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Title: Seasonal and Diurnal Changes in the Water Relations of Elk Sedge (Carex geyeri) and Pinegrass (Calamagrostis rubescens)

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Co-occurring plants of elk sedge and pinegrass were compared for diurnal fluctuations in xylem potential, abaxial diffusive resistance, and adaxial diffusive resistance. In addition, both species were measured for hygrometric osmotic potential (π) and the following parameters derived from the pressure-volume technique: osmotic potential at full turgor (π^{100}), osmotic potential at zero turgor (π^{0}), bound water fraction (B), and elastic modulus (E). Soil moisture, and diurnal fluctuation in ambient temperature and vapor density difference between leaf and air (VDD) were also measured.

Diurnal fluctuation in xylem potential indicated elk sedge had more negative midafternoon values (0.4-0.7 MPa) than pinegrass. In both species, predawn and midafternoon values were significantly ($p<0.05$ or 0.01) correlated to soil moisture. Elk sedge was apparently able to maintain lower xylem potentials than pinegrass because it had lower π^{0} and more rigid cell walls.

Hygrometric analysis of π would have resulted in different conclusions. In this case, π values were not significantly different ($p>0.05$) until late in the season, and then at one point pinegrass π

was more negative. The discrepancy between the two techniques apparently relates to bound water dilution of the osmotic system with the hygrometric technique.

Abaxial resistance was similar beween the two species whereas elk sedge generally had lower adaxial values. Elk sedge maintained low abaxial resistances (2-8 s cm^{-1}) to xylem potentials 0.5 MPa more negative than pinegrass. This probably relates to the lower osmotic potential in elk sedge. However, in both species abaxial resistance was linearly related to VDD. Thus, stomates respond to ambient humidity before severe tissue water deficit occurs. This may explain why threshold values of xylem potential were reached only late in the season as soil moisture dropped.

Elk sedge appears physiologically better adapted to cope with drought than pinegrass, based on the following factors: 1) more negative xylem potentials, 2) more negative osmotic potentials, 3) higher bound water fraction, 4) more rigid cell walls, and 5) maintenance of low diffusive resistance to more negative xylem potentials. However, both B and E were highly variable.

Seasonal and Diurnal Changes in the Water Relations of Elk Sedge (*Carex geyeri*) and Pinegrass (*Calamagrostis rubescens*)

by

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INTRODUCTION

Water is one of the most critical factors in plant growth and survival. Few plants growing in natural environments escape water stress for more than several days at a time (Hsiao et al. 1976). These authors further stated that understanding the mechanisms by which plants survive water deficits is of "prime significance" in plant physiology.

A majority of the studies dealing with water relations have involved annual crop species and woody plants. However, herbaceous inhabitants of arid and semi-arid rangelands have received relatively little attention, particularly in the United States. The importance of water under typical rangeland conditions cannot be overemphasized. Water availability is probably the single most important factor determining plant distribution on rangeland (Brown 1977). Water relations are critical in revegetation of rangeland, whether it be for mined land reclamation or range improvement.

Research into the mechanisms of drought adaptation should involve the simultaneous measurement of as many potentially important processes as possible at several stages of growth (Kramer 1974). This point is particularly important when one considers the tendency for different mechanisms to interact (Morgan 1980). If we eventually gain an adequate understanding of drought resistance mechanisms, breeding for

those characteristics will be possible. The general concept of drought resistance is too broad to serve as a basis for plant breeding, specific characteristics must be determined (Kramer 1980).

This study was conducted to evaluate some of the mechanisms by which elk sedge (Carex geyeri) and pinegrass (Calamagrostis rubescens) cope with water deficit. These two species are an important component of forested range in eastern Oregon. They both are able to tolerate the summer droughts common to eastern Oregon. Elk sedge is generally considered more drought tolerant than pinegrass, although no solid evidence of this is available. Thus a side-by-side comparison of these species was made on a site where their distributions overlapped. The specific objectives of the study were:

(1) To compare the diurnal course of xylem potential and diffusive resistance of both leaf sufaces for elk sedge and pinegrass;

(2) To relate measured diurnal courses of xylem potential and diffusive resistance to selected environmental variables;

(3) To compare parameters derived from the pressure-volume techniques for elk sedge and pinegrass;

(4) To assess osmotic adjustment in elk sedge and pinegrass using both hygrometric and pressure-volume techniques.

LITERATURE REVIEW

Water Flow Pathway

Anatomy

A general description of the water flow path within the plant would logically start at the root surface. The main water absorbing region of the root is thought to begin immediately behind the elongation zone and end where the endodermis undergoes secondary wall development (Tanton and Crowdy 1972). This zone generally contains an abundance of root hairs (extensions of epidermal cells) important in water absorption. As roots age they become highly suberized, a process that at one time was thought to almost totally limit the uptake ability of older roots. However, recent evidence suggests that older roots can be active in both water and nutrient uptake (Caldwell 1976, Fitter and Hay 1981).

Three pathways have been suggested for water flow between the root epidermis and xylem vessels: 1) vacuolar, from cell vacuole to vacuole; 2) cell wall, through cell walls except at the endodermis; and 3) symplastic, passing from protoplast to protoplast via plasmodesmata (Newman 1976, Molz et al. 1979). Some water flow probably occurs in all of the pathways listed. Newman (1976) felt the symplastic pathway best explains water movement through primary roots of corn (Zea mays); however, he concluded that the pathway has not been completely elucidated. Generally speaking, the cell wall pathway appears to be

most important (Tanton and Crowdy 1972, Epstein 1973, Milburn 1977, Salisbury and Ross 1978).

Water that is absorbed across the epidermis enters the cortex, which consists of several layers of large cells, the walls of which are highly permeable to water (Salisbury and Ross 1978). The cortex is bound on the inside by a single layer of close fitting cells called the endodermis. The cell wall pathway is blocked at the endodermis by a layer of suberin. The suberin layer, referred to as the Casperian strip, decreases the permeability of the cell walls and forces water to move into the endodermis protoplast (Tanton and Crowdy 1972, Milburn 1977). The degree and nature of suberization varies considerably with root age. Movement of the pathway into the protoplast would seem to provide a point where water and nutrient movement can to some extent be controlled (Milburn 1977). The escape of water from stele tissue may be most important in this regard. After passing across the endodermis, the water flow again returns to the cell wall until it reaches the xylem vessels, where it enters the lumen of mature xylem vessels (Tanton and Crowdy 1972).

The xylem system can be viewed as empty pipe conduits which function in long distance transport from roots to leaves (Epstein 1973). As xylem vessels reach the leaves they become finely branched, and it is at this point that water passes from vascular tissue to mesophyll cells. The classical view holds that the mesophyll walls are the evaporation sites which saturate the intercellular spaces. Water vapor escapes to substomatal cavities, is lost to the atmosphere

through stomates, and thus the pathway is completed (Meidner 1975). However, an alternate pathway has been suggested (Crowdy and Tanton 1970, Sheriff and Meidner 1974, Meidner 1975). The alternate pathway places the evaporation sites at the inner epidermal cell walls, and in particular at the subsidiary and guard cell walls. Meidner (1975) suggested this would locate the evaporation sites close to air spaces with the highest water vapor deficits.

The leaf water pathway may vary with plant type. Sheriff and Meidner (1974) proposed that bundle sheath extensions found in mesomorphic leaves are important in maintaining a close hydraulic link between the leaf epidermis and vascular tissue. However, this close hydraulic link does not exist in many xeromorphic species, and may serve as a mechanism to control water loss.

Soil-Plant-Atmosphere Continuum

The flow of water through the pathways described in the previous section can be viewed as continuous. When viewed in this manner, an analog to Ohm's Law can be applied to water flow through the plant. This approach was suggested by van den Honert (1948), and is generally referred to as the soil-plant-atmosphere continuum (SPAC). Kramer (1974) felt it a very useful unifying concept in the study of plant water relations, even though it is oversimplified. The system is analagous to Ohm's Law in that

$$\text{Flow} = \frac{\text{Driving Force}}{\text{Resistance}}$$

The driving force for water flow is the water potential gradient that exists between soil and atmosphere (Larcher 1975, Lange and Losch 1979, Meyer and Ritchie 1980). Some experimental evidence indicates a linear relationship exists between water potential and transpiration rate (Hailey et al. 1973, Newmann et al. 1974). This implies resistance is constant and a simple Ohm's Law analog is appropriate for the entire SPAC system. Other authors, however, have found inadequacies in the analog (Cowan 1965, Roberts and Knoerr 1978, Hinckley et al. 1978, Running 1980). Running (1980) suggested there are two basic problems with applying the analog: 1) non-steady state flow resulting from dynamic water exchange between plant tissues, and 2) variable flow resistances in different plant parts. He proposed the following equation to improve the model:

$$q = \frac{\Delta\varphi \text{ soil-root}}{r \text{ soil-root}} + \frac{\Delta\varphi \text{ root-xylem}}{r \text{ root-xylem}} + \frac{\Delta\varphi \text{ xylem-leaf}}{r \text{ xylem-leaf}} + \frac{\Delta\varphi \text{ leaf-air}}{r \text{ leaf-air}}$$

where q is the water flow through the entire system, $\Delta\varphi$ is the water potential gradient within each segment, and r is the resistance in each segment. Thus, potential gradients and resistance within each segment can be considered separately.

Plant Resistance and Capacitance

With theoretical development of SPAC has come an interest in the resistance to water flow in the plant system. The greatest resistance in the water flow pathway occurs at the gas phase (Lange and Losch

1979). Gas phase resistance is so much larger than other resistance in the plant it will control transpiration, and consequently water flow through the plant (Weatherley 1976). Root resistance is generally considered the largest resistance to liquid phase movement in the plant (Kramer 1974, Weatherley 1976). There are, however, reports of considerable shoot and leaf resistance in some species. Boyer (1974) considered the variable resistance to flow he found in sunflower (Helianthus annuus) to be associated with leaves rather than roots. Meyer and Ritchie (1980) studied resistance to flow in sorghum (Sorghum bicolor), and suggested a major resistance to flow lies at the plant crown. The authors considered root resistance only slightly greater than shoot resistance. Jarvis (1975) also determined that leaf resistance is substantial in some species. Thus, the magnitude of various resistances appears to be species specific.

In many cases resistance is highly dependent on flow rate (Boyer 1974, Kramer 1974, Weatherley 1976, Roberts and Knoerr 1978, Meyer and Ritchie 1980). The work of Boyer (1974) and Meyer and Ritchie (1980) revealed that resistance drops with increasing flow rate, then levels off and remains fairly constant with further increases in flow rate. Boyer proposed parallel flow pathways to account for this phenomenon. He suggested a protoplast pathway (supplying cell water needs for growth) with a resistance much higher than the cell wall pathway important in supplying transpirational needs. At high water flow rates the protoplast pathway would be relatively unimportant compared to the low resistance cell wall pathway. With a decline in flow rate the

protoplast pathway carries a larger proportion of the water flow, and total resistance increases. Black (1979) felt the 2-pathway hypothesis was insufficient to explain variable leaf resistance where little water is required for growth. In addition, he contended that in such a system the low resistance pathway would supply more water with increasing evaporative demand, avoiding transient stress. Given that transient stress does occur, the author maintained the mechanism of variable resistance has not been clarified.

An alternative explanation for variable flow resistance has been suggested by Meyer and Ritchie (1980). They considered plant capacitance, the ability of tissues to store and release water, a possible mechanism accounting for variable resistance. The resistance to water movement out of a capacitance (storage site) would be less than the main flow path resistance. Thus, transpiration would exceed uptake until the net exchange of water from a capacitance is zero, at which point equilibrium is reached. Larcher (1975) previously suggested the root cortex may store water and smooth out short-term fluctuations in absorption from the soil. Indeed, Huck et al. (1970) found that diurnally roots may shrink to 60% of their original diameter, more than twice the change found in foliage. Probably the most striking example of plant capacitance is found in large trees such as Douglas-fir (Pseudotsuga menzesii) which can store enough water in sapwood to meet transpirational requirements for 10 days during midsummer (Waring and Running 1976).

Plant Water Potential

The concept of using water potential (ψ) to describe plant water status was introduced more than 20 years ago (Slatyer and Taylor 1960). As with many new concepts, its acceptance was fairly slow. However, the introduction of water potential unified the description of plant water relations. Kramer (1974) considered this modernization in terminology an important advancement in the study of plant water stress.

Water potential is defined as free energy per gram molecular weight or the chemical potential of water (Salisbury and Ross 1978). It is difficult to measure absolute values of chemical potential; so the water potential of a system must be compared to a standard, usually pure water at standard pressure and temperature (Kramer et al. 1966, Milburn 1977). The water potential of the reference system is generally set at zero. Although water potential is defined in terms of free energy, it is physiologically more relevent to deal with pressures, and thus water potential is expressed in units of pressure (Kramer et al. 1966). However, Slavik (1974) felt there was no direct evidence that physiological activity of water was proportional to its water potential.

A major advantage of using water potential terminology is that it allows separation of the components of water potential. Water potential of plant tissue is often broken down with the following equation:

$$\varphi = p + \pi + \tau$$

where p is the turgor potential, π is osmotic potential, and τ is matric potential (Gardner and Ehlig 1965; Kramer 1969, 1974; Richter 1976; Salisbury and Ross 1978). The osmotic and matric potentials are negative in sign, and turgor potential is generally positive, although negative values have been reported. Although this additive approach is generally accepted there are certain limitations that must be recognized.

The separation of osmotic and matric potentials is hardly clear-cut. Gardner and Ehlig (1965) stated that the partition of energy between osmotic and matric components was arbitrary. Dainty (1976) suggested that the osmotic and matric components interact. He explained that the solid-liquid interface is electrically charged, and thus contains an electrical double layer. The charge attracts cations, concentrating them along the interface causing a more negative osmotic potential than exists in the bulk solution. In this way the solid phase will influence water potential through both matric and osmotic effects. In a typical plant cell, water potential of the vacuole consists of turgor and osmotic potentials, while the primary force operating in the cell wall is matric potential. Thus, as Weatherley (1970) pointed out, in a multiphase system there are difficulties in simply adding average values for the various components. It has also been suggested that matric potential arises from an inconsistent definition of pressure in the standard thermodynamic equation (Passioura 1980). Given the difficulties in separating matric and

osmotic components, and the fact that matric potential is thought to be relatively small in the normal range of water potentials, many researchers have chosen to define ψ as $p + \pi$ (Milburn 1977, Heathcote et al. 1979, Kramer 1980, Monson and Smith 1982).

Turgor Potential

The turgor pressure of a cell is the positive pressure in excess of atmospheric pressure pushing outward on the cell walls (Brown 1977). An excellent explanation of turgor is provided by Fitter and Hay (1981). They used ψ_{vac} to designate water potential in the vacuole and ψ_{apo} for apoplastic water potential, and explain tugor as follows:

> Since ψ_{vac} is lower than ψ_{apo}, water tends to flow inwards across the cytoplasm, raising the vacuolar water potential but also increasing the volume of the vacuole. In a plant lacking cell walls, this flow of water would continue until either the cell burst or the difference in water potential was abolished by dilution of the vacuolar sap. However, in a leaf, cell volume is limited by the cell walls and only relatively small inflow of water can be accommodated by the elasticity of the cell walls. Consequently, hydrostatic pressure (turgor pressure) develops in the vacuole, pressing the cytoplasm against the inner surface of the cell walls, and raising the vacuolar water potential. As turgor pressure rises, adjacent cells press against one another, with the result that a leaf, originally in a wilted, flaccid condition, becomes increasingly turgid. At equilibrium, turgor pressure has reached its maximum value, and there is no tendency for water to flow from apoplast to vacuole.

The relationship between turgor pressure and vacuole volume is not generally linear because as the wall stretches resistance to deformation increases (Meidner and Sheriff 1976).

Maintenance of turgor pressure is critical to plant growth, as turgor is considered the driving force for cell wall extension (Cleland

1971). However, as Hsiao et al. (1976) point out, expansive growth depends not only on turgor, but also on cell wall properties which allow cell wall relaxation under stress. The elongation rate is not necessarily proportional to turgor pressure, but rather proportional to turgor in excess of some critical value (Cleland 1971, Salisbury and Ross 1978). In addition, Kirkham et al. (1972) detected a critical turgor value for cell division. These authors found that cell division in radish (Raphanus sativus) cotelydons was greatly stimulated by increasing turgor from 0.5 to 0.6 MPa, and cell enlargement stimulated as turgor increased above 0.3 MPa. In addition to influencing cell division and elongation, loss of turgor appears to seriously interfere with a number of biochemical processes, including protein synthesis (Hellebust 1976).

Direct measurement of turgor pressure would require connection of a pressure gauge to a cell vacuole (Milburn 1977). This approach has been used in large algal cells (Green 1968), guard cells (Edwards and Meidner 1979), and in spiderwort (Tradescantia virginiana) leaf cells (Zimmerman et al. 1980). Unfortunately such measurements require fairly sophisticated equipment and are not routinely made. Instead turgor pressure is generally calculated using the equation $\psi = p + \pi$. In this procedure total potential and osmotic potential are measured, and turgor potential is obtained through subtraction. A common practice has been to measure total potential with either a psychrometer or pressure bomb, then freeze and thaw the plant tissue, and obtain a measure of osmotic potential using psychrometric techniques. The

freezing and thawing is assumed to destroy membrance integrity and thus eliminate turgor pressure. In recent years the pressure-volume technique has been used to obtain estimates of turgor potential. Both psychrometric and pressure bomb techniques will receive more detailed explanations in later sections.

There have been numerous reports of negative turgor values (Warren Wilson 1967, Noy-Meir and Ginzberg 1969, Johnson and Caldwell 1976, Adams et al. 1978, Johnson 1978), which would indicate that cell walls are under tension. A plant that could generate negative turgor potentials would be better able to extract water from dry soils through an increase in suction tension (Lange and Losch 1979). However, it is becoming increasingly obvious that plants do not develop substantial negative turgor values, rather that the values are an artifact of the freezing and thawing procedure used in psychrometric analysis of osmotic potential. The problem is that relatively pure water of the apoplast dilutes solute containing water of the symplast when the frozen tissue is thawed (Tyree 1976, Campbell et al. 1979, Markhart et al. 1981, Henson 1982). The dilution of symplastic water will raise the osmotic potential (make it less negative), thereby making low turgor potential appear negative when the subtraction procedure is used. The magnitude of error will depend on the amount of water contained in the cell wall and the proportion of cell wall to symplast (Markhart et al. 1981). In addition, the error will increase as stress intensifies (Henson 1982), because the cell wall water content remains fairly constant over the physiological range of water potentials.

However, the symplast will dehydrate with increasing stress, thus increasing the dilution factor.

Osmotic Potential

The osmotic potential of a solution arises from the presence of solutes. The addition of solutes almost always causes the total potential of a solution to become more negative (Milburn 1977, Salisbury and Ross 1978). The decrease in total potential caused by addition of solutes can be attributed at least partially to the increase in entropy of the system (Brown 1977). One must also consider that each ion in solution is charged and will attract water molecules, thereby increasing the attraction among the remaining water molecules and reducing their kinetic energy (Brown 1977, Milburn 1977). For dilute solutions the V'ant Hoff equation explains the relationship between osmotic potential and solute concentration:

$$\pi = NRT$$

where N is the concentration of dissolved molecules or ions, R is the universal gas constant, and T is the absolute temperature (Larcher 1975). As solutions become more concentrated ions tend to interact, and there will be deviations from the V'ant Hoff relationship.

There is good evidence that many plant species are able to adjust osmotic potentials in response to stress (Zimmerman 1978). There are two ways osmotic potential of a cell might be adjusted:

(1) cell dehydration which concentrates existing solutes (passive adjustment)

(2) increases in solute content of cell either by uptake or internal production of osmotically active substances (active adjustment). For many crops, Hsiao et al. (1976) estimated dehydration would account for only a 0.2 to 0.3 MPa drop in osmotic potential before turgor became zero. Several recent studies have shown cell solute levels to increase during stress (Jones et al. 1980, Wilson et al. 1980). Thus, interest has focused on active adjustment, and some authors reserve the term osmotic adjustment for the active accumulation of solutes (Hsiao et al. 1976, Turner and Jones 1980).

The primary adaptive advantage of osmotic adjustment is related to maintenance of turgor (Hsiao et al. 1976). As discussed previously turgor maintenance is critical to growth. In addition, it has been demonstrated that plants which osmotically adjust to water stress are able to maintain high stomatal conductances to lower water potentials than those which do not (Turner and Jones 1980). Osmotic adjustment will also allow maintenance of higher photosynthetic rates as stress is imposed (Jones and Rawson 1979).

It appears that the rate at which water stress is imposed can have an effect on osmotic adjustment. Jones and Rawson (1979) found that osmotic adjustment in sorghum was 0.5 to 0.6 MPa if the decline in predawn water potential was 0.15 or 0.7 MPa/day; however, no significant osmotic adjustment occurred if stress was imposed at a rate of 1.2 MPa/day. Similarly, Turner and Jones (1980) indicated that

sorghum plants dried slowly over a several week period maintained higher turgor pressure at water potential values below -0.5 MPa than plants dried quickly over several hours (thereby limiting osmotic adjustment). Hsiao et al. (1976) observed osmotic adjustment in sorghum plants stressed at a rate of about 0.01 MPa/day. To obtain relevant results one must consider the rate of stress a plant would encounter growing in the field.

Adjustment in osmotic potential is often temporary if water stress is relieved. Henson (1982) found that much of the osmotic adjustment in pearl millet (Pennisetum americanum) was lost within 24 h of rewatering. Several crop and pasture species have been reported to lose osmotic adjustment within seven to ten days of rewatering (Jones and Turner 1980, Wilson et al. 1980). Redmann (1976) found that osmotic potential values of several native graminoids were closely correlated to rainfall and thus soil moisture. Again in this case, osmotic adjustment was lost as soil moisture increased.

Certain aspects of osmotic adjustment have not been adequately studied. Mechanisms for osmotic adjustment have been suggested (Kluge 1976), however our knowledge of how plant cells regulate their solute concentrations is deficient (Hellebust 1976). The benefits of osmotic adjustment have been elaborated on; however, potential detrimental influences are seldom mentioned. High cell solute levels are known to detrimentally affect enzyme activity and protein hydration in some cases (Wiebe 1972). In an excellent review of osmotic adjustment,

Turner and Jones (1980) considered the cost of producing solutes for osmotic adjustment as another subject deserving of study.

Matric Potential

The matric potential of a plant cell results from forces of capillarity, adsorption, and hydration (Warren Wilson 1967, Brown 1977). In general, matric potential is a measure of the tenacity with which surfaces attract water molecules (Salisbury and Ross 1978). The matric force exerted by a surface decreases with distance from the surface, and there is no sharp distinction between molecules which are bound to the surface and those which are not (Miller 1972). Matric forces lower the free energy of water below that of pure water, hence matric potentials are negative (Brown 1977).

As mentioned previously, there are some problems encountered in separating the matric component from total water potential. Consideration must be given to the evidence that osmotic and matric potentials interact (Warren Wilson 1967, Kramer 1969, Dainty 1976, Markhart et al. 1981). Matric potential can vary considerably from one cell phase to another. It is generally accepted that matric potential is most important in the cell wall (Dainty 1976, Brown 1977, Turner 1981). Matric potential can be appreciable in the cytoplasm if the colloid content is high, but it is considered minor in the vacuole (Miller 1972). When dealing with the cell as a whole, matric potential is thought to be minor, except in severely desiccated tissue (Wiebe 1966, Kramer 1969, Hsiao et al. 1976, Tyree 1976). However, the ratio

of cell wall to protoplast will influence the effect of matric potential on cell water relations (Miller 1972).

Pressure Chamber

The pressure chamber was first proposed in the early part of this century (Dixon 1914 as cited in Ritchie and Hinckley 1975). However, its use was abandoned until Scholander and his colleagues redesigned the device in the early 1960's (Scholander et al. 1964, 1965). The pressure chamber was shown to be a useful tool in the study of plant moisture stress (Boyer 1967, Waring and Cleary 1967), and has gained wide acceptance. Many articles describing total water potential as measured by the pressure chamber have appeared in the literature since the later 1960's. Ritchie and Hinckley (1975) reviewed theory and use of the pressure chamber in ecological research.

In the original articles by Scholander et al. (1964, 1965) a method for separating total leaf water potential into its components was described. However, the technique saw little use until Tyree and Hammel (1972) provided a sound theoretical analysis of the parameters derived. These authors found that the pressure-volume (P/V) curves originally described by Scholander et al. (1964, 1965) allowed quantitative estimation of several parameters important in the study of plant water relations. These parameters include osmotic potential at various water contents, the proportion of plant water contained in the cell and cell wall, and cell wall elasticity. In addition, the P/V

technique allows analysis of the relationship between total leaf water potential and relative water content (RWC).

Pressure-Volume Technique

The P/V curve as originally described consisted of a graph with % cell water removed on the x-axis and the inverse of total water potential on the y-axis (Scholander et al. 1964). To obtain a P/V curve, a twig was inserted into the pressure chamber and a balancing pressure obtained. The balancing pressure being the point at which sap first exudes from the leaf or stem protruding from the pressure chamber. More pressure is then added and the sap forced out of the cut end is collected and weighed. The pressure required to drive off each successive amount of water is recorded. In this way a graph of 1/pressure and water removed can be plotted (Figure 1). The curvilinear portion of the line represents both turgor and osmotic potentials, while osmotic potential is the primary factor influencing the linear portion. Once turgor is lost, the removal of water across the semipermeable cell membranes will concentrate the osmotically active solutes in the cell vacuole and the relationship between water loss and balancing pressure becomes linear.

There have been attempts to use alternative transformations when deriving P/V curves. Richter (1978) suggested using P and the inverse of water removed on the y-axis and x-axis, respectively. However, Tyree and Richter (1981) compared the possible transformations and

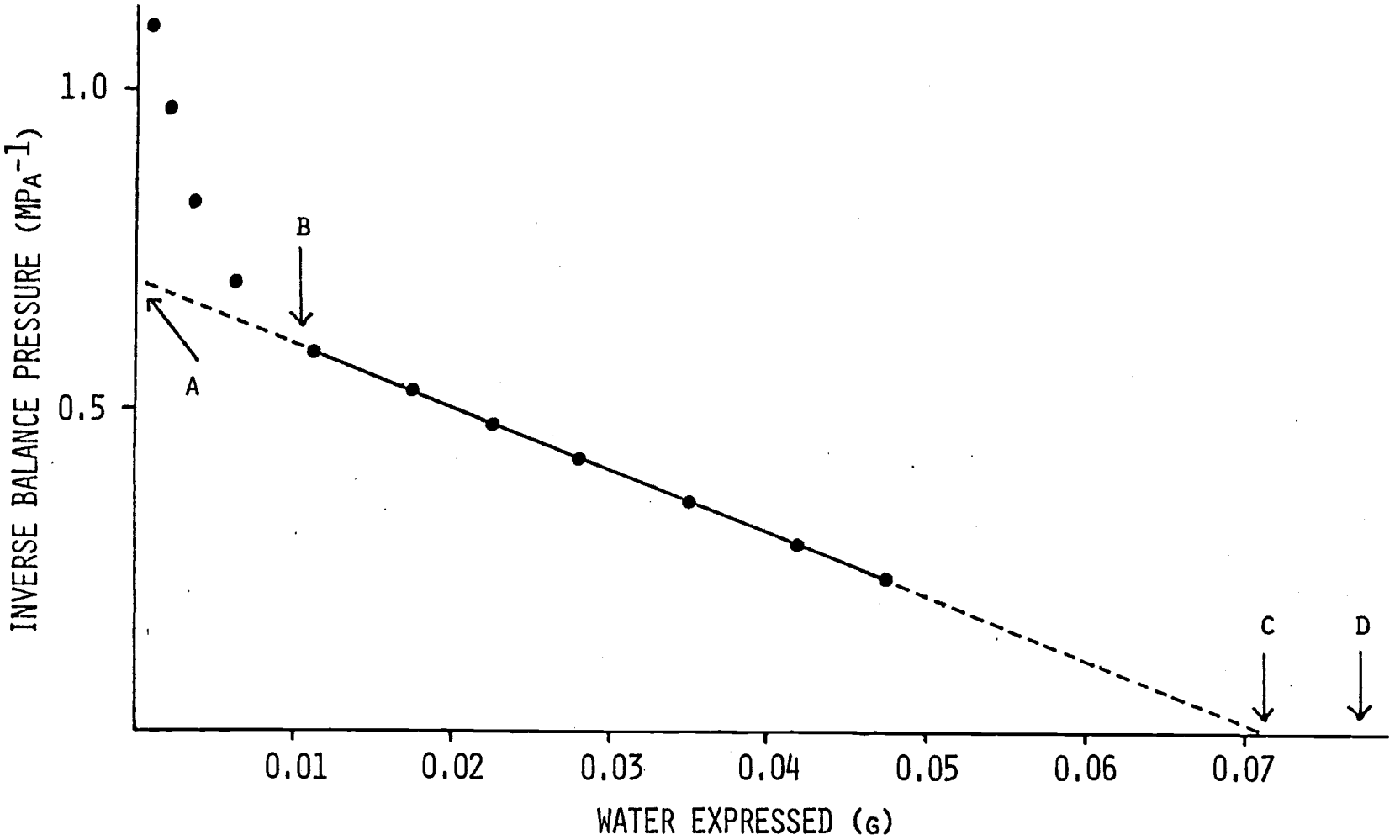

Figure 1. Typical pressure-volume curve. The letters represent the following: A is osmotic potential at full turgor, B is osmotic potential at zero turgor, C is total symplastic water, and D is total water content (obtained by subtracting dry weight from fully turgid weight). Bound water is obtained by subtracting C from D.

concluded 1/pressure vs. water removed to be the most useful plot in deriving P/V parameters.

The general procedure used in constructing P/V curves involves collection and weighing of sap expressed at various pressures. However, some species express only small amounts of sap when placed under pressure. The difficulty in collecting this small amount of sap rendered the technique useless for many herbaceous species, particularly the graminoids. A simple modification of the technique allowed its use on plants which express little sap (Campbell et al. 1979, Wilson et al. 1979). The modification consisted of determining weight loss from a leaf by weighing the whole leaf rather than collecting and weighing expressed sap.

Osmotic Potential

As indicated previously, osmotic adjustment is an important mechanism in drought adaptation. The P/V technique allows estimation of osmotic potential at any water content (Hellkvist et al. 1974); however, osmotic potential at full turgor (π^{100}) and osmotic potential at zero turgor (π^{0}) are most often considered. Cheung et al. (1975) suggest that π^{100}, π^{0}, and cell wall elasticity (E) are all closely associated with osmoregulation in a species.

Adjustment to increasingly negative π^{0} values allow positive turgor to be maintained as total leaf water potentials drop, and may be adaptive as substrate water becomes limiting (Roberts and Knoerr 1977). The advantage of more negative π^{0} values is that they allow the plant

to maintain water uptake and positive turgor at lower leaf water potential (Roberts et al. 1980). The tendency for π^{100} and π^{0} to become more negative as soil moisture declines has been observed in many native and crop species (Roberts and Knoerr 1978, Wenkert et al. 1978, Campbell et al. 1979, Jones and Turner 1980, Roberts et al. 1980, Wilson et al. 1980). Wilson et al. (1980) found that adjustment of π^{100} helped tropical grasses maintain positive turgor for the first 28 days of a drying cycle, but after that leaves apparently never achieved positive turgor.

Elastic Modulus

Elastic modulus is a potentially important parameter because it determines the rate of change in turgor pressure with changes in cell water content. A cell with rigid walls will drop its turgor pressure in reponse to a given change in water content more than one with less rigid walls (Cheung et al. 1975). Elastic modulus generally refers to cell wall rigidity; however, a confusing number of similar parameters have appeared in the literature (Wenkert et al. 1978). A relatively straightforward definition was proposed by Tyree et al. (1978):

$$E = \frac{\Delta P}{\Delta F}$$

where E is elastic modulus, P is turgor pressure, and F is a measure of the cellular volume by which the cell wall is stretched beyond the

symplastic volume at zero turgor. A similar definition was suggested by Turner (1981):

$$E = \frac{\Delta P}{\Delta \text{ Symplastic Water}} \times 100$$

thus, elastic modulus is dependent on changes in both turgor pressure and cell volume (Jones and Turner 1978).

It is not clear whether elastic modulus is constant with varying turgor pressures. In some cases it appears that elastic modulus increases as turgor increases (Hellkvist et al. 1974, Tyree et al. 1978, Wenkert et al. 1978, Wilson et al. 1980). Detailed work with wheat (Triticum aestivum) indicated elastic modulus was fairly constant at high turgor values, but varied in the low turgor region (Melkonian et al. 1982). Wenkert et al. (1978) suggested elastic modulus remains fairly constant under field conditions, but that fast drying in the pressure chamber causes values to vary.

Elastic modulus may be greatly influenced by a plant's prior stress history. Stressed plants should have a greater fraction of cell wall material, thicker cell walls, and more lignification, all of which would contribute to greater tissue rigidity (Jones and Turner 1978, Wilson et al. 1980, Melkonian et al. 1982). Research with sunflower indicated stress had little effect on elastic modulus (Jones and Turner 1980).

Campbell et al. (1979) measured elastic modulus ranging from 100 to 300 bars in wheat, and concluded its variability was too great for

use in evaluating drought adaptation in wheat cultivars. This parameter may, however, be of value in comparing drought tolerance between species (Ladiges 1975, Campbell et al. 1979).

Influence of Water Loss on Water Potential

Several ecological examples might help point out the adaptive significance of adjustment in osmotic potential and elastic modulus. Cheung et al. (1975) used the P/V technique to study the water relations of *Salix lasiandra*, a mesophyte, and *Ginkgo biloba*, a more drought resistant species. At 15% symplastic water loss (roughly incipient plasmolysis for both species), the total water potential was -2.2 MPa for *G. biloba*, but only -1.2 MPa for *S. lasiandra*. The greater drop in water potential of *G. biloba* was attributed to lower π^{100} and more rigid cell walls. *S. lasiandra* lost a substantial portion of its symplastic water fraction at fairly high water potentials, and thus would have to grow in moist soil to maintain favorable turgor.

Roberts and Knoerr (1977) used the P/V technique to study several forest species in the North Carolina piedmont. They found that *Ilex opaca* developed a total water potential of -1.7 MPa at a water deficit of 0.05 (where water deficit is water loss/turgid water content). The fairly negative total water potential was due largely to rapid turgor loss which allows *I. opaca* to extract water from fairly dry soils without undergoing a large leaf water deficit. During the same time period, *Acer rubrum* developed a total water potential of -0.2 MPa at

the same water deficit, suggesting this species requires moist soils. The disadvantage of the rapid turgor loss by I. opaca is reflected in turgor values at water deficits of 0.05; A. rubrum is able to maintain 1.4 MPa of turgor, and I. opaca only 0.4 MPa thus there would seem to be a trade-off in that A. rubrum maintains higher turgor (and presumably higher growth rates) in moist soils, but would undergo more severe water deficits than I. opaca to extract moisture from dry soils.

Osmotic and Bound Water Fraction

Another advantage of the P/V technique is that it allows an estimate of the water fraction held by the cell wall (bound water) and that contained in the symplast (osmotic water). The osmotic water fraction at full turgor is an important parameter in that it is the portion of water lost as water deficits develop (Roberts and Knoerr 1977). The bound water fraction is tightly held by cell wall material, and thus is unavailable for exchange in the normal physiological range of water potentials (Hellkvist et al. 1974, Tyree and Richter 1981).

Bound water may be directly correlated with volume of cell wall material (Boyer 1967). Cell wall composition could also influence the amount of bound water. However, Wilson et al. (1980) found little change in cell wall composition or thickness to explain variation of bound water in several tropical grasses. The factors controlling bound water fraction have not been well elucidated.

The relationship between bound water fraction and drought-resistance is also less than clear. Ladiges (1975) reported bound

water to correlate well with drought-resistance in three populations of Eucalyptus viminalis; more drought-resistant populations had a higher bound water fraction. However, Roberts and Knoerr (1977) could not establish a clear relationship between bound water fraction and environmental water availability; a range of species adapted to very different water regimes had similar bound water fractions. In several varieties of soybean (Glycine max), bound water fraction was not found to be a major factor in evaluating plant response to stress (Wenkert et al. 1978).

Seasonal changes in bound water fraction have been observed in many species. Studies of several tree species from a mixed deciduous forest in North Carolina revealed a general increase in bound water throughout the growing season (Roberts and Knoerr 1977, Roberts et al. 1980). In Sitka spruce (Picea sitchensis), Hellkvist et al (1974) observed that bound water increased from fall through spring, reached a high point in April, then declined during the summer. They also noticed a similar trend in dry weight fraction (dry weight/turgid weight). However, Campbell et al. (1977) observed a fairly constant bound water fraction in wheat.

Psychrometry

The idea of using a thermocouple junction to measure plant water potential was first proposed by Spanner (1951). A number of improvements were necessary before thermocouple psychrometers became widely accepted. It wasn't until the mid-1960's that psychrometers

were routinely used in the measurement of plant water potential (Kramer 1972). Many aspects of the development, construction, and theory of psychrometers are discussed in Brown and Van Haveren (1972).

A thermocouple psychrometer may contain one or more thermocouple junctions, i.e., junctions where two small wires of different metals are soldered together. The two metals have different electron densities and thus a small potential difference is created at the junction (Van Haveren and Brown 1972). When a current passes through the junction in one direction heat is liberated from the junction, when it moves in the opposite direction heat is absorbed. This phenomenon is referred to as the Peltier effect. Thus, when current moves in the proper direction the thermocouple junction can be cooled below the ambient temperature.

There are many different thermocouple techniques for measuring plant water potential, this discussion will deal with use of the single-junction psychrometer for measuring either wet-bulb depression or dewpoint depression. The single junction thermocouple psychrometer contains one bimetallic junction located inside a chamber in which the plant sample can be sealed. The sample must be allowed ample time to equilibrate with the air in the chamber, the equilibration time varies greatly depending on the nature of the sample. Once vapor equilibrium has been achieved, either the wet bulb depression (psychrometric mode) or dewpoint depression (hydrometric mode) is used to assess the vapor pressure in the chamber. The voltage output of the junction is read

with a microvoltmeter. Vapor pressure is related to water potential by the following equation:

$$\varphi = \frac{RT}{V} \ln \frac{e}{e_0}$$

where φ is water potential, R is the universal gas constant, T is absolute temperature, V is the partial molal volume of water, e is the vapor pressure of air at T, and e_0 is the saturated vapor pressure of pure free water at T (Brown 1977, Wiebe 1981).

When using a single junction psychrometer in the psychrometric mode, the junction serves alternatively as dry bulb and wet bulb (Slavik 1974). The output of the junction is read on a microvoltmeter, then Peltier cooling is used to condense water on the junction. The junction thus becomes a wet bulb and the temperature depression resulting from evaporative cooling is used to assess the vapor pressure gradient between the junction and the surrounding atmosphere (Van Haveren and Brown 1972). The output of the thermocouple is calibrated against salt solutions of known water potentials. A serious problem of this technique has been the need for extreme accuracy in the measurement of the wet bulb depression (Slavik 1974), and thus the need for very tight temperature control. Size and construction material of the chamber and thermocouple can influence results in the psychrometric mode (Mohsin and Ghildyal 1972).

An alternative to the psychrometric mode was described by Neumann and Thurtell (1972). They felt many of the problems associated with

psychrometers could be overcome if the dewpoint depression rather than wet bulb depression was used to assess vapor pressure in the psychrometer chamber. It appears that temperature control is less critical if the dewpoint technique is used (Turner 1981). The basic equipment is the same whether using the psychrometric or hydrometric mode, however, the microvoltmeter circuitry must be altered somewhat for dewpoint measurements. Peltier cooling is again used to condense water on the junction, however, in this case the microvoltmeter will maintain the junction at a temperature where water is neither lost nor gained from the surrounding atmosphere, i.e., the dewpoint (Campbell et al. 1973). As with the wet bulb techniques, microvolt output is calibrated against salt solutions of known water potentials.

Psychrometers have been commonly used to measure both total water potential and osmotic potential of plant samples. The technique used for measuring osmotic potential is described in detail by Brown (1972). Basically, total water potential of a plant sample is measured, the sample is then frozen and thawed, and water potential again measured. Freezing eliminates turgor pressure and the remaining component of water potential after freezing is assumed to be osmotic potential. Turgor potential can be estimated by subtracting osmotic potential from total water potential (e.g. Ackerson et al. 1977, Johnson 1978). However, as Brown (1972) points out, freezing eliminates the compartmentaliation normally found in plant cells and mixes the cellular contents. Thus there exists the problems alluded to earlier in this paper concerning the dilution of cell contents with apoplastic

water. The dilution effects can lead to apparent negative turgor values (Tyree 1976, Campbell et al. 1979).

Stomatal Function

Higher plants must take in carbon dioxide (CO_2) to maintain growth and function, yet must limit the amount of tissue water lost to the atmosphere (Salisbury and Ross 1978, Ludlow 1980). The plant must control water loss because the leaf mesophyll is sensitive to desiccation. A solid epidermal covering over the mesophyll would limit water loss, however CO_2 diffusion into photosynthetic cells would be virtually eliminated. Plants have not evolved a membrane which is permeable to CO_2 yet relatively impermeable to water vapor (Raschke 1976, Cowan 1977). Plants are able to regulate gas exchange across the relatively impermeable epidermis by controlling stomatal aperture. Stomata refers specifically to the pore itself, however, the term is often used to indicate the whole stomatal complex, including guard cells (Salisbury and Ross 1978). Guard cells are the pair of cells surrounding the pore, and the specialized epidermal cells adjacent to the guard cells are subsidiary cells.

Guard cells ultimately exercise control over the opening and closing of the stomata. Stomates open when guard cells take in water and swell (Ayler et al. 1973, Hsiao and Acevedo 1974). Cellulose microfibrils arranged around the circumference of the guard cell limit their ability to expand in diameter, thus they expand in length when water uptake occurs (Alyer et al. 1973, Salisbury and Ross 1978). The

cellulose arrangement, called radial micellation, causes the guard cells to buckle as their turgor increases. Since the guard cells are attached to each other at the ends, buckling causes opening of the stomata (Salisbury and Ross 1978).

Although many of the basic mechanisms of stomatal action are poorly understood (Raschke 1975), it does appear that guard cells raise their turgor pressure by developing low solute potentials and osmotically taking in water from other epidermal cells (Hsiao and Acevado 1974, Edwards and Meidner 1979). Exchange of potassium ions between subsidiary cells and guard cells is apparently important in this regard (Levitt 1976). In grasses, the subsidiary cells are thought to serve as ion storage sites (Raschke 1975).

The degree of stomatal opening is important in plant gas exchange. The control stomates exert over gas exchange is generally expressed in terms of resistance to diffusion (Fitter and Hay 1981). Both resistance and its inverse, conductance, have been used to describe plant gas exchange. The rate of gas exchange of a particular gas is determined by the concentration gradient of the gas (driving force) and the sum of resistances to gas flux (Moore 1977). Thus, an Ohm's law analog similar to that used to describe water flow in the plant has been applied to gas exchange. The one-dimensional nature of resistance model has been questioned by Parkhurst (1977), who proposed a three-dimensional model in dealing with photosynthesis.

The Influence of Stomatal Conductance on Photosynthesis and Transpiration

Photosynthesis

In order for photosynthesis to occur, CO_2 must diffuse into the leaf and then find its way to the carboxylation site in the chloroplast. The path of CO_2 within the leaf depends greatly upon the photosynthetic pathway of a particular plant, an aspect which will be considered only briefly in this discussion. A general formula for photosynthesis is as follows:

$$P = \frac{[CO_2]_a - [CO_2]_{chl}}{r'_a + r'_s + r'_m}$$

where P is photosynthesis; r'_a, r'_s, and r'_m are resistances to CO_2 diffusion at the boundary layer, stomata, and mesophyll, respectively; and $[CO_2]_a$ and $[CO_2]_{chl}$ are CO_2 concentrations in ambient air and at the chloroplast, respectively (Moore 1977). In this case r'_m is a fairly broad term including all resistances to CO_2 movement from the time it moves across the epidermis until it is fixed in the chloroplast. Thus mesophyll resistance provides an indication of a leaf's photosynthetic efficiency when the influence of stomata and the boundary layer are removed (Jones and Slatyer 1972).

The importance of the various resistances has been debated for many years. Penman and Schofield (1951) considered mesophyll resistance the controlling factor in photosynthesis except where stomates were closed or nearly so. However, Brix (1962) discovered

that stomatal aperture was very important in controlling photosynthesis. Similarly, Hinckley et al. (1978) found photosynthesis related to stomatal conductance in four tree species. Wong et al. (1979) altered the capacity of leaves to fix CO_2 and found that stomatal resistance to CO_2 transfer changes almost linearly with CO_2 assimilation rate. While stomatal movement and photosynthetic rate may respond independently to the same factors, Wong et al. (1979) suggest there is a direct link between the two processes. There is evidence that the close relationship between stomatal conductance and photosynthesis varies slightly at low leaf water potentials, and mesophyll resistance becomes relatively more important (Boyer 1970, Beadle et al. 1973). Boundary layer resistance has not been considered in this discussion because it is seldom large enough to limit photosynthesis, particularly in narrow leaves (Beadle et al. 1973, Gifford 1974, Williams 1974).

A number of factors may influence the relative importance of stomatal and nonstomatal resistances. Water stress appears to influence both stomatal and nonstomatal resistances simultaneously (Hsiao and Acevedo 1974, Boyer 1976). Relative changes in the resistances may be species specific. Hsiao and Acevedo (1974) felt the discovery of some nonstomatal control of photosynthesis in a few species should not obscure the critical influence stomates have on photosynthesis as water stress develops. Light intensity may also influence the proportions of the various resistances. Boyer (1976) has suggested that stomatal control may be most important at high light

levels where the CO_2 flux is great, and mesophyll resistance more important at low light levels. Possibly most important in any consideration of resistances to CO_2 assimilation is a plant's photosynthetic pathway. One of the advantages of the C-4 pathway is its ability to reduce mesophyll space CO_2 concentrations to very low levels and effectively carry CO_2 to the carboxylating sites (Fitter and Hay 1981). Thus mesophyll resistance in C-4 species may be only one-fifth that of C-3 species (Gifford 1974).

Transpiration

Plant water loss is controlled primarily by stomatal aperture. The overall importance of transpiration to world water cycles was pointed out by Raschke (1975): "one-half to six-sevenths of the water precipitated on the land returns to the atmosphere by evapotranspiration from vegetation. On the average transpiration through stomata is almost three times larger than evaporation from soil." Water loss through stomata is also critically important to individual plants.

The model used to describe transpiration is again an Ohm's Law analog, with several changes from the photosynthesis model:

$$T = \frac{[H_2O]_1 - [H_2O]_a}{r_a + r_s}$$

where T is transpiration; $[H_2O]_1$ and $[H_2O]_a$ are the water vapor concentrations in the leaf intercellular spaces and ambient air,

respectively; and r_a and r_s are the resistances of the boundary layer and stomates, respectively (Hsiao and Acevedo 1974, Moore 1977). The driving force for transpiration is the difference in vapor pressure between water within the leaf and in the bulk air (Salisbury and Ross 1978). The vapor pressure in the leaf is generally assumed equal that over a free water surface at leaf temperature (Farquhar and Raschke 1978). The assumption that the intercellular spaces are saturated may not always hold (Moore 1977), this point will be considered in the following discussion. In contrast to photosynthesis, where CO_2 is actively taken up by the leaf, transpiration is considered a passive physical process, where water is transferred along a concentration gradient (Brown 1977).

The transpiration model presented above does not include a mesophyll resistance, a point which has been the subject of some controversy. Farquhar and Raschke (1978) found no evidence for the presence of a mesophyll wall resistance to transpiration under physiological conditions. However, the authors hesitated to extend their conclusions to arid zone plants. Indeed, there is evidence that vapor tensions may develop in mesophyll walls of some species under severe stress (Jarvis and Slayter 1970). Mesophyll wall vapor tensions would cause intercellular vapor concentrations to be less than saturated, violating a basic assumption of the transpiration model. Under most circumstances it is probably still safe to assume that the intercellular spaces are saturated with water vapor.

The transpiration model also ignores nonstomatal (cuticular) water loss. However, the epidermal covering of the leaf is considered hydrophobic and thus offers considerable resistance to diffusion of water vapor (Larcher 1975). Diffusion resistance of the cuticle is generally 10 to 100 times that of the lowest resistance of the stomata (Raschke 1975). Xerophytes in general, and mesophytes under even moderate water stress lose little water across the cuticle (Larcher 1975, Raschke 1975).

Transpiration can influence the energy budget of a leaf, which in turn affects other physiological processes. There are three major processes by which plants dissipate heat: 1) emission of long-wave radiation, 2) convection of heat, and 3) transpiration (Fitter and Hay 1981). Plants are able to exercise short-term control over transpiration, and thus in many cases it is the most effective method of heat dissipation (Gates 1976). Plants with low transpiration rates may have leaf temperatures 10 C above ambient air temperatures (Gates 1975, Larcher 1975). However, small leaves often stay close to air temperatures even at low transpiration rates (Campbell 1977).

High leaf temperatures can in turn influence transpiration through effects on the vapor pressure gradient. Vapor pressure approximately doubles for every 10 C increase in temperature (Salisbury and Ross 1978). Thus, if leaf temperature increased before transpiration commenced, the driving force for water loss would be greater. Tenhunen and Gates (1975) found that water use by common milkweed (Asclepias syriaca) was dependent upon three factors: 1) water vapor

concentration of the air, 2) leaf temperature, and 3) resistance in the diffusion pathway. These factors certainly interact, but the importance of leaf temperature to water loss is demonstrated. However, factors other than transpiration may help reduce leaf heat load. Ehleringer (1980) compared pubescent and nonpubescent species of Encilia, which are suffrutescent desert shrubs with drought deciduous leaves. He found pubescence greatly reduced midday absorbance, and calculated that transpiration would be reduced by 34% compared to nonpubescent species. There is good evidence that leaf orientation is also very important to the leaf energy budget (Campbell 1977). Therefore, the relationship between leaf temperature and transpiration is influenced by other factors, and depends greatly on plant adaptations.

Water Use Efficiency

The relationship between transpiration and photosynthesis is generally expressed as water use efficiency (water used to produce a unit weight of dry matter) or transpiration ratio (transpiration/photosynthesis). Water use efficiency (WUE) can be influenced by physiological processes other than transpiration and photosynthesis, but generaly transpiration ratio and WUE are similar.

Low levels of environmental CO_2 limit a plant's ability to develop a steep CO_2 gradient between leaf and air. As Larcher (1975) points out, at an air temperature of 20 C and relative humidity of 50% the water vapor gradient is about 20 times as sharp as the CO_2 gradient.

In addition, water molecules are smaller than those of CO_2 and diffuse at least 1.5 times faster (Larcher 1975, Moore 1977). Thus it is not surprising that large amounts of water are used in producing plant material. Black (1973) lists the WUE of C-3 and C-4 plants as 450-950, and 250-350 g H_2O/g dry weight, respectively. The higher WUE of C-4 plants can be attributed to their CO_2 pumping system which allows them to maintain the same photosynthetic rate as a C-3, but with smaller stomatal opening (Ehleringer 1979). There are a wide variety of adaptations within each pathway that effect water use efficiency.

It is possible that a degree of stomatal closure could exert a larger proportional effect on transpiration than on photosynthesis because of the length of the CO_2 pathway (Meidner and Mansfield 1968). It appears that the transpiration ratio can be improved when partial stomatal closure is induced artificially (Mansfield 1976). Raschke (1976) also cites evidence indicating that partial stomatal closure improves water use efficiency by reducing transpiration more than photosynthesis. The author considered transpiration linearly related to conductance, with photosynthesis following saturation kinetics, a very non-linear function with respect to conductance. This contrasts with the findings of Wong et al. (1979), that epidermal conductance to CO_2 transfer is linearly related to assimilation rate.

The argument that WUE is improved by partial stomatal closure was considered by Hsiao and Acevedo (1974). The authors note that the model used for representing transpiration does not include a mesophyll resistance, while the photosynthetic model does. Thus, as mentioned

previously, stomatal resistance might be relatively less important for photosynthesis compared to transpiration. Hsiao and Acevedo argued that while such a situation can occur, and might explain some experimental results, the bulk of research indicates that as stress becomes severe enough to increase stomatal resistance, mesophyll resistance also increases. There may not be a gain in WUE if stress reduces photosynthesis through increases in mesophyll resistance, and this would explain field studies indicating that WUE remained relatively constant for a given species as water levels were varied (Hsiao and Acevedo 1974). The rate at which stress is applied can influence WUE (Jones and Rawson 1979). The observation that artifically induced stomatal closure increases WUE and water stress induced closure does not, might be explained by the lack of significant increases in mesophyll resistance with artifical closure.

Factors Influencing Stomatal Conductance

It has been well established that stomatal conductance and transpiration tend to cycle both diurnally and on a more short term basis. Lange and Losch (1979) have identified five types of daily transpirational courses: 1) dome shaped curves, 2) single-peaked curves, 3) single-peaked curves with a shoulder, 4) two-peaked curves, and 5) daily courses with more than two peaks. Generally, progression from type 1 to type 4 is associated with increasingly adverse environmental conditions. The authors state that daily transpirational cycles in well-watered plants cannot always be explained by

environmental factors, endogenous rhythms in stomatal aperture may also be important.

Cyclic variations in stomatal aperture can take on several different forms. Barrs (1971) cites evidence of short term cycles of 2-4 minutes and longer term cycles of 10-15 minutes in corn. The short term oscillations may be caused by a CO_2-regulating system within the leaf, with longer term oscillations controlled by the water regulation system. The water-based oscillations could result from root absorption lagging behind transpiration. Barrs (1971) felt the CO_2 and water based explanations consistent with experimental results, however, he cautioned there are exceptions. Self-sustaining oscillations of about 40 minutes in duration have been observed in many species (Farquhar and Cowan 1974).

In discussions of diurnal stomatal conductance one must also consider behavior during the night. Evaporative demand is generally much less at night than during the day, a fact that is put to good use by the water-efficient CAM photosynthetic pathway. There is a less clear advantage for night-time opening in C-3 species. It is not unusual for stomata of dicotyledons to open just prior to the beginning of the photoperiod (Meidner and Mansfield 1965); however, in this case there may be an advantage in that CO_2 can diffuse into the intercellular spaces just prior to the beginning of photosynthetic activity. Munchow et al. (1980) found stomata of the C-3 species kenaf (Hibiscus cannabinus) open at midnight, and state that night-time transpiration can be 20% of the total during nights with high

advection. These authors found no nocturnal opening of stomata in sorghum, which apparently is characteristic of monocotyledons.

Given that CO_2 uptake is one of the primary functions of stomata, one might expect photosynthesis to influence stomatal conductance. Raschke (1975) felt there was good evidence for stomatal opening in response to low levels of intercellular CO_2. In this manner, stomatal conductance would be related to the photosynthetic capacity of the mesophyll. If stomatal conductance of CO_2 changes in the same proportion as assimilation rate, then intercellular CO_2 cencentration (Ci) can be calculated by the following equation:

$$Ci = Ca - A/g$$

where Ca is ambient CO_2 concentration, A is assimilation rate of CO_2, and g is diffusive conductance of the epidermis to CO_2 transfer (Wong et al. 1979). The intercellular CO_2 concentration tends to remain constant, except in cases of rapidly applied water stress (Osmond et al. 1980).

Stomates also respond to water stress. Johnson et al. (1974) found that transpiration was linearly related to flag leaf water potential in both barley (Hordeum vulgare) and wheat. There are examples of stomates responding more to leaf turgor than total leaf water potential (Hinckley et al. 1978). In some species conductance is unaffected by leaf water potential to a point, then declines in either a linear or curvilinear fashion (Ludlow 1980). Douglas fir exhibited a major decrease in stomatal conductance if xylem water potential dropped

below -2.0 MPa (Running 1976). A threshold response of conductance to leaf water potential has been widely demonstrated (Hsiao 1973), however, the response depends on species, growing conditions, and stress history (Hsiao et al. 1976).

The manner in which stress is applied influences conductance. Field-grown plants often maintain high conductance values to lower leaf water potentials than container-grown plants (Ritchie 1974). The author suggested exposure to prolonged deficit in the field allows modification of stomatal response, whereas container-grown plants are usually stressed more quickly. Indeed, Jones and Rawson (1979) found rapid stress rates resulted in a threshold response of stomates, while stomates closed gradually over a 1.5 MPa range when slower rates of stress were used. This is certainly an important point when comparing field and greenhouse studies.

Stomates may become acclimated to stress through prior experience. Sorghum stomata completely closed during an initial drying cycle, but when droughted after an initial drying and wetting cycle, they remained partially open (Sullivan and Easten 1974). Prior stress conditioning allowed cotton (Gossypium hirsutum) plants to maintain comparable stomatal resistance to leaf water potentials 1.4 MPa below non-conditioned plants (Brown et al. 1976).

Although a great many factors are important, it has generally been assumed there were two variable feedback loops influencing stomatal conduction; one dependent on leaf CO_2 level and one on leaf water status (Lange and Losch 1979). Using the water-regulated loop as an

example: when leaf water potential falls to some level as a result of transpirational water loss, stomata begin to close allowing leaf water potential to recover--following classical feedback theory (Ludlow 1980). However, feedback response cannot explain observations that increased evaporative demand can actually reduce transpiration before leaf water potential is affected (Farquhar 1978). The direct response of stomata to evaporative demand is feedforward in nature (Cowan 1977). The feedforward response requires only that water be lost from the leaf without passing through the stomates, and that stomates respond to the loss (Farquhar 1978).

There are advantages to the feedforward response, especially for plants growing in areas of high evaporative demand. Schulze et al. (1972) detected stomatal response to humidity in three ecologically diverse species growing under desert conditions. This response has also been observed in alpine and arctic species found in typically dry sites (Johnson and Caldwell 1976), and may be fairly widespread in arid-zone plants (Lange and Losch 1979). Direct stomatal response to humidity insures reduction in transpiration before any detrimental effects of low leaf water potential can occur (Ludlow 1980).

The feedforward response is also consistent with the theoretical optimization of gas exchange presented by Cowan and Farquhar (1977). Under this system, optimum stomatal behavior for gas exchange requires that the partial differential quotient $\partial T/\partial P$ (where T is transpiration and P is photosynthesis) remain constant. Stated simply, stomates tend to open under conditions allowing rapid photosynthesis and close when

transpiration will be high (Farquhar et al. 1980). To optimize gas exchange, plants must be able to directly respond to environmental conditions, specifically evaporative demand (Lange and Losch 1979). The experimental results of Farquhar et al. (1980) support the theory that plants vary stomatal aperture to keep the differential quotient constant, optimizing carbon gain with respect to water loss.

There are a number of environmental factors that may influence intercellular CO_2 concentration, leaf water status, and evaporative demand, thereby affecting stomatal conductance and transpiration. As Raschke (1975) states, when responding to environmental variables, it is uncertain which feedback loop ultimately controls stomatal aperture. The response may be further complicated in species exhibiting a feedforward response. As Smith and Geller (1980) point out, there are a number of leaf and environmental parameters that interact to determine stomatal conductance and transpiration. And, of course, the physiological adaptations of each species must be considered.

Environmental water supply will influence stomatal conductance through its effects on leaf water status. However, in mesophytes stomatal closure of water stressed leaves may take several days to reverse once adequate water is supplied (Fitter and Hay 1981). Stomatal closure in response to water stress is species specific. Earlier closure with the onset of water stress is a mechanism for conserving water in some species (Sullivan and Eastin 1974). The desert shrub jojoba (Simmondsia chinensis) maintained appreciable leaf conductance to very low soil water potential (-2.0 MPa), a situation

that would kill many mespohytes (Adams et al. 1978). Tundra species exhibit different stomatal response to soil moisture depending on the sites to which they are adapted (Johnson and Caldwell 1976). Cotton transpiration was correlated to decreasing soil moisture (Pallas et al. 1967). Position within the plant canopy can influence conductance. Stevenson and Shaw (1971) found that under soil moisture stress, leaf resistance in the middle of the canopy increased 2 h earlier in the day and to a greater extent than upper leaves of soybeans.

In some species adjustment of leaf area may serve to maintain conductance as moisture stress increases. Under controlled conditions, Black and Squire (1979) covered some leaves of unirrigated pearl millet (Pennisetum typhoides) and groundnut (Arachis hypogaea) and detected increased stomatal conductance of the remaining leaves. Campbell and Harris (1977) felt that big sagebrush (Artemisia tridentata) controlled long-term water loss primarily by adjusting leaf area.

Light indirectly influences stomatal conductance through effects on photosynthesis and intercellular CO_2 concentration (Raschke 1975). Stomatal closure at low light levels is often an advantage because CO_2 gain is low and water loss can be substantial (Kaufmann 1976). In a study of 4 native tree species, Kaufmann (1982) found photosynthetic photon flux density and absolute humidity difference between leaf and air the two most important variables in explaining stomatal conductance. However, secondary factors such as air temperature and water stress did intermittantly influence conductance. Pospisilova and Solarova (1978) studied snap bean (Phaseolus vulgaris) and determined

that generally stomatal conductance increased in response to increasing photon flux density. However, with decreasing leaf water potential, the photon flux density necessary for major increases in stomatal conductance became greater. At leaf water potentials lower than -1.0 MPa, the highest photon flux density used did not induce photoactive stomatal opening. This illustrates the interactive nature of environmental factors.

Direct response of stomata to ambient humidity or the vapor pressure deficit between leaf and air (VPD) was discussed previously as a feedforward response. In species not exhibiting a feedfoward response, increasing VPD can influence stomatal aperture by increasing transpiration, thereby lowering leaf water potential, and stomata respond in a feedback manner. There are numerous reports of stomatal response to humidity in both native and crop species (Schulz et al. 1972, Hall et al. 1976, Farquhar et al. 1980).

Stomatal response to temperature is often indirect and thus difficult to separate from other factors. Absorbed solar radiation can cause leaf temperatures to rise well above ambient temperature, which increases the VPD (Smith and Geller 1980). On the other hand, evaporative cooling via transpiration lowers leaf temperatures (Raschke 1975). Soil moisture can influence the potential for evaporative cooling. Pallas et al. (1967) noted that cotton leaves were as much as 3.4 C above ambient temperatures when soil moisture was low. Losch (1979) found that increasing ambient temperature from 20 to 28 C increased stomatal opening if no water stress existed, and decreased

stomatal aperture if water stress had been applied. In some cases an optimum response curve, with stomatal closure at high and low temperatures occurs (Hall et al. 1976).

One must also consider that stomata on the adaxial (upper) and abaxial (lower) leaf surfaces may react differently to environmental conditions. There is often a difference in stomatal density on the two surfaces. Higher densities on the abaxial surface have been found in cotton (Pallas et al. 1967), snap bean (Kanemasu and Turner 1969), and heartleaf arnica (Arnica cordifolia) (Young and Smith 1980). On the other hand, Ledent and Journet (1978) examined 120 genotypes of winter wheat, and Dernoeden and Butler (1979) examined 12 genotypes of Kentucky bluegrass (Poa pratensis) and in all cases stomatal density was higher on the adaxial side.

Abaxial and adaxial stomatal conductance also varies with species. Sionit and Kramer (1976) found soybeans had higher abaxial conductance at all water potential and growth stages tested, however, no major differences between the two surfaces were detected in sunflower. With snap beans, Kanemasu and Turner (1969) noted abaxial conductance unaffected by leaf water potentials above -1.1 MPa, however, adaxial resistance increased sharply at about -0.8 MPa. Solaroa et al. (1977) worked with snap bean, and also measured greater conductance on the abaxial surface, but the response of the two surfaces corresponded. Stress preconditioning in cotton allowed abaxial stomates to maintain comparable conductance to leaf water potentials 1.4 MPa lower than plants not preconditioned, however no adjustment in adaxial stomates

occurred (Brown et al. 1976). Sharpe (1973) also found abaxial conductance higher than adaxial in cotton, as did Sanchez-Diaz and Kramer (1971) with sorghum. The differences between upper and lower surfaces decreased in corn with increasing water stress (Sanchez-Diaz and Kramer 1971). The responses of the two surfaces in the desert shrub jojoba depended on plant water status (Adams et al. 1978). Well watered jojoba plants exhibited abaxial conductance equal to or greater than adaxial values, while under water stress adaxial values were considerably higher. The authors suggest higher conductance of the upper surface could be a cooling mechanism for this desert plant. In general, it appears that the conclusions of Sharpe (1973) should be heeded, i.e., that measuring stomatal conductance of one surface does not adequately describe leaf resistance, and that the two surfaces may respond differently to changing environmental conditions.

STUDY SITE

The study was conducted on the Hall Ranch of the Eastern Oregon Agricultural Research Center, located 19 km southeast of Union in Union County, Oregon. The study area is situated in the foothills of the Wallowa Mountains in the northeastern portion of the state, at an elevation of approximately 1200 m.

The community dominating the site resembles the mixed conifer-pinegrass, ash soils community type described by Hall (1973). Overstory vegetation was primarily ponderosa pine (Pinus ponderosa), but also contained Douglas fir and larch (Larix occidentalis). There was limited tree regeneration on the site. The understory vegetation was dominated by elk sedge, pinegrass, and heartleaf arnica.

Soils on the study site are Typic Vitrandepts belonging to the Tolo series. The soils are silt loams, with the top 10 cm containing 22, 55, and 23% clay, silt, and sand, respectively. This series is formed from volcanic ash over buried soil, and is generally deep (100-150 cm) and well-drained. The aspect of the site is north-facing with 15-20% slope.

The study area normally receives the bulk of precipitation during the winter and spring. Summers are typically hot and dry, with daytime temperatures often reaching 32-35 C. During the study years there were occasional summer thunderstorms. Precipitation data were collected at a weather station located 1.6 km from the study site. The average precipitation for 1971-1981 was 61.0 cm, with the study years above

average; 66.8 and 65.3 cm for 1980 and 1981, respectively. Precipitation for May, June, July, and August totalled 9.9, 5.1, 3.3, and 0.8 cm, respectively for 1980 and 7.1, 7.4, 2.5, and 2.5 cm, respectively for 1981.

METHODS

1980 Study

Field Measurements

During the 1980 study season pinegrass was the only species studied. The study began in May and continued until the end of July when pinegrass approached senescence. On each sampling date both water relations and environmental factors were measured.

Xylem potential was measured in the field at approximately 4 h intervals beginning 600 (PDT). At each sampling time eight samples were measured using a pressure chamber (PMS, Corvallis, OR). Moist towling was placed in the pressure chamber to limit vapor loss, and a pressurization rate of 0.025 MPa s^{-1} was used. Tillers were randomly selected and the most recently expanded leaf blade used for each measurement.

Total water potential was also measured at each sampling time using sample chamber psychrometer/hygrometers (model C-52, Wescor, Logan, UT) in conjunction with a microvoltmeter (model HR-33T, Wescor). Two sample chambers were used, allowing measurement of two samples for each sampling time. The hygrometric or dew point mode was used, and readings were taken after 2 and again after 4 h of equilibration. The sample chambers and microvoltmeter were enclosed in styrofoam boxes with 5 liter water heat sinks to help reduce thermal gradients encountered in the field. The sample chambers were calibrated with standard NaCl solutions prior to each set of measurements. Ambient

temperature and relative humidity were measured at each sampling time with a sling psychrometer. Solar radiation throughout each sampling date was measured with a recording pyranograph (model R-401, Weather Measure Corp). Soil moisture was determined gravimetrically at the 0-10 and 10-30 cm depths on each sampling date. Four random samples were taken at the two depths. A soil moisture release curve was constructed from pressure plate readings and percent soil moisture converted to soil water potential.

Lab Measurements

Leaf samples were also collected and frozen on dry ice at each sampling time. At the end of the day the samples were placed in a freezer at -20 C. After several days, samples were removed from the freezer and allowed to thaw for 2-3 h. The samples were loaded into sample chambers in a humid box to minimize vapor loss during loading. Samples were allowed a five minute equilibration period before readings of osmotic potential were made. Two samples were measured for each sampling time. Sample chambers were recalibrated every ten samples.

1981 Study

During the 1981 season both pinegrass and elk sedge were studied. All physiological parameters studied were measured for both species. Field work began in May and continued through the end of August. Again, both water relations and environmental parameters were measured diurnally on each sampling date.

Field Measurements

Xylem potential was measured at approximately 2 h intervals beginning just prior to sunup (predawn). At each sampling time four samples of each species were measured using the pressure chamber. Tillers were randomly selected and the most recently expanded leaf blade used. In addition, rhizomes were collected three times between predawn and midafternoon for pressure chamber measurements.

Diffusive resistance was measured each sampling date at 4 h intervals beginning approximately 730 (PDT). Four measurements of abaxial (lower) and adaxial (upper) leaf surfaces of each species were taken using a diffusive resistance porometer (model LI-60 with LI-15S sensor, Lambda Instruments, Lincoln, NE). Leaf temperature was measured with a thermistor located in the sensor head.

Ambient temperature, relative humidity, solar radiation, and soil moisture were measured in the same manner as they were in 1980. However diurnal measurements were taken at 2 h intervals in 1981.

Lab Measurements

Samples of each species were collected at approximately 1400 (PDT) and frozen on dry ice. At the end of the day samples were placed in a freezer at -20 C. As in 1980, sample chambers were used to determine osmotic potentials of the samples. Four randomly selected leaf samples of each species were measured.

Four times during the sampling season pressure-volume curves were constructed for each species. Entire tillers, including a portion of

the root system, were collected in the field and placed in dark styrofoam boxes containing about 2 cm of water in the bottom. Ice was used to keep the samples cool. About six tillers of each species were collected. Tillers were allowed to rehydrate overnight and pressure-volume measurements taken the following day. At most, two pressure-volume curves for each species were made during any given day. The extra tillers were collected in case xylem breakage occurred during a pressure-volume run. A minimum of three days was necessary to obtain four pressure-volume curves for each species, thus the date of sampling presented in the text represents the midpoint.

The pressure-volume curves were constructed using a technique similar to that of Wilson et al. (1979). The most recently expanded leaf was cut from a tiller, enclosed in a small plastic bag, and the cut end inserted through a split rubber bung. The bung was constructed from a laboratory stopper. The entire assembly was weighed and placed in a pressure chamber. Balancing pressure, the point where sap first appeared at the cut end, was noted. The pressure was then increased 0.25 MPa and maintained until sap no longer exuded from the cut end. Sap was blotted from the cut leaf. The pressure was released very slowly, and the leaf and bung weighed. The assembly was again placed in the pressure chamber and repressurized at a rate of 0.008 MPa s^{-1} until a balance pressure was obtained. The entire procedure was repeated until at least 10 points of balance pressure and water lost were obtained for each leaf. Pressure-volume curves were constructed from the data (Figure 1), and least square analysis used to plot a line

through the linear portion of the graph. The parameters π^{100}, π^{0}, and B were obtained as shown in Figure 1. Cell wall elasticity was calculated as change in turgor per change in relative water content (RWC), where

$$RWC = \frac{\text{Sample Wt} - \text{Dry Wt}}{\text{Turgid Wt} - \text{Dry Wt}} \times 100.$$

In this case elastic modulus was calculated from the midpoint of the curvilinear portion of the graph to the point where turgor was lost. Thus the calculation is rather arbitrary and should be considered primarily for relative comparisons.

Two samples of each species were analyzed for cell wall content using the method of Van Soest (1967). Samples were collected along two 30 m transects on seven dates during the study season. Leaf materials similar to those used for water relations measurements were collected. On three occasions during the study season leaf samples of both species were weighed and leaf impressions made. Leaf area was measured with a leaf area meter (Model LI-3000, Li-Cor, Lincoln, NE), and specific leaf weight calculated. Four samples, each consisting of two leaf blades were analyzed for each species.

RESULTS AND DISCUSSION

1980 Study

There are many reports of diurnal changes in xylem potential for both woody plants (Klepper 1968, Goode and Higgs 1973, Cline and Campbell 1976, Running 1976) and herbaceous crops (Jordan and Ritchie 1971, Biscoe et al. 1976, Hsiao et al. 1976, Ackerson et al. 1977, Turner and Long 1980). The generally observed diurnal trend is one of high xylem potential values in the morning, decreasing (becoming more negative) until midafternoon, then increasing during late afternoon and evening. Hsiao et al. (1976) stated that "midday depression of water potential of leaves or shoots of exposed plants is probably ubiquitous on sunny days."

There is less literature available on perennial herbaceous species. Pavlik (1980) observed typical trends in xylem potential for several sand dune species, as did Jackson (1974) with orchardgrass (Dactylis glomerata) and perennial ryegrass (Lolium perenne). Young and Smith (1980) observed a much smoother diurnal curve of xylem potential for sun plants than for shade plants of heartleaf arnica, indicating forest overstory can influence trends in xylem potential.

In this study measurement of pinegrass xylem potential indicated this species also follows the typical diurnal pattern (Figure 2). In some species there is recovery of xylem potential to near predawn values by early evening (Pavlik 1980, Turner and Long 1980), however, this was not the case with pinegrass. In fact, on 6-10 there was no

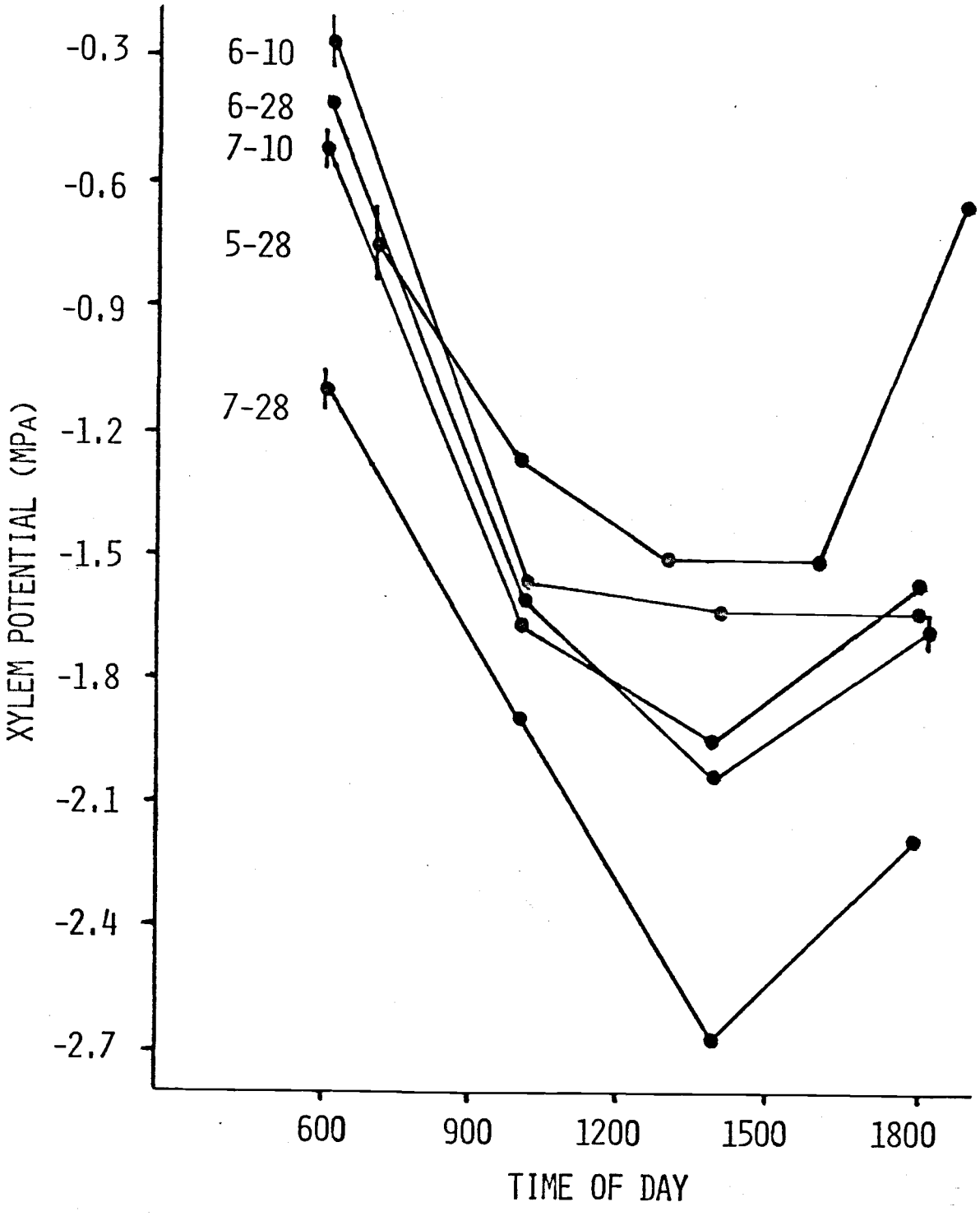

Figure 2. Diurnal variation in xylem potential for pinegrass during 1980. Dates are indicated to the left of each curve. Vertical lines represent maximum standard error for each curve.

recovery in xylem potential values by 1800 h. The lack of recovery appears to result from the fact that temperature and relative humidity (RH) remained unchanged between 1400 and 1800 h. Conversely, there was almost complete recovery of xylem potential on 5-28. On this date temperature declined from 16 C at 1400 h to 8 C at 1900 h and RH increased from 50 to 87% during the same period. The decrease in evaporative demand allowed recovery of xylem potential.

On any given day most of the variation in RH can be accounted for by changes in temperature, the actual vapor density remains fairly constant. The lowest correlation between temperature and RH occurred on 7-28 ($r = -.94$); the lowest correlation coefficient on the other dates (5-28, 6-10, 6-28, 7-10) was -.98. Without major airmass changes it is typical for vapor density to remain constant on a diurnal basis (Campbell 1977). Thus temperature plays an important role in the diurnal variation of xylem potential in pinegrass.

Diurnal variation in osmotic potential of pinegrass also occurred (Figure 3). Again, values generally declined from morning to afternoon, leveling or increasing by evening. Once again the major exception occurred on 6-10 when there was a continual decline in osmotic potential until 1800 h. Apparently the lack of recovery of xylem potential and consequent lack of rehydration of cell tissue accounted for the continual decline in osmotic potential.

Diurnal variation of osmotic potential has been demonstrated in several species. Concurrent diurnal trend in leaf water potential and osmotic potential was observed for wheat growing in moist soil (Biscoe

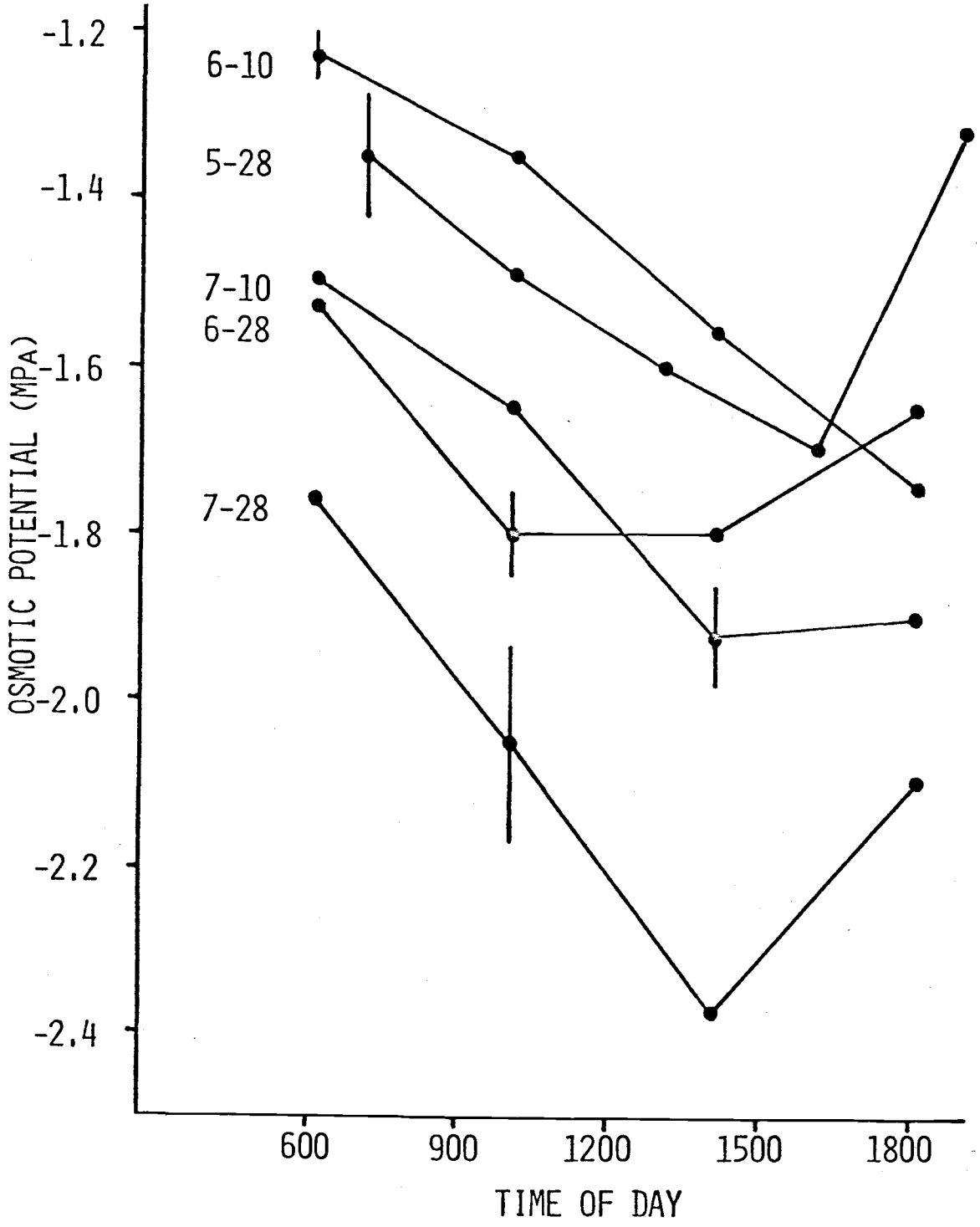

Figure 3. Diurnal variation in osmotic potential for pinegrass during 1980. Dates are indicated to the left of each curve. Vertical lines represent maximum standard error for each curve.

et al. 1976), cotton and sorghum (Ackerson et al. 1977), and corn (Hsiao et al. 1976). However, Biscoe et al. (1976) observed daily variation, but no definite diurnal trend in osmotic potential for wheat growing in dry soil. Campbell and Harris (1977) noted diurnal fluctuation in osmotic potential of big sagebrush to be greatest early in the season. In the study being reported a consistent trend for osmotic potential to decline from morning to afternoon existed throughout the season (Figure 3). There was no apparent tendency for diurnal variation to subside as the season progressed and the soil dried. Sampling for most negative diurnal osmotic potential would be best accomplished in midafternoon. Seasonal osmotic adjustment will be considered in the discussion of 1981 results.

The two most commonly employed instruments for measuring leaf water status are the pressure chamber and psychrometer/hygrometer. Agreement between the two instruments has varied depending on the species (Ritchie and Hinckley 1975). These authors suggested agreement between the two methods may be better for herbaceous than for woody plants.

The need for rigid temperature control has limited the use of psychrometers in the field. However, with the advent of the dewpoint hygrometer (Campbell et al. 1973), exact temperature control became less important. This development should decrease the necessity for elaborate equipment in making field measurements, a point particularly important on remote sites.

The potential for using dewpoint hygrometry in the field without temperature control was tested against the standard pressure bomb technique. Leaf discs were placed in sample chamber hygrometers, which in turn were placed in insulated boxes with a water heat sink to help eliminate temperature gradients. Wiebe et al. (1971) suggested a styrofoam box with heat sink for achieving temperature control. The comparison of pressure chamber and hygrometer measurements was conducted diurnally and seasonally to include variability encountered in typical field sampling. A total of 26 points were compared (Figure 4). The correlation coefficient between the two techniques ($r = .93$) was highly signifiant ($p<0.01$). This correlation coefficient is very similar to the value obtained for wheat ($r = .95$) by Campbell and Campbell (1974). The wheat study involved use of a leaf hygrometer attached to the leaf in situ rather than leaf discs placed in sample chamber hygrometers.

Although agreement between the two techniques was generally good, the data showed some scatter (Figure 4). Several sources of error may account for the discrepancies: 1) applied pressure forcing water into voids or xylem elements not previously containing water (Boyer 1967), 2) water loss after excision of leaf material (Turner and Long 1980), 3) difficulty in determining pressure chamber endpoint (Campbell and Campbell 1974), 4) the presence of solutes in xylem sap (Boyer 1967), 5) lack of equilibrium between the leaf sample and air in the sample chamber, and 6) physiological changes in leaf material during the equilibration period (Talbot et al. 1975). Factors 1-4 can influence

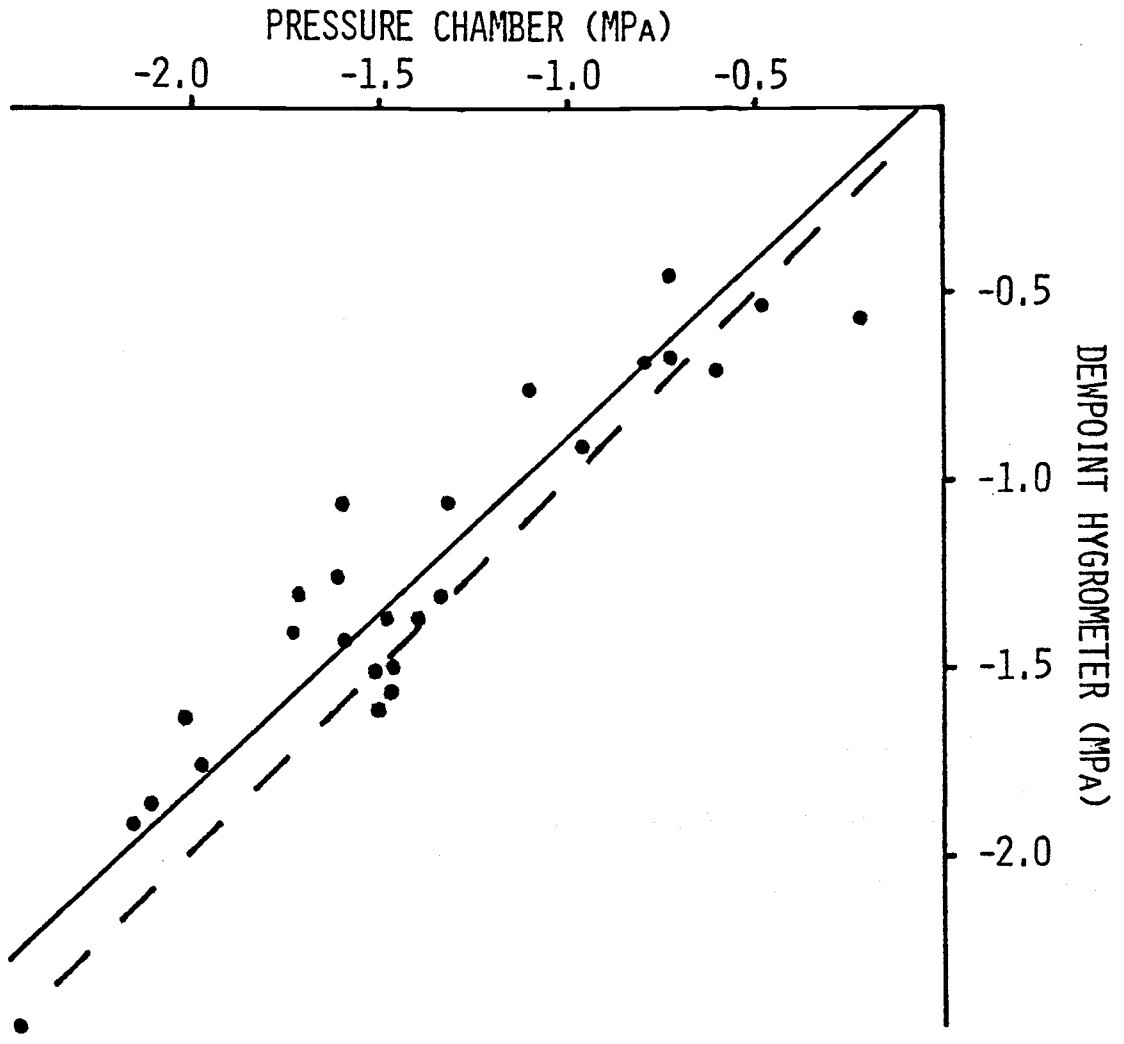

Figure 4. Relationship between leaf water potential of pinegrass measured with pressure chamber and dewpoint hygrometer (r = .93, slope = 1.06, intercept = -0.27). Solid line represents regression, dashed line the 1:1 slope.

pressure chamber readings, while 5 and 6 influence hygrometer values. With pinegrass the pressure chamber endpoint determination seemed straightforward as long as the pressurization rate was .025 MPa s^{-1} or less. Equilibration in the sample chamber hygrometer is probably the major factor limiting use of this technique in the field, unless many sample chambers are available for use. The 2 h equilibrium time was not sufficient, and in some cases readings were still changing slightly after 4 h. The pressure chamber required only several minutes for each sample reading.

It was reassuring that agreement between the two techniques was generally good, as they are intended to measure essentially the same parameter. With some plant material, pressure chamber measurements may not be practical, and in these cases the sample chamber hygrometer would be recommended for field use. However, the ease and speed of pressure chamber measurements make this technique more desirable, especially when many measurements are to be taken. Errors in pressure chamber measurements can be minimized by using slow pressurization rates and limiting water loss of samples beween the time of excision and measurement.

1981 Study

Xylem Potential

During 1981 xylem potential was measured diurnally for elk sedge and pinegrass to determine how these species respond when growing side-by-side. Diurnal variation in xylem potential was measured on six

dates during 1981 (Figures 5-10). The first four dates were characterized by very rapid decline in xylem potential during the morning for both species. By 8-10 the predawn values for both species were approximately -1.5 MPa, which corresponds closely to soil moisture levels (Table 1). Diurnal variation in xylem potential is almost nonexistent on 8-26; this apparently related to plant senescence, a point that will be discussed later.

TABLE 1. Soil moisture potential (MPa) at various dates during 1980 and 1981.

	1980				
Depth (cm)	5-28	6-10	6-26	7-10	7-27
0-10	-0.02	-0.02	-0.02	-0.03	-0.27
10-30	-0.04	-0.04	-0.03	-0.09	-1.10

	1981						
	5-18	6-5	6-30	7-13	7-27	8-10	8-26
0-10	-0.01	-0.01	-0.03	-0.02	-0.23	-1.50	-1.43
10-30	-0.03	-0.03	-0.09	-0.07	-0.85	-1.40	-1.50

On all dates studied elk sedge maintained more negative xylem potentials than pinegrass. The difference between the two species ranged from 0.7 MPa on 6-5 to 0.4 MPa on 8-10 for midafternoon values (Figure 11). The trends, however, are very similar, with a highly significant ($p<0.01$) correlation between the two species ($r = .96$).

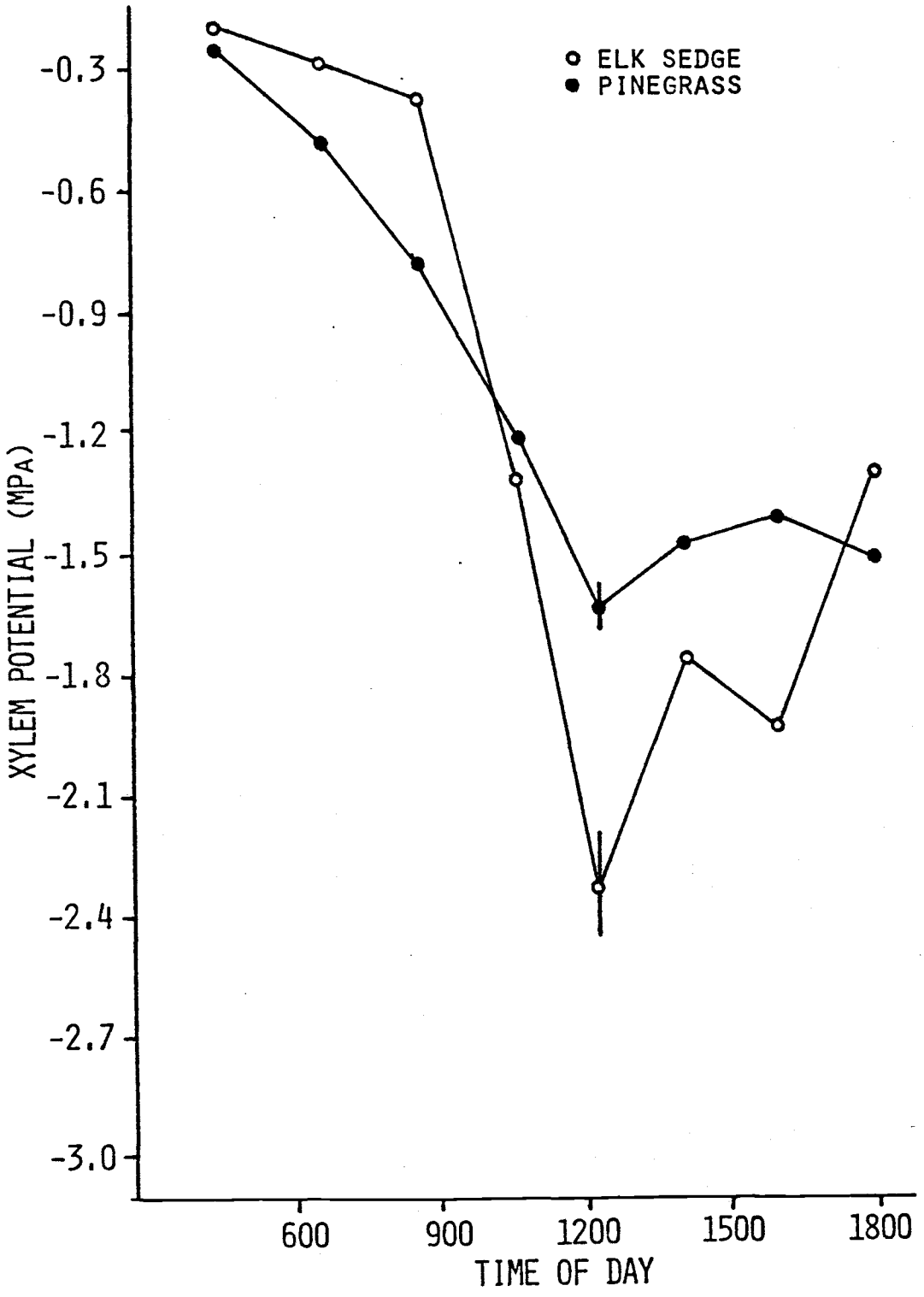

Figure 5. Diurnal variation in xylem potential of elk sedge and pinegrass on 6-5-81. Vertical lines represent maximum standard error for each curve.

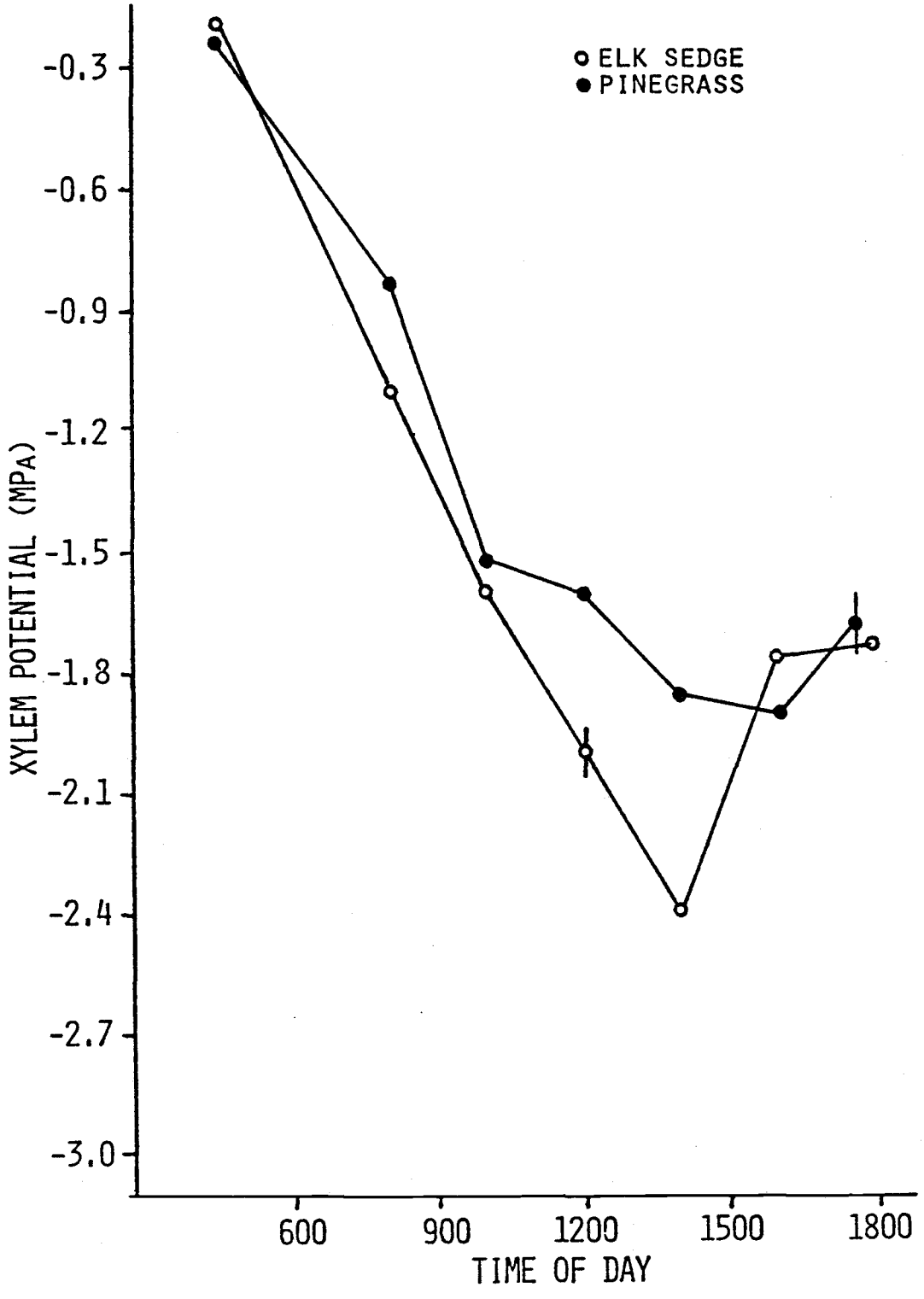

Figure 6. Diurnal variation in xylem potential of elk sedge and pinegrass on 6-30-81. Vertical lines represent maximum standard error for each curve.

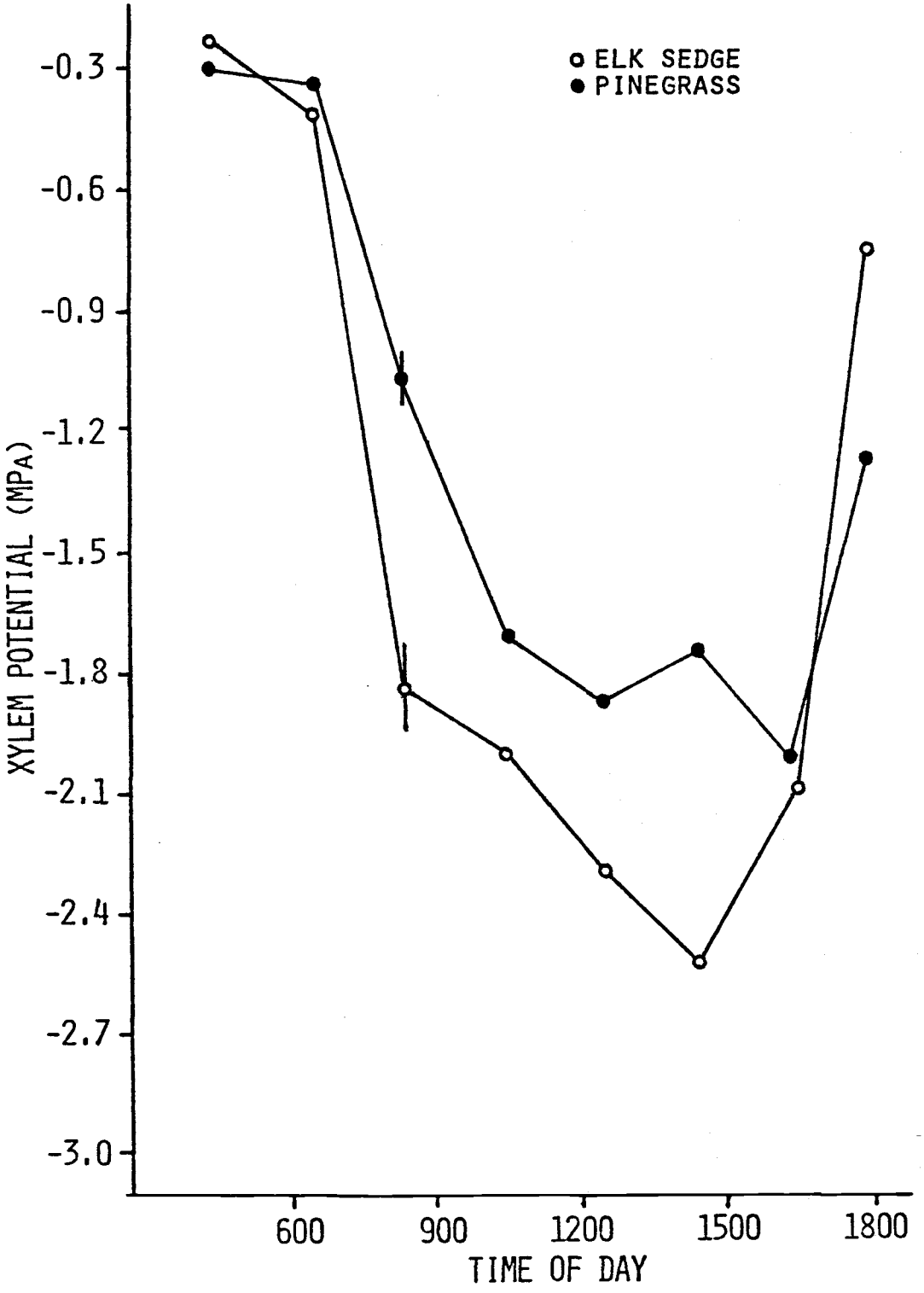

Figure 7. Diurnal variation in xylem potential of elk sedge and pinegrass on 7-13-81. Vertical lines represent maximum standard error for each curve.

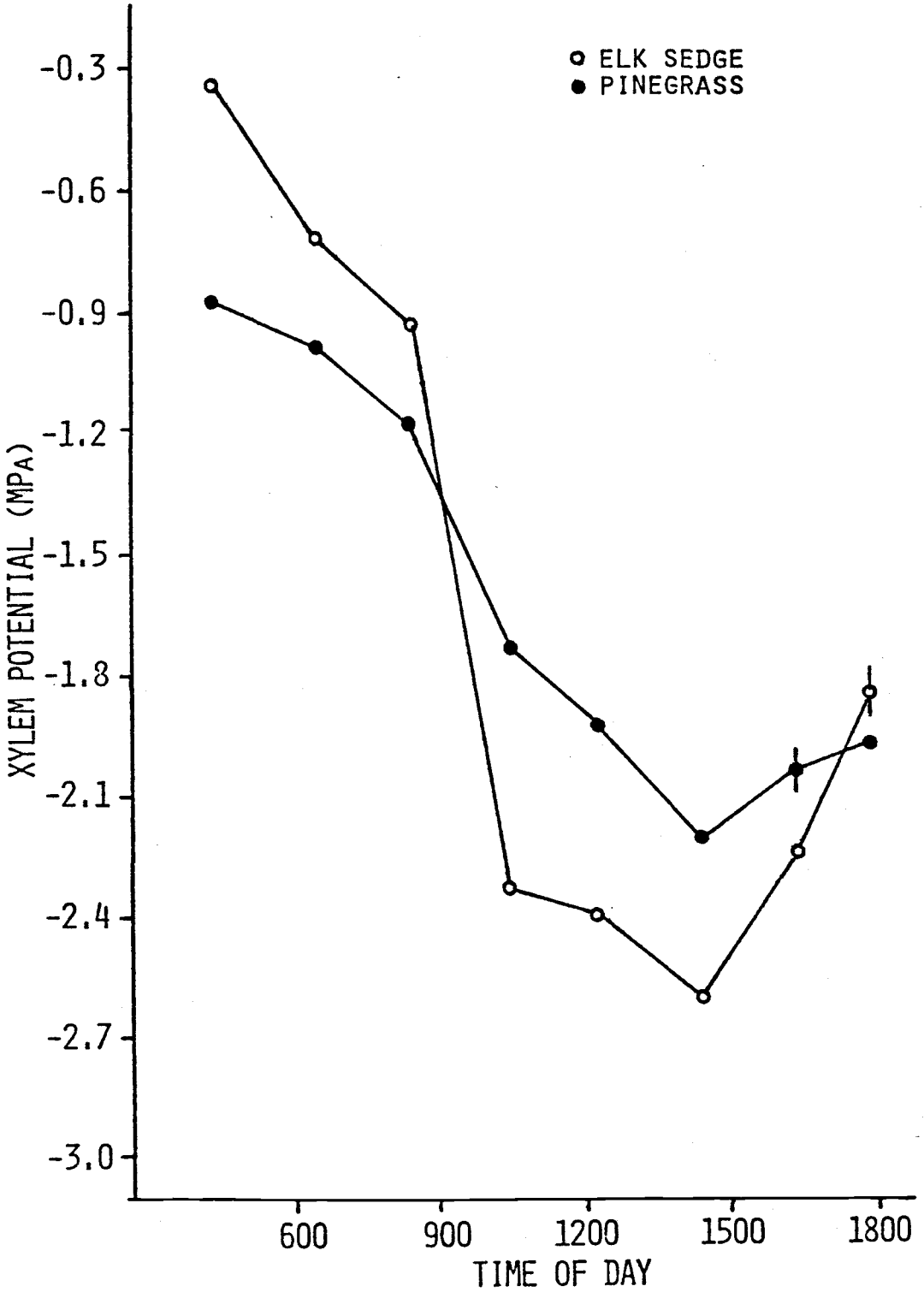

Figure 8. Diurnal variation in xylem potential of elk sedge and pinegrass on 7-27-81. Vertical lines represent maximum standard error for each curve.

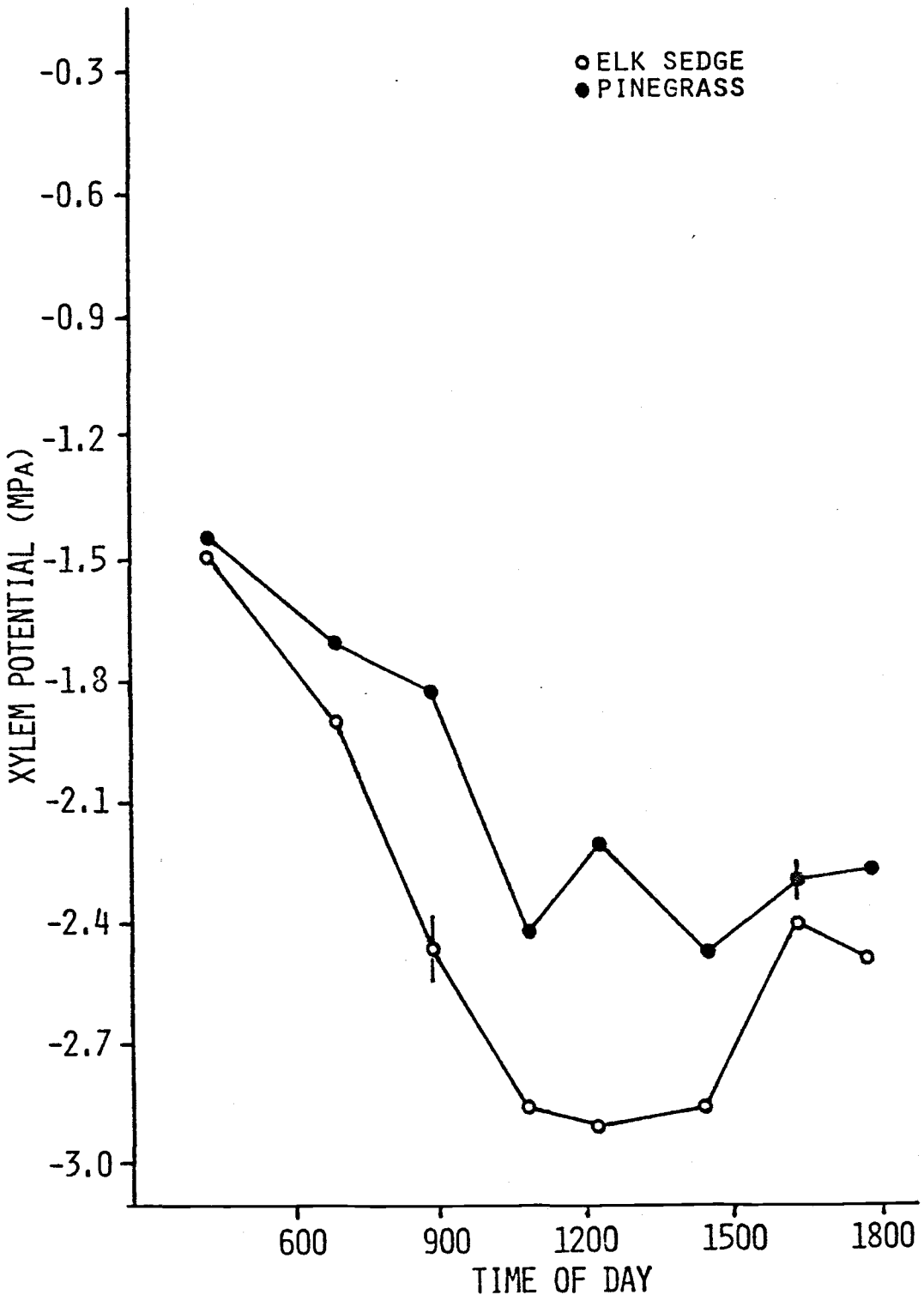

Figure 9. Diurnal variation in xylem potential of elk sedge and pinegrass on 8-10-81. Vertical lines represent maximum standard error for each curve.

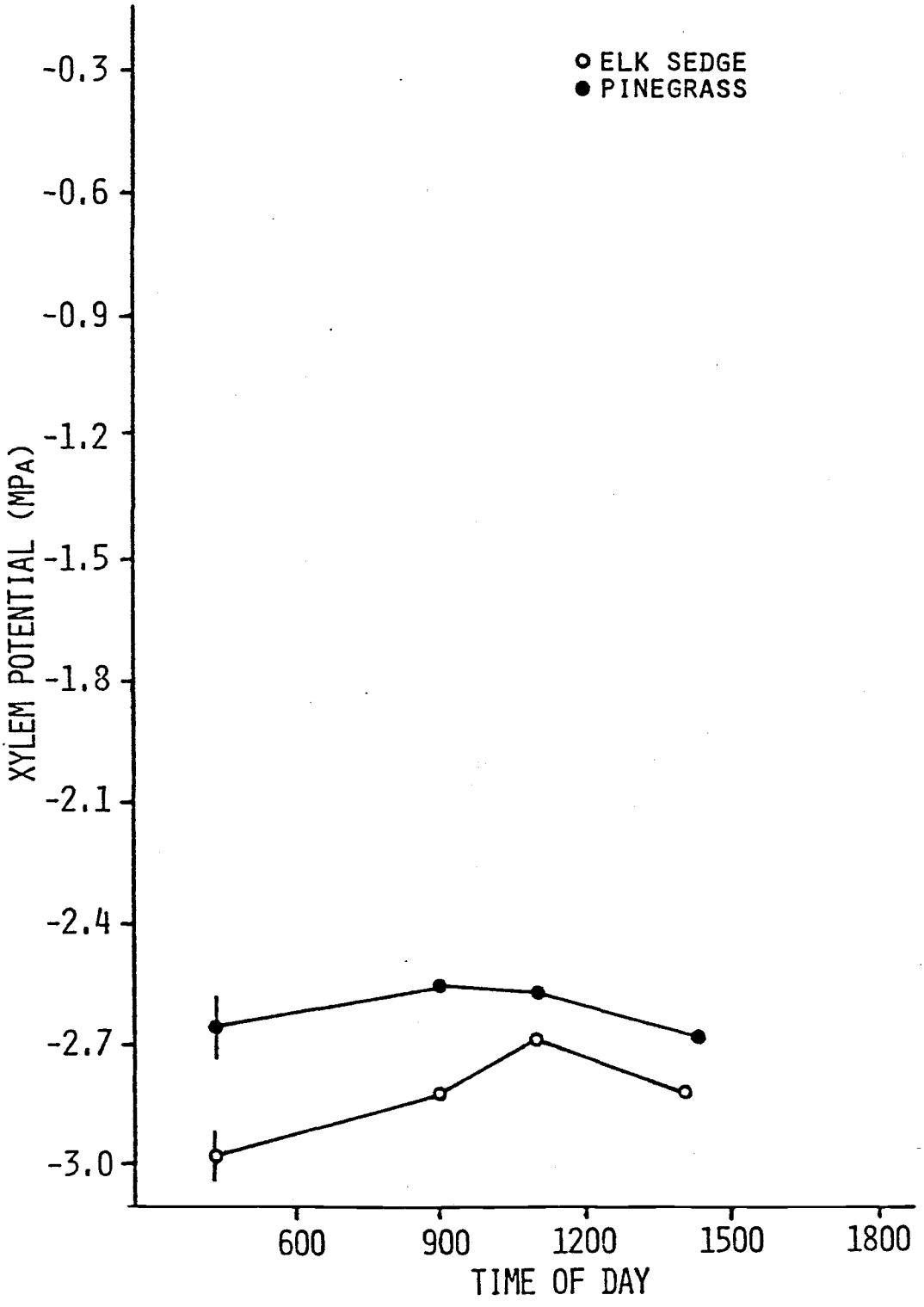

Figure 10. Diurnal variation in xylem potential of elk sedge and pinegrass on 8-26-81. Vertical lines represent maximum standard error for each line.

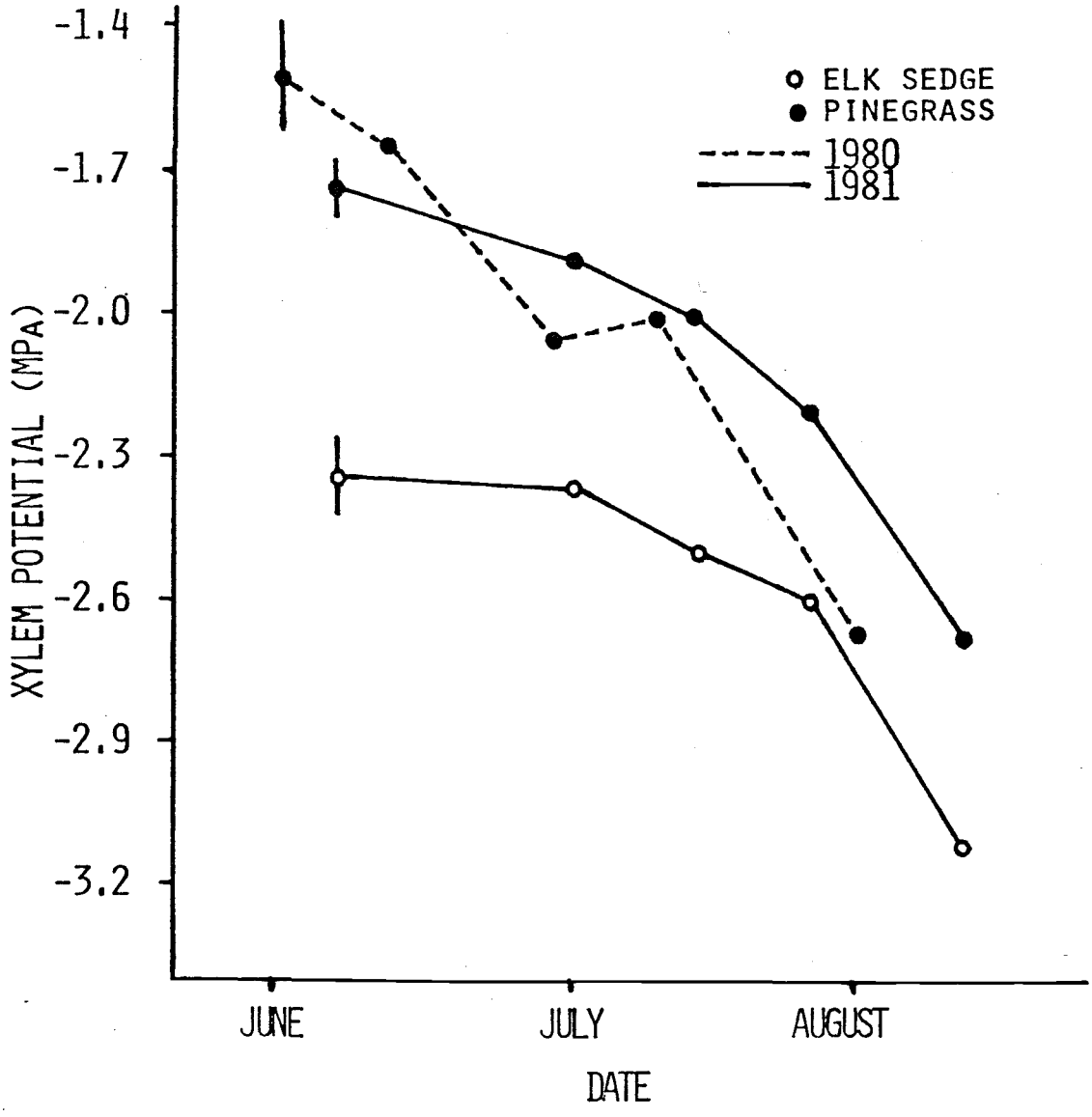

Figure 11. Seasonal variation in midafternoon xylem potential for elk sedge and pinegrass. Vertical lines represent maximum standard error for each curve.

Visual signs of senescence in pinegrass appeared several weeks earlier in 1980 than in 1981, and the most negative afternoon xylem potential was reached about 10 days earlier the first year (Figure 11). Soil moisture at the end of July was less the first year (Table 1), although differences were small. Temperatures were warmer in 1980 than 1981, another factor that may have influenced senescence. For example, maximum daily temperature was 36.0 C on 7-27-80 and 27.5 C on 7-27-81.

During the period of physiological activity, predawn xylem potentials of the two species were similar (Figure 12) except on 7-27 when soil moisture began to drop (Table 1). Elk sedge maintained a higher predawn value at that point. Predawn xylem potential was generally more negative than soil moisture potential; however, most of the variation in soil water potential could be accounted for by either predawn or midafternoon xylem potential (Table 2). Predawn xylem potential was generally a better indicator of soil moisture than midafternoon values, the exception being elk sedge at the 10-30 cm depth. Elk sedge apparently responds more to soil moisture at 0-10 cm and pinegrass to the 10-30 cm depth. All correlations were significant ($p<0.05$ or 0.01) and xylem potential could be used successfully to detect trends in soil moisture. These correlations are higher than reported in big sagebrush by Branson and Shown (1975). However, these

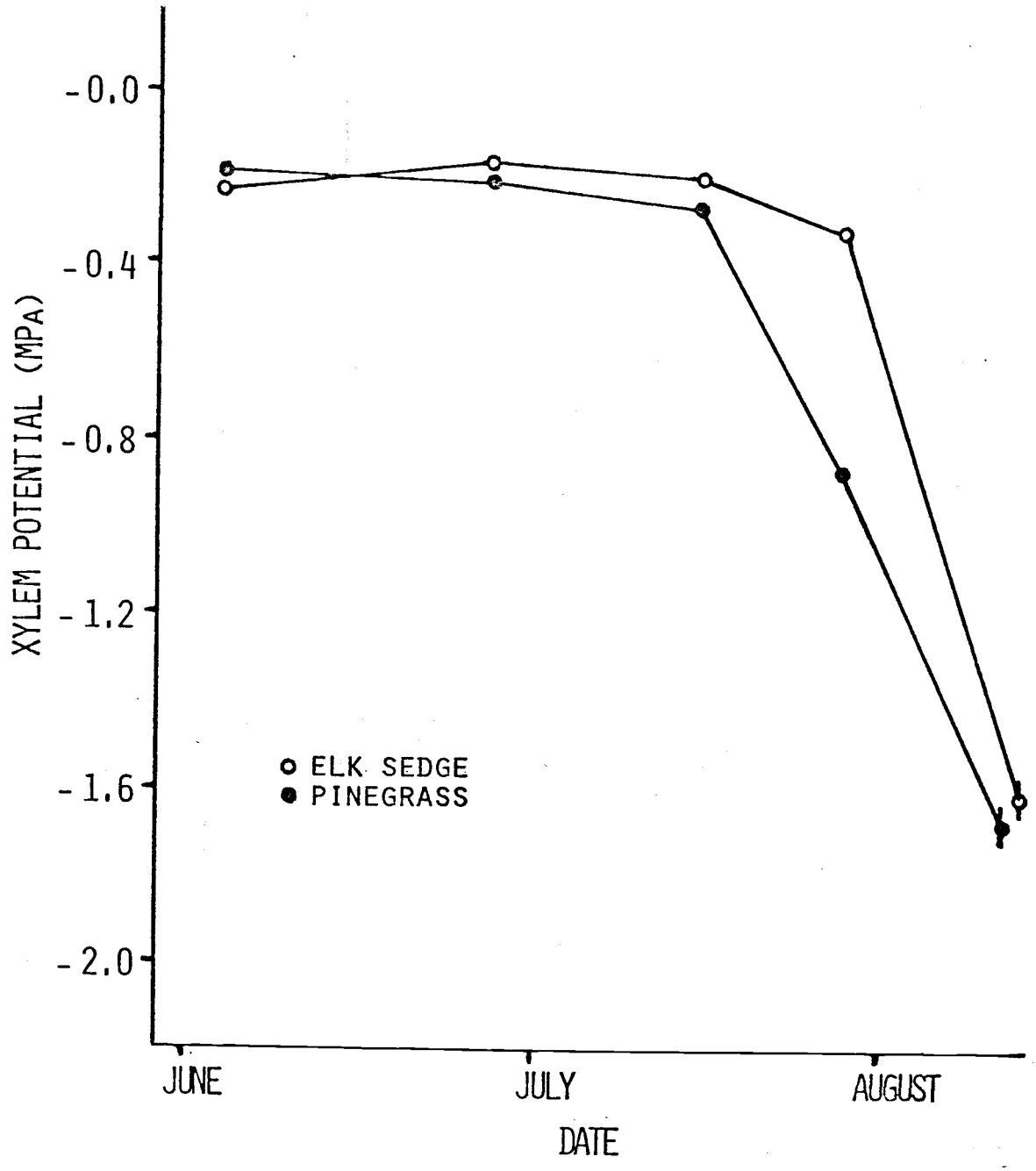

Figure 12. Seasonal variation in predawn xylem potential for elk sedge and pinegrass during 1981. Vertical lines represent maximum standard error for each curve.

TABLE 2. Coefficient of determination (r^2) between soil water potential at two depths and xylem potentials of elk sedge and pinegrass measured predawn and midafternoon.[1]

	Elk sedge		Pinegrass	
Xylem potential	0-10 cm	10-30 cm	0-10 cm	10-30 cm
Predawn	.99	.77*	.91	.98
Midafternoon	.95	.86	.82*	.89

[1]Correlations for five dates beginning 6-5-81 and ending 8-10-81.
*Significant at the .05 level, all other values are significant at the .01 level.

authors measured xylem potential only once during the day, and made no mention of diurnal trends. In addition, big sagebrush has a fairly complex rooting system which would confound the relationship. Rooting pattern, period of physiological activity, and physiological adaptations must be considered before using xylem potential of a particular species to predict soil moisture.

Xylem potentials of rhizomes were very different than those of leaf samples. Rhizome potentials were higher than -0.2 MPa until 7-27 when they reached -0.4 MPa in pinegrass. On 8-10 values for both species were approximately -0.8 MPa during midafternoon. Rhizome xylem potential did not change more than 0.3 MPa between predawn and midafternoon for either species on any of the measurement dates. High xylem potentials in the rhizome occurred during periods when leaf xylem potentials approached -2.5 MPa for elk sedge and -2.0 for pinegrass. Gradients in water potential between leaves and roots have been found in a number of species, these results have been summarized by Hellkvist

et al (1974). Rhizome xylem potentials were more negative than soil water potential until 8-10.

An attempt was made to collect rhizome xylem sap and measure osmotic potential. Negative sap osmotic potentials would influence pressure chamber measurements. Unfortunately, it was difficult to collect enough sap to make reliable measurements. However, sap potentials in other studies seldom exceeded -0.2 MPa in either shoots or roots (Boyer 1967, DeRoo 1969, Ritchie and Hinckley 1975).

Explanation of the differing leaf and rhizome xylem potentials may involve plant resistance to water flow. Hellkvist et al. (1974) concluded that the difference in water potential between leaves and roots of sitka spruce (Picea sitchensis) was largely the result of resistance to flow in the trunk. Similarly, Meyer and Ritchie (1980) considered sorghum to have a major resistance to flow in the crown. The crown represents the junction point between shoot and rhizome, and a difference in water potential between the two components could be explained by crown resistance.

Osmotic Potential and Pressure-Volume Parameters

Osmotic adjustment is a mechanism by which elk sedge could maintain lower xylem potentials than pinegrass. There are numerous reports of osmotic adjustment in the literature (Hsiao et al. 1976, Roberts and Knoerr 1977, Jones and Rawson 1979, Turner and Jones 1980, Wilson et al. 1980). The advantages of osmotic adjustment relate to

turgor maintenance (Hsiao et al. 1976) and possibly adjustment of stomatal resistance (Ludlow 1980).

When measured with the hygrometric technique, osmotic potential values for the two species were significantly different ($p<0.05$) only on 7-27 and 8-10 (Figure 13). The trend for pinegrass was similar for the two years, except that the decline in osmotic potential started earlier in 1980.

Osmotic potential measured by the P/V technique presented a different picture (Table 3). Samples used for the hygrometric analysis were collected midafternoon when xylem potentials were most negative, and thus are more comparable to osmotic potential at zero turgor (π^0) than at full turgor (π^{100}). The P/V measurements indicate elk sedge had more negative osmotic potentials than pinegrass, both at full turgor and zero turgor. During the end of July when soil moisture began to decline, elk sedge had a π^0 value approximately 0.5 MPa more negative than pinegrass. Thus elk sedge could achieve more negative xylem potentials without losing turgor. And indeed, on 7-27 (Figure 8), elk sedge had midafternoon xylem potentials 0.4 MPa more negative than those of pinegrass.

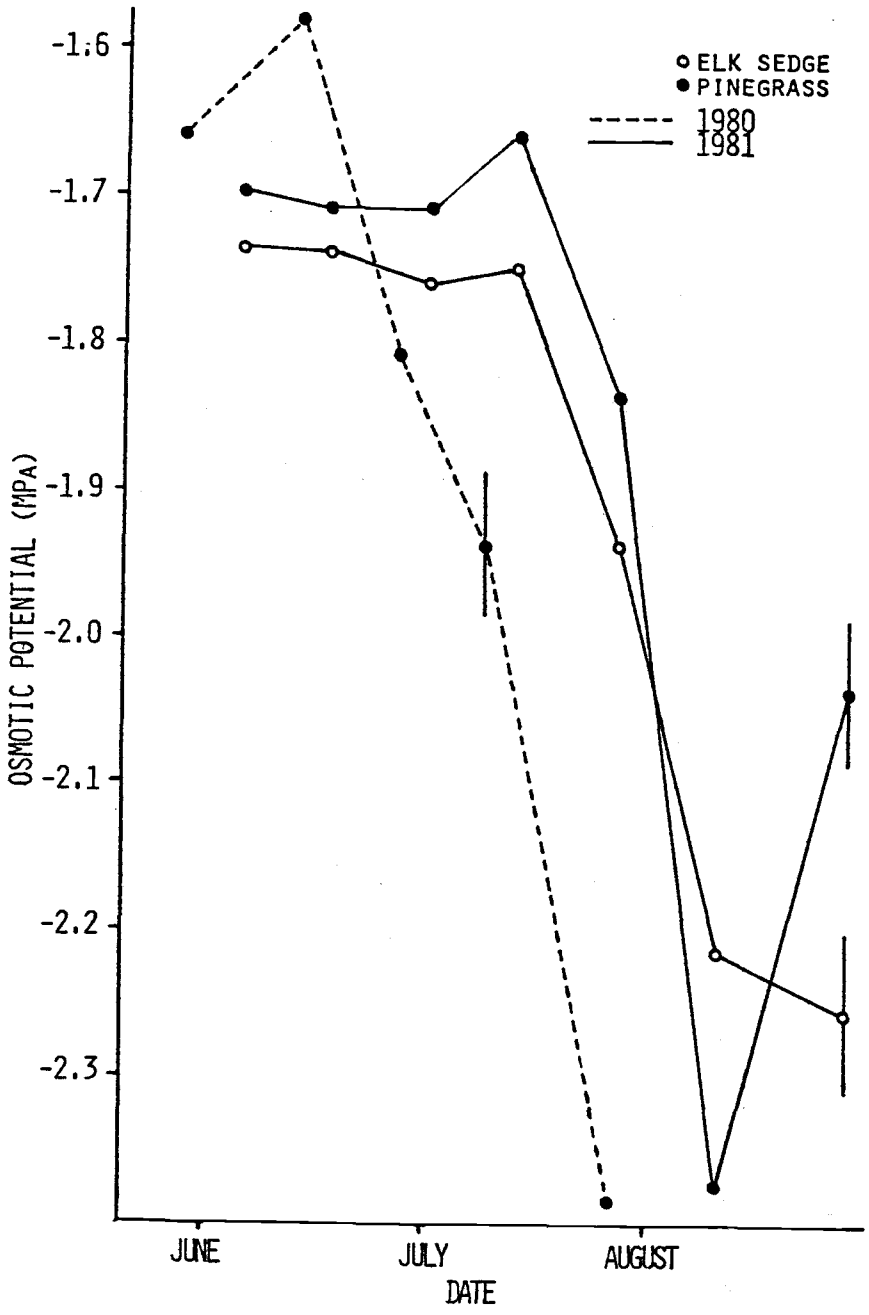

Figure 13. Seasonal variation in osmotic potential of elk sedge and pinegrass as measured by the hygrometric technique. Vertical lines represent maximum standard error for each curve.

TABLE 3. Parameters derived from the pressure-volume technique for pinegrass (Caru) and elk sedge (Cage) during 1981.

	Date							
	6-9		7-8		7-27		8-11	
	Caru	Cage	Caru	Cage	Caru	Cage	Caru	Cage
π^{100} (MPa)								
$\bar{x}$[1]	-1.15**	-1.56	-1.66*	-1.90	-2.00*	-2.51	-1.95**	-2.43
CV[2]	7.7	5.3	2.1	5.1	8.8	4.8	5.0	3.6
π^{0} (MPa)								
$\bar{x}$	-1.63**	-2.34	-2.18	-2.43	-2.48*	-3.02	-2.39**	-3.16
CV	3.8	2.2	6.5	4.1	3.7	1.5	1.5	4.1
B (%)								
$\bar{x}$	17.0	19.4	25.9	38.3	18.0*	52.3	21.0*	45.8
CV	42.4	52.6	37.0	18.4	38.9	8.0	37.1	15.3
E (MPa)								
$\bar{x}$	3.00**	7.56	2.80*	11.87	6.23*	22.30	3.88	10.63
CV	25.7	12.7	50.7	18.5	36.4	11.1	40.7	31.0

Legend: π^{100} = osmotic potential at full turgor, π^{0} = osmotic potential at zero turgor, B = bound water, E = elastic modulus.

[1]Average of four measurements.

[2]Coefficient of variation (%).

*, ** Values for elk sedge and pinegrass are signifiantly different at the .05 and .01 levels, respectively.

It has been recognized that hygrometric analysis results in artificially high values of osmotic potential (Brown 1972, Tyree 1976, Campbell et al. 1979, Turner 1981, Markhart et al. 1981). The technique allows dilution of osmotic water in the vacuole with relatively pure apoplastic (bound) water. The difference in osmotic potential between the techniques studied is presented in Table 4. The discrepancy is greater for elk sedge, and relates well to bound water fraction (B) in this species. The correlation between the difference

in the two techniques (Table 4) and B (Table 3) was significant ($p<0.05$) for elk sedge ($r = .90$). However, there was a very poor correlation between the two parameters for pinegrass ($r = .32$). Apparently factors other than B were influencing one or both of the measurement techniques in pinegrass.

TABLE 4. Difference between osmotic potential measured by the hygrometric technique and osmotic potential at zero turgor measured by the pressure-volume technique.[1]

	6-9	7-8	7-27	8-11
Elk sedge	0.61**	0.68**	1.09**	0.94**
Pinegrass	-0.07	0.50**	0.65**	0.02

[1]All values presented in MPa, positive values indicate pressure-volume value was more negative.

** Signicant at the 0.01 level.

The relationship between B and cell wall content (CWC) was also tested. Actual seasonal changes in CWC between 6-9-81 and 8-10-81 were only 2 and 4.7% for pinegrass and elk sedge, respectively. A significant ($p<0.05$) correlation existed between B and CWC for elk sedge ($r = .92$), but not for pinegrass ($r = .68$). The relationship may relate more to changes in cell wall components than actual total cell wall fraction as Wilson et al. (1980) suggest. The change in B for elk sedge went from 19.4 to 52.3% during a period when CWC changed by less than 4%.

Elastic modulus (E) is another factor of importance in plant water relations. Elk sedge had more rigid cell walls than pinegrass (E is

inversely related to cell wall elasticity); the difference being significant ($p<0.05$) until the last date (Table 3). The ramifications of cell wall elasticity have been well summarized by Cheung et al. (1975): "a cell with more rigid walls will drop its turgor pressure (and therefore water potential) in response to a given change in water content more than one with less rigid walls." Elk sedge is thus able to drop xylem potential more per unit loss of water than pinegrass. It should be noted that E was highly variable, and there are problems in the calculation of this parameter using standard P/V techniques (e.g. Melkonian et al. 1982).

Pressure-volume measurements were attempted on 8-26-81 for both species, however, typical P/V curves were not observed. The reader is referred to Figure 1 on page 20 for an example of a typical P/V curve. Curves for elk sedge exhibited discontinuities and a distinct linear phase was difficult to detect. The relationship in pinegrass was strictly linear in most cases, showing no curvilinear phase. However, the slopes of the lines were inconsistent. In fact, on 8-11 only the lower portion of the curvilinear phase was detectable for pinegrass. I suspect that senescence and subsequent loss of membrane integrity caused the problems with the P/V measurements. It has been demonstrated that membranes can become leaky at low tissue water contents (Gaff 1980). Apparently the plants were no longer maintaining appreciable turgor, a suggestion supported by the lack of diurnal fluctuation in xylem potential on 8-26 (Figure 10).

Leaky membranes and the transfer of carbon and nitrogen to underground storage organs might help explain the late season increase in osmotic potential in pinegrass (values became less negative). The increase appeared both in P/V (Table 3) and hygrometric (Figure 13) measurements. Elk sedge has an evergreen growth habit, with leaves living for several or more years; this makes interpretation of senescence more difficult for elk sedge than for pinegrass whose tillers die back each year.

It might also be noted that midafternoon osmotic potential measured with the hygrometric technique reached about the same value (-2.4 MPa) both years as visual signs of senescence in pinegrass appeared. It is interesting to speculate that some level of osmotic potential might trigger senescence, however, as Thomas and Stoddart (1980) pointed out, a number of factors influence senescence.

Diffusive Resistance

There were definite diurnal trends in diffusive resistance of both leaf surfaces for the two species (Figures 14-18). Early in the season diffusive resistance declined or remained essentially unchanged from midday to evening. However, on 7-13 there was an initial decrease in resistance, then continual increase throughout the afternoon. The trend on 7-27 and 8-10 was for increasing resistance throughout the day, although there were exceptions. Elk sedge showed a slight decline in resistance from 730 to 1130 on 7-27. The VDD was low during the early morning (2.0 g/m^3) but increased sharply by 1130 (20.5 g/m^3).

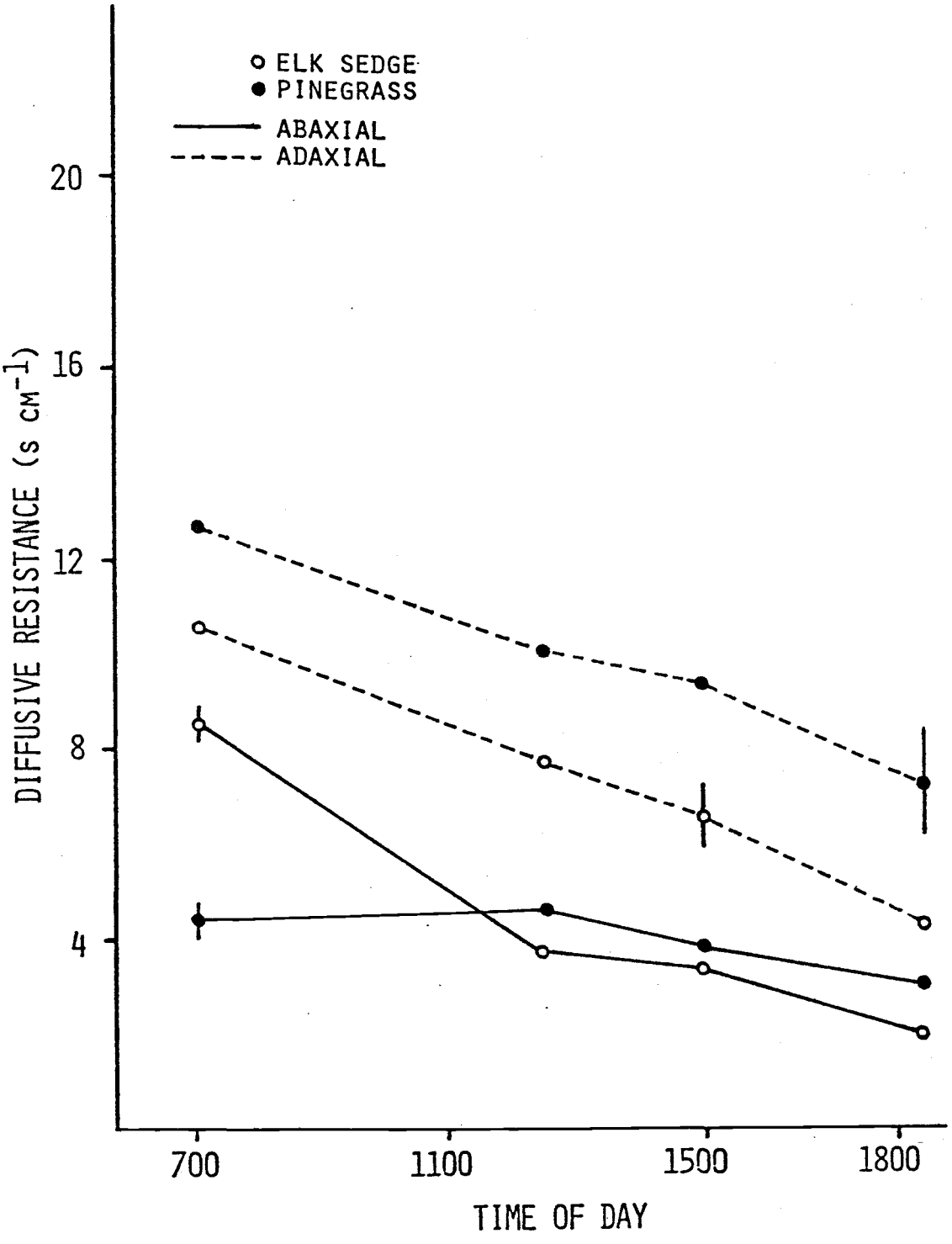

Figure 14. Abaxial and adaxial diffusive resistance of elk sedge and pinegrass on 6-5-81. Vertical lines represent maximum standard error for each curve.

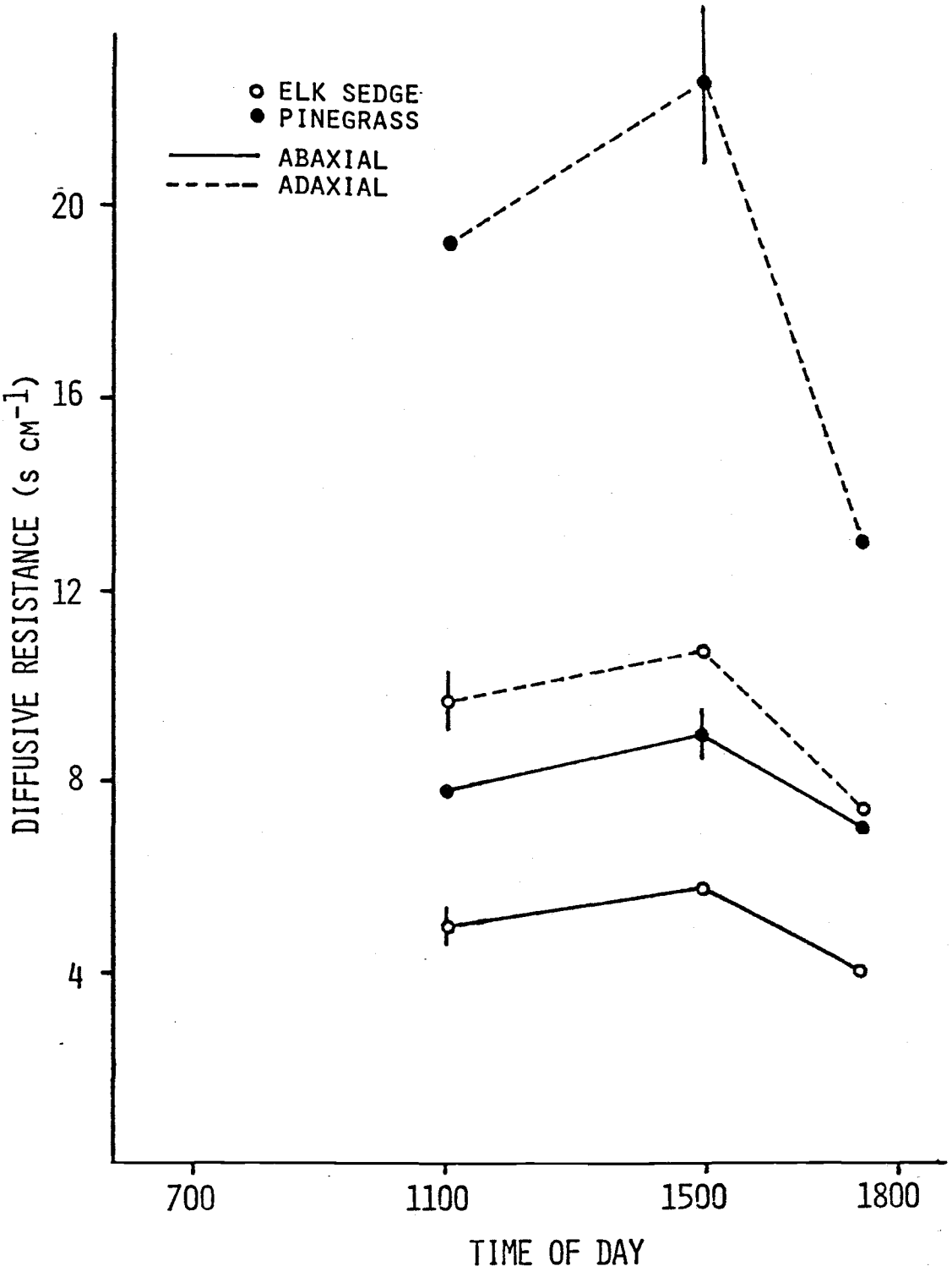

Figure 15. Abaxial and adaxial diffusive resistance of elk sedge and pinegrass on 6-30-81 (early morning measurements were not taken because vegetation was wet). Vertical lines represent maximum standard error for each line.

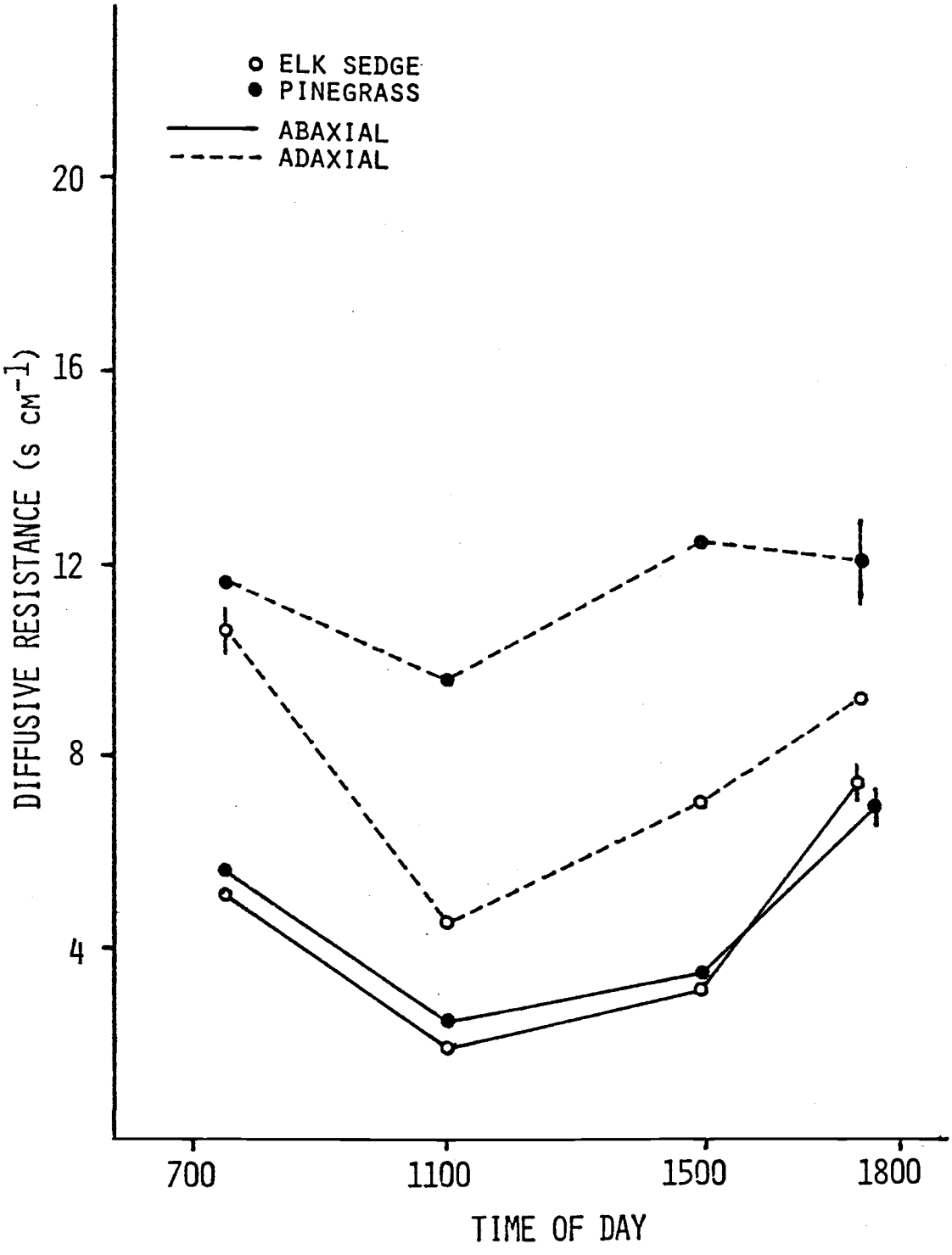

Figure 16. Abaxial and adaxial diffusive resistance of elk sedge and pinegrass on 7-13-81. Vertical lines represent maximum standard error for each curve.

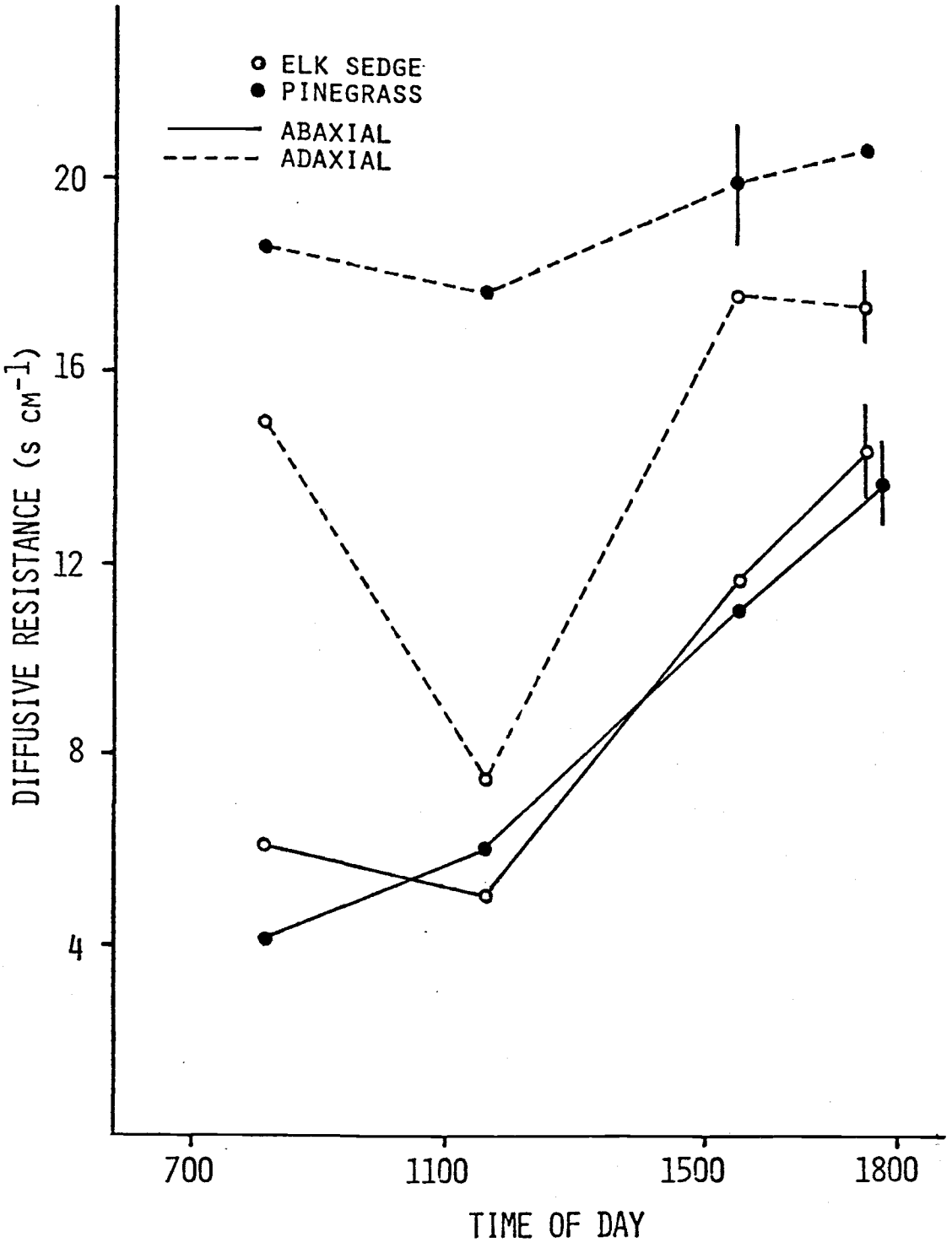

Figure 17. Abaxial and adaxial diffusive resistance of elk sedge and pinegrass on 7-27-81. Vertical lines represent maximum standard error for each curve.

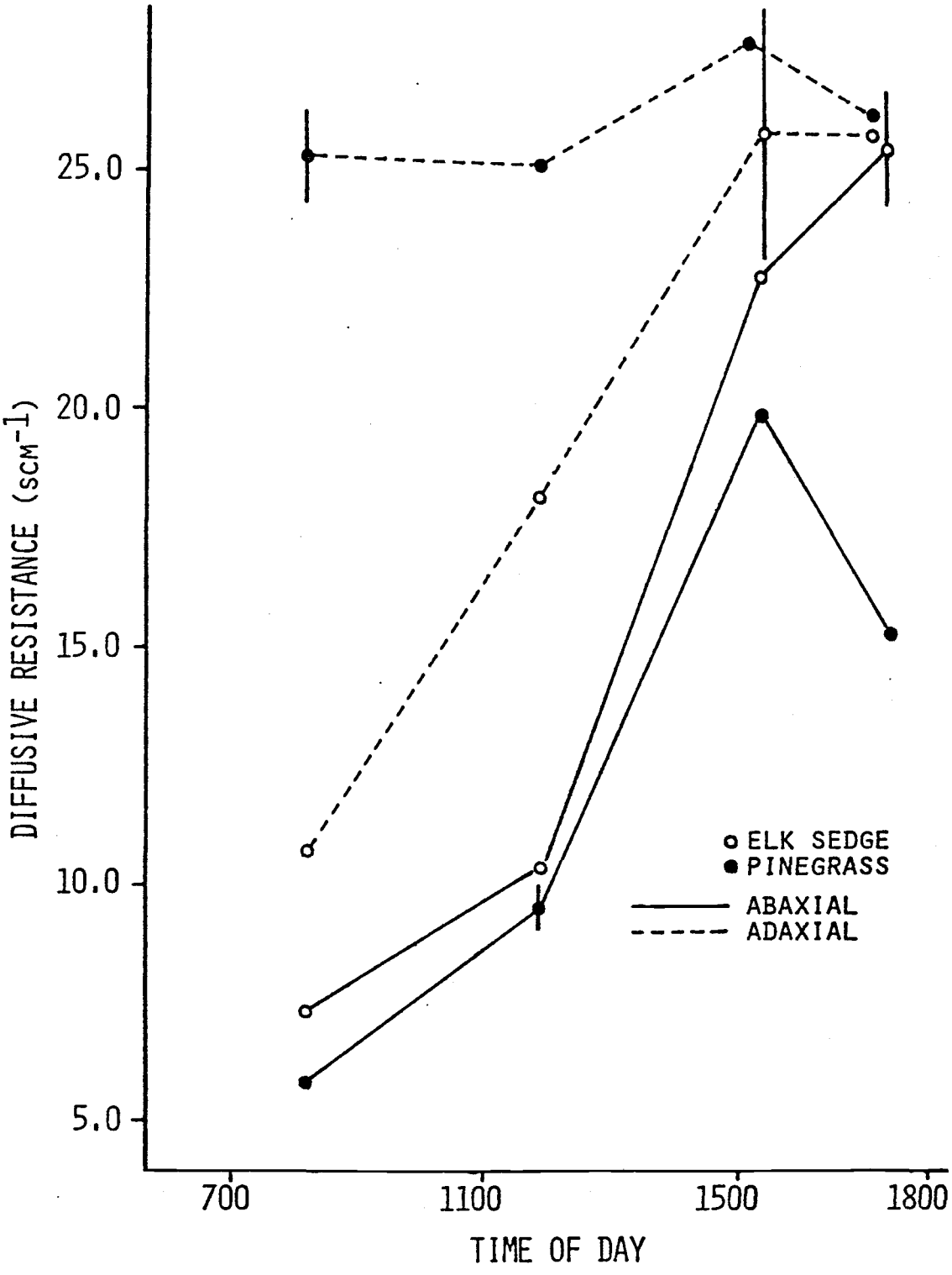

Figure 18. Abaxial and adaxial diffusive resistance of elk sedge and pinegrass on 8-10-81. Vertical lines represent maximum standard error for each curve.

Apparently elk sedge stomates were responding to the initially low VDD, and did not begin closing until afternoon. Overall, diffusive resistance increased considerably from 7-13 to 7-27 to 8-10. In fact, on 8-10 only abaxial stomates at 730 had diffusive resistance values below 9.0 s cm^{-1}.

There were definite differences between abaxial and adaxial resistance for both species. The abaxial resistances of the two species tested tended to be similar; however, elk sedge always had lower adaxial resistance than pinegrass. The correlation between abaxial and adaxial resistance was higher for elk sedge ($r = .95$) than for pinegrass ($r = .77$), although both correlations were highly significant ($p<0.01$).

There have been many reports of differing diffusive resistance on abaxial and adaxial leaf surfaces. Higher adaxial resistance has been reported in soybeans (Sionit and Kramer 1976), snap beans (Kanemasu and Turner 1969, Solaroa et al. 1977), and cotton (Sanchez-Diaz and Kramer 1971, Sharpe 1973). However, Biscoe et al. (1976) reported higher abaxial resistance in wheat. In the study being reported there can be little question that resistance was higher on the adaxial surface of both species.

There have been few suggestions in the literature as to the adaptive advantages of differing diffusive resistances on the upper and lower leaf surfaces. Adams et al. (1978) measured higher adaxial than abaxial resistance in well watered plants of the desert shrub jojoba, but the opposite trend was found for plants growing in dry soil. The

authors felt that lower adaxial resistance might be a mechanism for cooling jojoba leaves, which are 1 mm or more thick and heat up under high radiation loads.

The importance of transpirational cooling in the species studied is difficult to assess. Elk sedge leaves are approximately twice as thick as those of pinegrass with specific leaf weights for elk sedge, ranging from 6.5 to 10.2 mg/cm^2 on 6-8-81 and 8-12-81, respectively; while those of pinegrass were 3.2 and 4.6 mg/cm^2 on the same dates. Yet there was never more than 1 C difference in leaf temperature between the two species, even during days with relatively high radiation. However, the radiation level was never more than 383 W/m^2 and was highly variable from one moment to the next because of irregularity in the overstory canopy.

Assessment of the adaptive significance of dissimilar diffusive resistances of the upper and lower leaf surfaces will require further research in a number of areas. The water use efficiency of the two surfaces should be examined. The influence of leaf thickness and other morphological and anatomical characteristics on distribution of CO_2 within the leaf is another consideration (eg. Nobel 1980).

The generally lower resistance values should allow more daily carbon gain per leaf area for elk sedge compared to pinegrass (Figures 14-18). Other factors are certainly important, but photosynthesis is greatly influenced by stomatal resistance (eg. Turner and Jones 1980, Frank 1981). Ludlow (1980) suggested that increased carbon gain from stomatal adjustment can improve water relations if the carbon is used

in any of the following ways: (1) to produce roots that can explore new soil volume and extract more water; (2) help maintain existing roots and shoots; and (3) to assist in the osmotic adjustment mechanism. Ludlow was referring to seasonal adjustment in a species stomatal response, however, his assessment could also be used in comparing species. In the present case, elk sedge maintains a more negative osmotic potential than pinegrass, and it can be assumed that osmotic adjustment carries with it an energetic cost (Kluge 1976, Turner and Jones 1980).

Stomates of many species exhibit a threshold response to water potential (Hsiao 1973, Running 1976, Jarvis 1980, Ludlow 1980). Reported threshold values range from -1.0 to -1.5 MPa for a number of crop species (Hsiao 1973), and -0.8 to -2.5 MPa for conifers (Jarvis 1980). There are reports of non-threshold response of stomates in some species (Adams et al. 1978, Jones and Rawson 1979). Jones and Rawson (1979) found that the rate of water stress influenced stomatal response in sorghum. High rates of stress resulted in a threshold response, lower rates did not.

The response of elk sedge and pinegrass abaxial diffusive resistance to xylem potential is presented in Figure 19. Abaxial resistance is considered because it was more important in gas exchange than adaxial resistance. The linear correlation between abaxial diffusive resistance and xylem potential was significant ($p<0.05$) for pinegrass ($r = .67$), but not for elk sedge ($r = .43$). However, the correlations were both significant ($p<0.01$ for pinegrass and $p<0.05$ for

Figure 19. Relationship between xylem potential and abaxial diffusive resistance for elk sedge and pinegrass. Points represent diurnal values taken on five dates beginning 6-5-81 and ending 8-11-81.

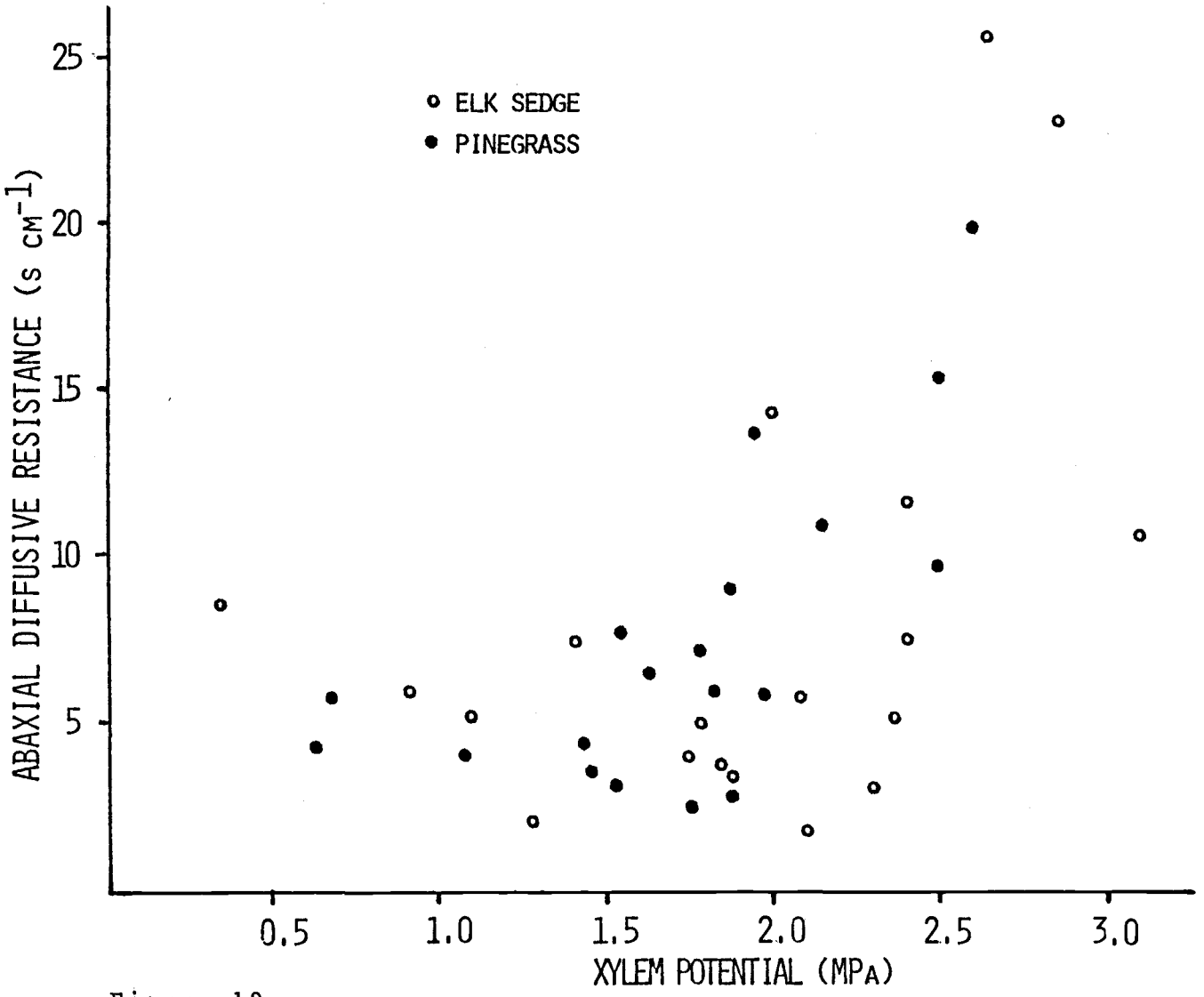
ELK SEDGE
PINEGRASS
ABAXIAL DIFFUSIVE RESISTANCE (s cm^{-1})
25
20
15
10
5
0.5
1.0
1.5
2.0
2.5
3.0
XYLEM POTENTIAL (MPa)

Figure 19.

elk sedge) when a polynomial model ($Y = A + B_1X + B_2X^2$) was used. The correlation coefficients increased to .81 for pinegrass and .61 for elk sedge. The polynomial model suggests a threshold response, with large increases in abaxial resistance after some value of xylem potential is reached. However, as illustrated in Figure 19, the threshold for pinegrass (approximately 2.0 MPa) is less negative than for elk sedge (approximately 2.5 MPa). Thus elk sedge maintains low resistance values (2-8 s cm^{-1}) to xylem potentials 0.5 MPa more negative than those of pinegrass. This corresponds closely to the difference in osmotic potential between the two species (Table 3).

Whereas diffusive resistance was relatively unchanged over a wide range of xylem potentials, there was a fairly linear response to VDD, particularly in the range of 10-32 g/m^3 (Figure 20). The correlation coefficient between abaxial diffusive resistance and VDD in the 10-32 g/m^3 range was .85 for pinegrass and .80 for elk sedge using the linear model; both values were significant ($p<0.01$). However, in this case the addition of a polynomial term to the model did not significantly ($p>0.05$) improve the correlation for either species.

Direct response of stomates to humidity has been reported in a number of species (Schulze et al. 1972, Farquhar et al. 1980, Kaufmann 1982), and is considered a mechanism by which plants reduce transpiration before the detrimental effects of low water potential can occur (Ludlow 1980). The humidity response of stomates in the species

Figure 20. Relationship between vapor density difference between leaf and air (VDD) and abaxial diffusive resistance for elk sedge and pinegrass. Points represent diurnal values taken on five dates beginning 6-5-81 and ending 8-11-81.

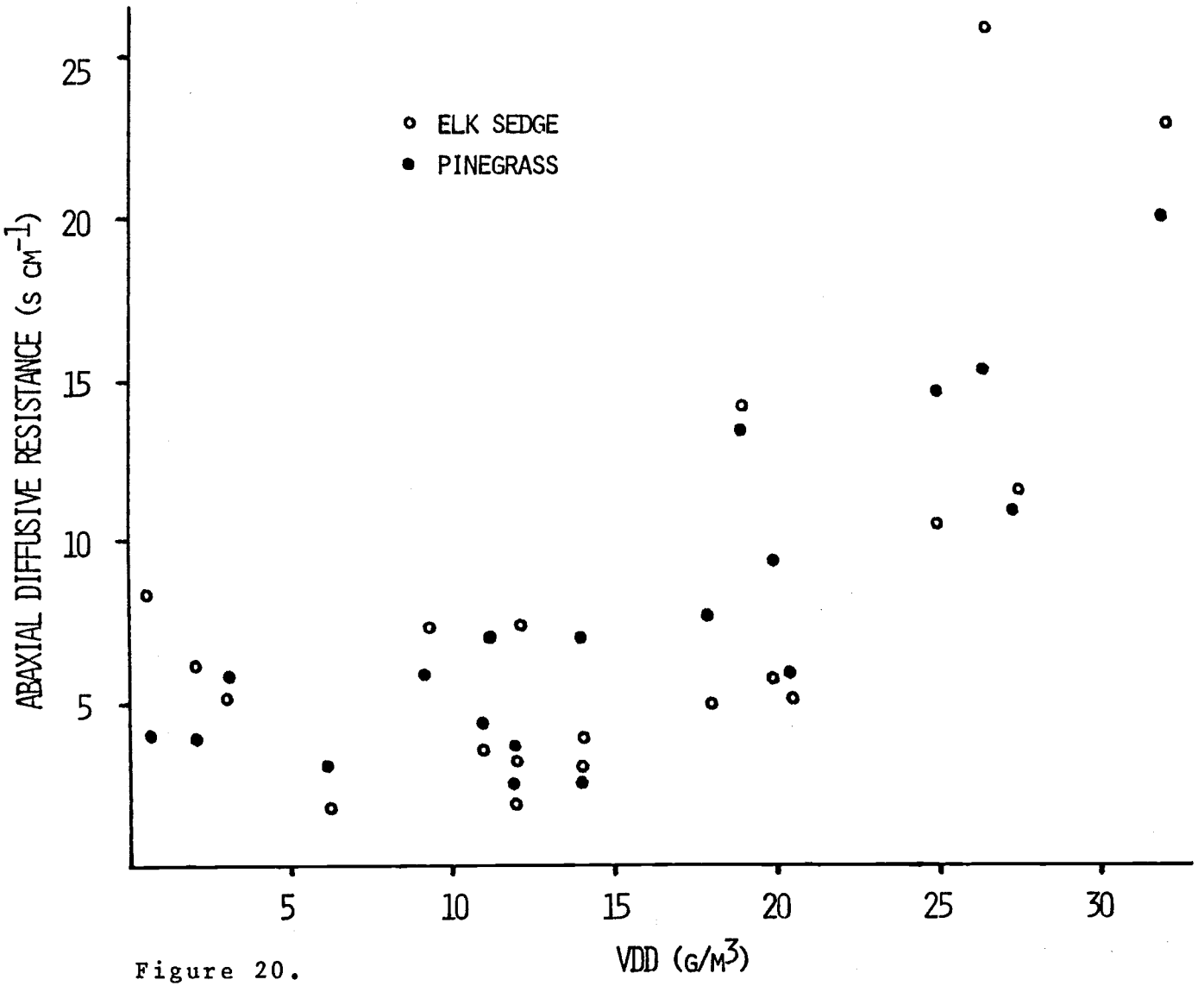
ELK SEDGE
PINEGRASS
ABAXIAL DIFFUSIVE RESISTANCE (s cm^{-1})
VDD (g/m^3)
5
10
15
20
25
30

Figure 20.

reported here may have kept the plants from reaching threshold xylem potentials, except late in the season when soil moisture was low. Such behavior would obscure a threshold response.

CONCLUSIONS

The results of the 1980 study clearly indicated diurnal trends in xylem and osmotic potentials of pinegrass. Both values generally reached most negative values at midafternoon; there was also seasonal decline in response to soil moisture depletion. When proper precautions are taken, the pressure chamber and sample chamber hygrometer show good agreement ($r = .93$) when used under field conditions. However, the pressure chamber is quicker and more convenient.

Diurnal trends in xylem potential were also measured in 1981, for both elk sedge and pinegrass. Elk sedge, a plant generally considered more drought resistant than pinegrass, had midafternoon xylem potentials 0.4 to 0.7 MPa more negative than those of pinegrass during the period of physiological activity. At first glance one might assume elk sedge was more stressed than pinegrass, however, measurements of other water relations parameters suggested that was not the case. It appeared elk sedge had adaptations which allowed it to achieve more negative xylem potentials than pinegrass and still remain physiologically active.

The two factors probably most important in maintaining lower xylem potential in elk sedge are osmotic potential and cell wall elasticity. When we compare π^0 and E for the two species, elk sedge has more negative π^0 values and more rigid cell walls. Thus, for a given loss of water elk sedge will have lower total water potential than pinegrass. Elk sedge also maintained higher levels of B during the

period both species were physiologically active, however, the value of B in assessing drought resistance has not been clearly established (Roberts and Knoerr 1977, Wenkert et al. 1978). In the present study higher values of B appeared to fit into a general group of characteristics suggesting elk sedge to be more drought resistant than pinegrass.

There were obvious differences in π values measured with hygrometric and P/V techniques. Differences between the two techniques were greater for elk sedge than pinegrass, which apparently relates to the higher bound water fraction in elk sedge. The discrepancy between the two techniques also changed with time. Use of the hygrometric technique would have obscured the comparison of osmotic adaptations in these two species.

Abaxial diffusive resistance was higher than adaxial resistance for both species. Abaxial resistance was generally similar for the two species; differences in adaxial resistance were more apparent, with elk sedge having lower adaxial resistance. If CO_2 movement through the stomates is the primary factor limiting photosynthesis in these two species, elk sedge should have higher carbon gain per leaf area. This does not necessarily mean elk sedge will have higher aboveground productivity than pinegrass, excess energy may be used in the drought resistance mechanisms (eg. osmotic adjustment and possibly root growth). Research into the energetic costs of drought resistance is certainly warranted; our understanding of this subject is limited.

Diffusive resistance of both species remained relatively unchanged over a wide range of xylem potentials. At some point diffusive resistance increased sharply, apparently showing a threshold response. This did not occur until late in the season when soil moisture declined. The xylem potential at which diffusive resistance sharply increased was 0.5 MPa more negative for elk sedge than pinegrass, which roughly corresponded to the difference in osmotic potential between the two species. This supports the assertion of Ludlow (1980) that osmotic adjustment influences stomatal response. Diffusive resistance was more correlated to VDD than xylem potential, and the relationship was linear. This follows the feedforward response of stomates to atmospheric humidity reported in the literature (eg. Farquhar et al. 1980).

Stomatal action, by itself, may be insufficient in assessing drought resistance, since it is influenced by the protoplasmic tolerance of drought in a given species. Stomates may exhibit low diffusive resistance if a plant's protoplasm is resistant to water deficit. Or, as Wilson et al (1980) suggested, species which have low protoplasmic tolerance to water deficit may require tight stomatal control of water loss and have high diffusive resistance as soil moisture declines. Thus a combination of factors must be considered in assessing drought resistance. Diurnal trends in xylem potential and diffusive resistance, π^{o}, B, and E should provide an adequate picture of species response to water deficit; however it should be noted that B and E were highly variable. These parameters should be measured as

often as practical over the season, and particularly during the period when soil moisture begins to decline.

In the present study elk sedge appears better able to cope with soil water deficit than pinegrass based on a combination of the following physiological factors: 1) more negative xylem potentials, 2) more negative osmotic potentials (P/V technique), 3) higher bound water fraction, 4) more rigid cell walls, and 5) maintenance of low diffusive resistance to more negative xylem potentials. Additional research should include more species and a range of sites if these conclusions are to be supported or refuted.

An understanding of drought resistance mechanisms will allow better matching of plant material to environmental conditions for revegetation. Potentially the range of plant material available for a particular type of site can be improved by breeding for particular characteristics. Plant physiologists must improve both knowledge of drought resistance mechanisms and methods of screening for particular adaptations. It is time we started considering interaction of stress factors. For example, how does defoliation influence the water relations of a particular plant? Leaf area removal by livestock could be an important tool in managing soil water storage and use in some areas.

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APPENDICES

APPENDIX A

List of Symbols

φ	–	total water potential
P	–	turgor potential
π	–	osmotic potential
τ	–	matric potential
π^{100}	–	osmotic potential at full turgor
π^{0}	–	osmotic potential at zero turgor
B	–	bound water
E	–	elastic modulus
VDD	–	vapor density difference between leaf and air
CWC	–	cell wall content
RWC	–	relative water content

APPENDIX B

Diurnal Course of Vapor Density Difference Between Leaf and Air (VDD) and Ambient Temperature on Measurement Date During 1981.

Date	Time	VDD (g/m^3)	Ambient Temp. (C)
6-5-81	750	0.0	9.0
"	1100	11.0	16.0
"	1500	12.0	21.0
"	1850	6.2	15.0
6-30-81	1100	18.0	23.0
"	1450	20.0	29.0
"	1750	14.0	25.0
7-13-81	750	3.0	12.0
"	1100	12.0	17.0
"	1500	14.0	20.0
"	1750	11.2	18.0
7-27-81	800	2.0	12.0
"	1130	20.5	25.0
"	1525	27.5	27.5
"	1750	19.0	25.0
8-10-81	825	9.2	16.0
"	1200	25.0	28.0
"	1550	32.0	33.0
"	1750	26.5	31.0

APPENDIX C

Analysis of Variance Tables for Pinegrass Regressions

Linear Regression of Abaxial Diffusive Resistance (Dependent Variable) on Xylem Potential (Independent Variable).

Source	DF	Sum of Squares	Mean Square	F - Value
Total	18	396.0074		
Regression	1	178.5360	178.5360	13.96
X	1	178.5360	178.5360	13.96
Residual	17	217.4714	12.7924	

Polynomial Regression of Abaxial Diffusive Resistance (Dependent Variable) on Xylem Potential (Independent Variable).

Source	DF	Sum of Squares	Mean Square	F - Value
Total	18	396.0074		
Regression	2	260.4555	130.2277	15.37
X	1	178.5360	178.5360	21.07
X^2	1	81.9194	81.9194	9.67
Residual	16	135.5519	8.4720	

Linear Regression of Abaxial Diffusive Resistance (Dependent Variable) on Vapor Density Difference Between Leaf and Air (Independent Variable)[1].

Source	DF	Sum of Squares	Mean Square	F - Value
Total	13	332.6893		
Regression	1	239.1386	239.1386	30.67
X	1	239.1386	239.1386	30.67
Residual	12	93.5507	7.7959	

[1]VDD in the 10-32 g/m^3 range.

APPENDIX C. continued

Polynomial Regression of Abaxial Diffusive Resistance (Dependent Variable) on Vapor Density Difference Between Leaf and Air (Independent Variable)[1].

Source	DF	Sum of Squares	Mean Square	F - Value
Total	13	332.6893		
Regression	2	247.2042	123.6021	15.90
X	1	239.1386	239.1386	30.77
X^2	1	8.0657	8.0657	1.04
Residual	11	85.4851	7.7714	

[1]VDD in the 10-32 g/m^3 range.

APPENDIX D

Analysis of Variance Tables for Elk Sedge Regressions

Linear Regression of Abaxial Diffusive Resistance (Dependent Variable) on Xylem Potential (Independent Variable).

Source	DF	Sum of Squares	Mean Square	F - Value
Total	18	788.6200		
Regression	1	150.9008	150.9008	4.02
X	1	150.9008	150.9008	4.02
Residual	17	637.7192	37.5129	

Polynomial Regression of Abaxial Diffusive Resistance (Dependent Variable) on Xylem Potential (Independent Variable).

Source	DF	Sum of Squares	Mean Square	F - Value
Total	18	788.6200		
Regression	2	297.5711	148.7856	4.85
X	1	150.9008	150.9008	4.92
X^2	1	146.6703	146.6703	4.78
Residual	16	491.0489	30.6906	

Linear Regression of Abaxial Diffusive Resistance (Dependent Variable) on Vapor Density Difference Between Leaf and Air (Independent Variable)[1].

Source	DF	Sum of Squares	Mean Square	F - Value
Total	13	728.6800		
Regression	1	463.5411	463.5411	20.98
X	1	463.5411	463.5411	20.98
Residual	12	265.1389		

[1]VDD in the 10-32 g/m^3 range.

APPENDIX D. continued

Polynomial Regression of Abaxial Diffusive Resistance (Dependent Variable) on Vapor Density Difference Between Leaf and Air (Independent Variable)[1]

Source	DF	Sum of Squares	Mean Square	F - Value
Total	13	728.6800		
Regression	2	496.1144	248.0572	11.73
X	1	463.5411	463.5411	21.92
X^2	1	32.5733	32.5733	1.54
Residual	11	232.5656	21.1423	

[1]VDD in the 10-32 g/m^3 range.

APPENDIX E

Diurnal Variability in Xylem Potential (MPa)[1] of Elk Sedge and Pinegrass on Three Representative Dates

	Approximate Time (PDT)							
6-5-81	430	630	830	1030	1230	1430	1630	1800
Elk Sedge								
$\bar{x}$[2]	0.21	0.29	0.37	1.33	2.35	1.79	1.95	1.29
S.E.[3]	0.02	0.06	0.05	0.23	0.17	0.19	0.09	0.13
Pinegrass								
$\bar{x}$[2]	0.22	0.48	0.78	1.23	1.64	1.49	1.42	1.52
S.E.[3]	0.03	0.05	0.10	0.09	0.09	0.08	0.12	0.08
7-13-81								
Elk Sedge								
$\bar{x}$[2]	0.19	0.38	1.82	1.96	2.27	2.51	2.07	0.73
S.E.[3]	0.02	0.04	0.21	0.12	0.14	0.11	0.06	0.05
Pinegrass								
$\bar{x}$[2]	0.26	0.30	1.04	1.68	1.84	1.73	1.99	1.25
S.E.[3]	0.04	0.04	0.15	0.08	0.02	0.04	0.09	0.10
8-10-82								
Elk Sedge								
$\bar{x}$[2]	1.68	2.11	2.66	3.06	3.11	3.07	2.61	2.67
S.E.[3]	0.06	0.10	0.14	0.05	0.08	0.13	0.09	0.06
Pinegrass								
$\bar{x}$[2]	1.67	1.90	2.04	2.62	2.40	2.67	2.50	2.48
S.E.[3]	0.07	0.07	0.08	0.08	0.06	0.05	0.10	0.08

[1] All means are negative.
[2] Mean of four samples.
[3] Standard error.

APPENDIX F

Diurnal Variability in Abaxial and Adaxial Diffusive Resistance (S cm^{-1}) for Elk Sedge and Pinegrass on Two Representative Dates

	6-5-81				7-27-81			
	730[1]	1130	1500	1830	800	1130	1530	1730
Elk Sedge								
Abaxial								
$\bar{x}$[2]	8.5	3.7	3.4	1.9	6.2	5.1	11.6	14.3
S.E.[3]	0.6	0.4	0.3	0.2	0.1	0.9	1.4	2.2
Adaxial								
$\bar{x}$	10.5	7.8	6.5	4.1	15.0	7.5	17.8	17.4
S.E.	0.9	1.1	1.3	0.6	0.7	0.9	1.5	1.6
Pinegrass								
Abaxial								
$\bar{x}$	4.3	4.5	3.6	3.0	4.1	6.0	11.0	13.6
S.E.	0.7	0.6	0.4	0.4	0.6	1.2	1.3	1.8
Adaxial								
$\bar{x}$	12.6	9.9	9.3	7.1	18.8	17.7	20.1	20.8
S.E.	1.0	0.8	1.0	0.7	1.5	1.6	2.8	2.0

[1]Approximate time (PDT).
[2]Mean of 4-5 samples.
[3]Standard error.

APPENDIX G

Seasonal Changes in Cell Wall Content of Elk Sedge and Pinegrass During 1981

Date	Pinegrass	Elk Sedge
5-27	61.3	62.9
6-17	61.8	63.0
6-30	64.7	65.4
7-13	62.5	66.0
7-27	61.0	66.7
8-12	62.7	67.7
8-27	61.6	66.1