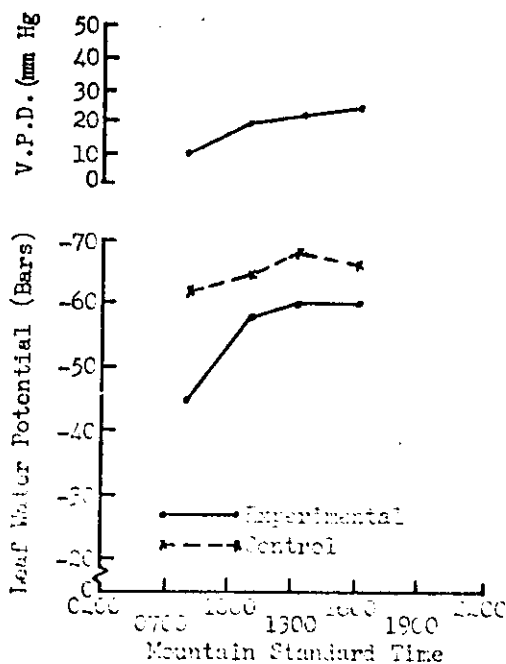


Figure 21c. August 6.

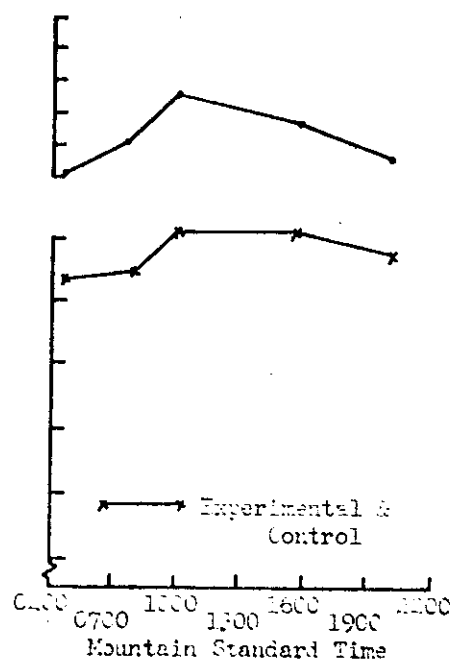


Figure 21d. August 11.

Fig. 21. The response of *B. gracilis* on Shingle-Renohill soil to a pulse of 13.0 mm of water applied at 0925 hours MST on August 2.

the data show that blue grama responds rapidly to a pulse of water. One reason for the rapid response may be the large amount of root biomass in the top 10 cm of soil. Another reason may be the presence of Endogone mycorrhizae on blue grama roots at the Pawnee (Darwin Davidson, personal communication). Safir, Boyer and Gerdemann (1971) report enhancement of water transport and reduction of resistance to water uptake by plants which have vesicular-arbuscular mycorrhizae. They showed that recovery from moderate water deficits in soybean was faster when mycorrhizae are present. There also may have been some foliar absorption of water, but that is difficult to measure.

In an area where much of the summer precipitation is from light thundershowers of short duration, the ability of a plant to respond rapidly to a small pulse of water could be a significant adaptation to survival in an arid to semiarid environment. Soil water evaporation is likely to be rapid on the short grass prairie, and a rapid uptake mechanism for the limited rainshower water would seem to be very adaptive.

#### Leaf Water Potential Study on the Irrigated and Irrigated-Fertilized Plots

By August 11 the water potential of leaf material on the soil transect was approaching the limits of measurement with the available instrumentation (about -70 bars), so the sampling area was shifted to the experimental plots just west of the IBP Headquarters building, Fig. 1. One of the plots had been subjected to sprinkler irrigation only, the other had been irrigated and fertilized (150 kg/ha nitrogen



on June 1, 1970). With fertilization and irrigation, the blue grama leaf area was about 10 times that of the irrigated-only plot (Knight, in press). Both plots had been irrigated periodically until the last week of July when the irrigation system failed. This provided an excellent opportunity to study the drying rate of blue grama and how leaf area affects the rate of drying. Also, at this time photosynthetic rates of blue grama were being measured by A. J. Dye and Joe Trlica on these same plots. It was hoped that the relationship between  $\text{CO}_2$  uptake and leaf water potential could be observed.

**Fig. 22** and Appendix D show the diurnal and two-week drying patterns for the two experimental plots. The diurnal patterns are similar to those found on the soil transect, the control of VPD being quite evident. For example, at 1000 hours and 1400 hours MST, August 18, light sprinkles occurred which depressed the VPD, with a corresponding increase in  $\Psi_{\text{leaf}}$  (**Fig. 23**). The  $\Psi_{\text{leaf}}$  on the irrigated and fertilized plot declined more rapidly during the 2 week period, most likely because of the larger amount of leaf area (**Fig. 22**).

Carbon dioxide uptake was measured on two consecutive days in both the irrigated and the irrigated and fertilized experimental plots. On August 25 the photosynthetic rate on the irrigated and fertilized plot was about  $20 \text{ mg CO}_2 / \text{dm}^2$  of leaf area/hr at 1100 hours MST at  $27^\circ\text{C}$ . The rate was considerably higher on the irrigated-only plot at about the same hour on the next day,  $52 \text{ mg CO}_2 / \text{dm}^2 / \text{hr}$ . The plot with the higher photosynthetic rate was also the plot with the lowest leaf area index and the highest  $\Psi_{\text{leaf}}$ . Since both days were clear with about

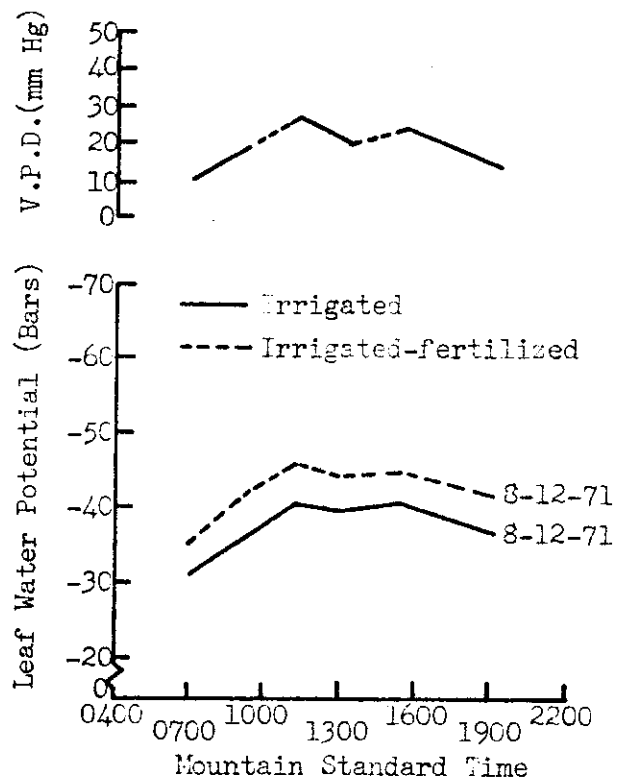


Fig. 22a. The responses of *B. gracilis* leaf water potential and vapor pressure deficit on the irrigated and irrigated-fertilized experimental plots on August 12.

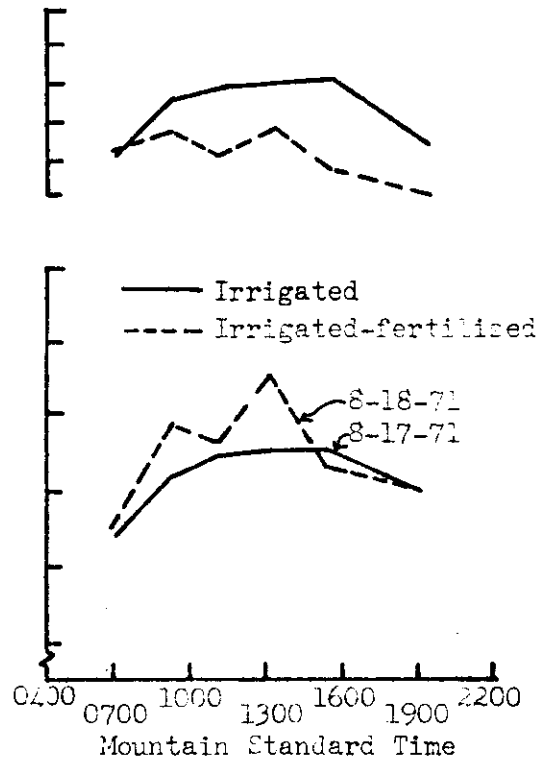


Fig. 22b. The responses of *B. gracilis* leaf water potential and vapor pressure deficit on the irrigated and irrigated-fertilized experimental plots on August 17 and August 18, respectively.

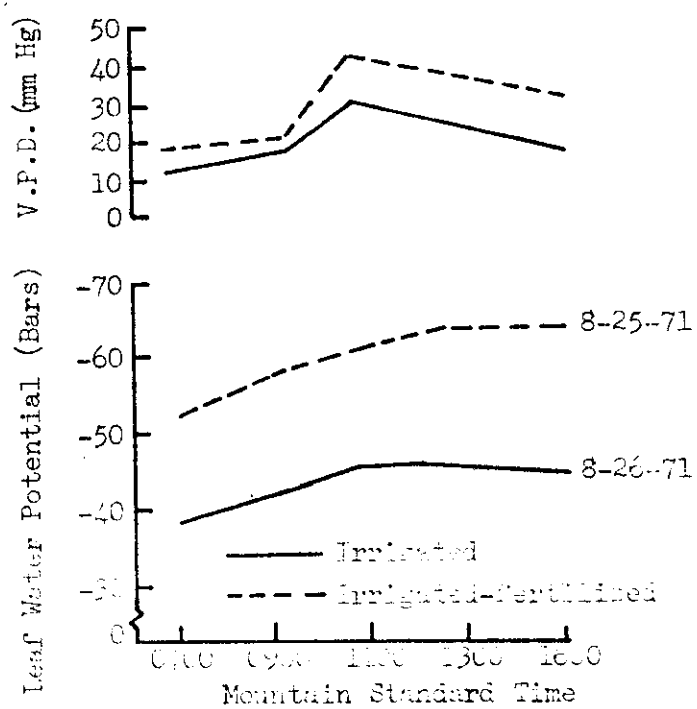


Fig. 22c. The responses of *B. gracilis* leaf water potential and vapor pressure deficit on the irrigated and irrigated-fertilized experimental plots on August 26 and August 25, respectively.

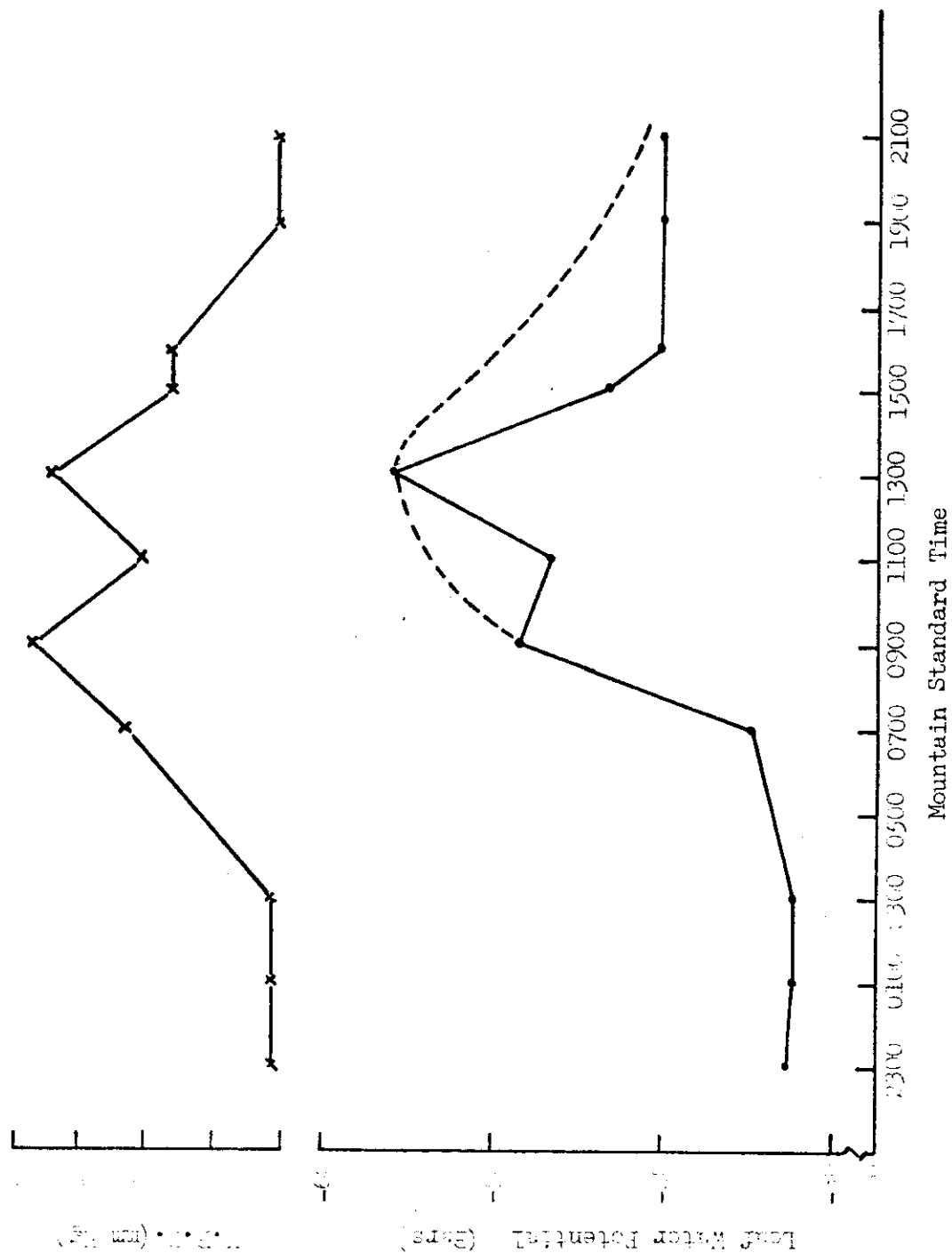


Fig. 23. The responses of leaf water potential to vapor pressure deficit on the irrigated-fertilized experimental plot on August 18. The dashed line represents a typical diurnal response on a warm, sunny day.

the same VPD and temperature (27°C on August 25 and 31°C on August 26) at the time of measurement, the lower photosynthetic rate seems best explained in terms of a lower  $\Psi_{\text{leaf}}$  resulting from the larger amount of leaf area. Although increased leaf water stress seems to cause a decrease in CO<sub>2</sub> uptake, it is interesting to note the relatively higher photosynthetic rates at very low  $\Psi_{\text{leaf}}$  (-38 to -62 bars). Boyer (1970b) reports reduction in photosynthesis in corn and soybeans when leaf water potential dropped below -3.5 and -11 bars, respectively. Blue grama appears to be photosynthetically active over a much wider range of  $\Psi_{\text{leaf}}$  (-38 to -62 bars). The significance of this will be discussed later.

#### Environmental Control of Leaf Water Potential

The objective of this part of the study was to examine the diurnal and seasonal trends in VPD and  $\Psi_{\text{soil}}$  in relation to  $\Psi_{\text{leaf}}$  to determine which factors exert the greater effect on  $\Psi_{\text{leaf}}$ . Data were analyzed by linear, multiple and stepwise regression (Steele and Torrie 1960) with leaf water potential the dependent variable in all cases.

Due to the small number of degrees of freedom, the data for the soil transect were pooled to assess the effect of VPD on the diurnal response of  $\Psi_{\text{leaf}}$ . The regression of  $\Psi_{\text{leaf}}$  on VPD indicates the relationship to be a quadratic function instead of linear. The regression model used was

$$y = a + Xb_1 + X^2b_2$$

where Y is  $\Psi_{\text{leaf}}$ , a is the y intercept, X is VPD and  $b_1$  and  $b_2$  are the regression coefficients. The regression equations for the data of

June 11 through August 11 are as follows:

June 11	$Y = -20.04 - 4.175X + 0.171X^2$	$R=0.85$
June 16	$Y = -25.05 + 0.245X - 0.012X^2$	$R=0.83$
June 23	$Y = -23.49 - 0.280X + 0.002X^2$	$R=0.77$
June 30	$Y = -28.42 - 1.906X + 0.062X^2$	$R=0.66$
July 7	$Y = -40.31 - 1.386X + 0.022X^2$	$R=0.83$
July 20	$Y = -52.22 - 1.566X + 0.060X^2$	$R=0.84$
August 2	$Y = -58.09 - 0.496X + 0.009X^2$	$R=0.71$
August 11	$Y = -64.11 - 0.484X + 0.007X^2$	$R=0.77$

All of the equations are significant at  $P = 0.05$ , with  $R$  values that indicate the significance of VPD as a control over  $\Psi_{\text{leaf}}$ .

Multiple and stepwise regression of soil water potential at the 2, 10, 20, 40 and 60 cm depths and VPD on leaf water potential yielded some perplexing results which may be due in part to the non-independence of soil water potential at the various levels. The analysis of the data shows soil water potential at 40 cm to be most important in explaining the variability in leaf water potential, accounting for 95 percent of the variability. These results may be due to the high correlation between soil water potential at certain levels. It would seem that  $\Psi_{\text{soil}}$  at the 10 and 20 cm depths would be most highly correlated with leaf water potential, since that is where most of the root biomass is located, but this is not indicated by the results.

## DISCUSSION

The measurement of leaf water potential with thermocouple psychrometers has become a fairly straight forward procedure. The major limitation is strict temperature control while measurements are being made. This problem was overcome in this study by the development of the instrument previously described which allowed for field measurements. Certain precautions must be taken when using thermocouple psychrometers, however. First, the junctions must be kept clean at all times. Second, under prolonged use the calibration curve may change, necessitating periodic calibration of the psychrometers. In spite of these limitations, thermocouple psychrometry measures a very sensitive indicator of plant water stress, water potential, and has become an increasingly important tool for studying soil and plant water relations.

Plant response to different levels of leaf water potential at various stages of growth may be responsible, in large part, for the success or failure of species establishment in a given area. Brown (1958), in studying grass leaf anatomy, stated that leaf anatomy may be correlated with environmental conditions of the areas occupied by the grass groups. He further stated that the chlorodoid types are characteristic of arid and semiarid hot regions with high light intensities. He writes, "there may, then, be a correlation of leaf anatomy with either or both high temperatures and light intensities. Perhaps the chlorodoid type leaf anatomy may also be in some way related to drought resistance". Hatch and Slack (1966) elucidated a new photosynthetic pathway in certain plants, the C-4 dicarboxylic



acid pathway. This C-4 pathway has been correlated with the type of leaf anatomy found in blue grama. Bender (1970) and George Williams (personal communication) found evidence that blue grama has the C-4 dicarboxylic acid pathway. Laetsch (1968) hypothesized that the biochemical, physiological and structural features shared by plants with the C-4 pathway are "adaptations to high light intensity in an environment in which water stress could frequently be the limiting factor for photosynthesis". C-4 species have been shown to require high light intensities and high temperatures for optimum photosynthetic rates. In addition, the phosphophenol-pyruvate-carboxylase enzyme system has a greater affinity for  $\text{CO}_2$  than the carboxy dismutase system (Walker 1962) which may result in a  $\text{CO}_2$  compensation point of near zero. Also, C-4 plants are not believed to photorespire (Moss 1962), which is an adaptation in areas of high light intensities, and is also important for the low  $\text{CO}_2$  compensation point of these species. Laetsch (1968) adds that the proximity of active photosynthetic sites to the vascular tissue is an efficient arrangement for the rapid transport of reactants and end products of photosynthesis.

All of these anatomical, biochemical and physiological characteristics may be responsible for the dominance of blue grama on the short grass prairie. The ability of blue grama to remain photosynthetically active at low water potentials (-40 to -60 bars) is interesting, to say the least, since results by Epper (1970b) show corn, another C-4 species, to have a much reduced photosynthetic rate at -16 bars. He further stated, on the basis of his results, that the C-4 pathway confers no particular ability to withstand low leaf water potentials.

This obviously needs further testing and should include C-4 species adapted to areas where water may be limiting throughout much of the growing season.

The ability of blue grama to respond rapidly to a pulse of water appears to be another significant adaptation (Smith 1972). Although no measurement of photosynthetic activities was made following watering, blue grama probably resumed active photosynthesis and growth.

The difficulties encountered in this study in attempting to statistically analyze the environmental effect of vapor pressure deficit and soil water potential on leaf water potential show that plant response is not a simple matter of one or two environmental factors. Interactions of all components of the environment and plant are complex and some are not easily detected or measured. Nonetheless, this type of analysis, with supporting data from other investigators, may shed some light on the interactions between plants and environment and thereby lead to a better understanding of ecosystem function. Information on the response patterns of blue grama  $\Psi_{\text{leaf}}$  **responds similarly** on different Pawnee soil should simplify the modeling effort, if that is possible.

## ACKNOWLEDGMENTS

Special acknowledgment is due to Bruce Van Haveren who helped us frequently with the technology of thermocouple psychrometry. He helped in the design of our multi-chamber sample holder and provided data on soil water potential in the study area. We are also grateful to A. J. Dye and Joe Trlica for data on CO<sub>2</sub> uptake; Freeman Smith and Frank Rauzi for infiltration data obtained during the simulated rainfall experiment; Don Jameson for suggestions offered during the course of this study; and A. Tyrone Harrison for helpful criticism of this manuscript. Without the long hours of field assistance by Mike Evans and Richard Fresh, much of the data in this paper could not have been collected.

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## APPENDIX A

Diurnal and seasonal trends of leaf water potential and vapor pressure deficit on the soil transect.

Date	Time (MST)	Ascalon soil		Renohill soil		Shingle-Renohill soil	
		$\Psi_{\text{leaf}}$	VPD	$\Psi_{\text{leaf}}$	VPD	$\Psi_{\text{leaf}}$	VPD
June 11	0430	-23.5*	0.62	-26.0	0.62	-23.5	1.28
	1000	-36.0	23.54	-31.5	25.48	-27.0	23.54
	1530	-40.5	23.26	-53.0	17.98	-39.5	23.26
	2000	-33.0	5.13	-47.5	5.13	-36.0	5.13
June 16	0430	-25.5	0.62	-26.5	0.62	-22.5	1.28
	1000	-29.5	29.36	-34.0	34.70	-26.0	29.36
	1530	-37.5	29.35	-29.0	31.00	-29.0	29.90
	2000	-33.5	2.76	-25.0	4.33	-25.0	5.30
June 23	0430	-20.5	0.67	-25.5	0.72	-25.5	0.67
	1000	-37.5	41.78	-27.5	41.78	-29.0	41.30
	1530	-30.5	35.00	-33.0	35.00	-31.0	35.00
	2000	-25.5	15.02	-28.0	17.97	-28.5	17.97
June 30	0430	-27.5	0.62	-30.5	0.62	-29.5	0.26
	1000	-31.0	23.05	-48.5	21.96	-40.5	23.87
	1530	-34.5	15.02	-43.0	15.02	-50.0	15.02
	2000	-27.5	6.38	-41.0	5.54	-44.5	6.38
July 7	0430	-37.5	1.28	-43.0	1.28	-44.0	1.28
	1000	-48.0	20.31	-55.0	20.31	-53.5	20.31
	1530	-53.0	17.60	-62.0	15.44	-59.5	18.77
	2000	-51.0	7.10	-53.0	7.10	-46.0	9.64
July 20	0430	-55.0	0.62	-55.0	0.62	-53.0	0.62
	1000	-62.0	17.01	-61.0	17.01	-58.0	17.01
	1530	-62.0	24.12	-66.0	24.12	-60.0	24.12
	2000	-59.0	7.43	-64.0	7.43	-56.0	7.43
August 2	0430	-59.0	0.62	-58.0	0.62	-58.0	0.62
	0800	-62.5	14.25	-65.0	14.25	-62.5	14.25
	1200	-63.5	29.37	-69.0	29.37	-63.0	29.37
	1530	-62.0	31.00	-69.0	31.00	-61.0	31.00
	2000	-60.0	8.33	-61.0	8.33	-60.0	8.33

APPENDIX A  
(Continued)

Date	Time (MST)	Ascalon soil		Renohill soil		Shingle- Renohill soil	
		$\Psi$ leaf	VPD	$\Psi$ leaf	VPD	$\Psi$ leaf	VPD
August 11	0430	-63.5	1.28	-66.0	1.28	-63.5	1.28
	0800	-65.0	12.44	-71.0	12.44	-65.0	12.44
	1000	-71.0	25.34	-73.0	25.34	-70.5	25.34
	1530	-72.0	19.28	-74.0	19.28	-71.0	19.28
	2000	-68.0	6.38	-70.0	6.38	-67.0	6.38

(\* each value is the mean of four separate determinations)

## APPENDIX B

Precipitation (mm) on the soil transect.

May total	51.8
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June 3	0.3
4	0.3
9	0.3
12	1.8
13	3.3
14	5.0
17	0.3
total	10.7

July 18	0.9
21	2.5
22	0.8
23	2.1
24	1.4
28	2.4
total	10.2

August 1	1.8
21	3.5
23	2.3
26	1.5
total	9.0

## APPENDIX C

Leaf water potential and vapor pressure deficit -  
simulated rainfall study

Shingle-Renohill soil

Date	Time (MST)	Leaf Water Potential (Bars)		VPD (mm Hg)
		Experimental	Control	
August 2	0430	-59.5	-59.5	0.62
	0800	-62.5	-62.5	14.25
	1000	-59.0	-62.5	22.10
	1200	-47.5	-63.0	29.37
	1530	-40.0	-61.0	31.00
	1900	-33.5	-61.0	17.60
	2000	-30.0	-59.5	8.33
August 3	0700	-28.0	-52.5	6.30
	1000	-40.0	-56.5	12.10
	1300	-43.5	-59.5	23.40
	1600	-46.5	-61.5	27.90
August 6	0800	-46.5	-62.0	10.00
	1100	-57.5	-64.0	18.70
	1330	-60.0	-68.0	23.20
	1600	-59.5	-66.0	26.50
August 11	0430	-63.5	-63.5	1.28
	0800	-65.0	-65.0	12.44
	1000	-70.5	-70.5	23.54
	1600	-71.0	-71.0	19.28
	2000	-67.0	-67.0	6.38

Ascalon Soil

Date	Time (MST)	Leaf Water Potential (Bars)		VPD (mm Hg)
		Experimental	Control	
August 3	0700	-30.0	-64.0	6.30
	1000	-39.0	-65.5	12.10
	1300	-51.0	-68.5	23.40
	2000	-46.5	-65.5	11.13
August 6	0800	-49.5	-64.0	10.00
	1100	-53.5	-68.0	18.70
	1600	-61.0	-70.0	26.50
	2000	-56.0	-68.0	9.65
August 9	0800	-59.5	-64.5	1.26
	1000	-65.0	-69.0	10.34
	1600	-68.5	-70.5	26.79
	2130	-64.5	-68.0	7.09
August 11	0430	--	-63.5	1.28
	0800	-64.0	-65.0	12.44
	1000	-69.0	-70.5	25.34
	1530	-70.5	-72.0	19.28
	2000	-67.5	-68.0	6.38

## APPENDIX D

Leaf water potential and vapor pressure deficit -  
irrigated-fertilized and irrigated experimental plots

Date	Time (MST)	Irrigated-Fertilized		Irrigated	
		$\Psi_{\text{leaf}}$ (Bars)	VPD (mm Hg)	$\Psi_{\text{leaf}}$ (Bars)	VPD (mm Hg)
August 12	0700	-35.5	9.8	-31.5	9.8
	0900	-42.0	18.0	-36.5	18.0
	1100	-46.5	25.5	-41.0	25.5
	1300	-44.0	19.4	-40.0	19.4
	1500	-45.0	23.0	-41.0	23.0
	1900	-42.0	12.0	-37.5	12.0
August 17	0700			-34.0	9.6
	0900			-42.0	26.1
	1100			-44.5	30.5
	1300			-45.0	32.9
	1500			-45.0	32.9
	1900			-40.0	17.8
August 17	2300	-32.5	0.9		
August 18	0100	-32.0	0.9		
	0300	-32.0	0.9		
	0700	-34.5	12.0		
	0900	-48.5	18.0		
	1100	-46.5	12.5		
	1300	-55.7	18.5		
	1500	-43.0	8.5		
	1900	-40.0	8.5		
	2100	-40.0	1.5		
August 25	0730	-42.2	18.9		
	0910	-58.1	20.8		
	1100	-61.7	42.8		
	1230	-64.0	39.1		
	1500	-64.0	31.3		
August 26	0730			-38.0	12.5
	0910			-42.5	17.6
	1040			-45.5	28.8
	1200			-46.0	25.6
	1500			-45.0	17.1