Transactions of the Nebraska Academy of Sciences and Affiliated Societies

Nebraska Academy of Sciences

1996

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Charles J. Bicak
University of Nebraska at Kearney

Troy M. Walz
University of Nebraska

Bicak, Charles J. and Walz, Troy M., "Xylem Pressure Potential of Two Perennial Grasses, *Bromus inermis* and *Andropogon scoparius*, on the Oldfather Prairie in Central Nebraska" (1996). *Transactions of the Nebraska Academy of Sciences and Affiliated Societies*. 78.
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1996. *Transactions of the Nebraska Academy of Sciences*, 23: 23–27

XYLEM PRESSURE POTENTIAL OF TWO PERENNIAL GRASSES, *BROMUS INERMIS* AND *ANDROPOGON SCOPARIUS*, ON THE OLDFATHER PRAIRIE IN CENTRAL NEBRASKA

Charles J. Bicak and **Troy M. Walz**

Department of Biology
University of Nebraska at Kearney
Kearney, Nebraska 68849

University of Nebraska
West Central Research & Extension Center
North Platte, Nebraska 69101

ABSTRACT

Xylem pressure potential of *Bromus inermis* and *Andropogon scoparius* was measured at predawn and at midday on the Oldfather Prairie west of Kearney, Nebraska (41° 42' N, 99° 08' W). This mixed-grass prairie is characterized by patches of *B. inermis* and *A. scoparius* growing in close proximity. Ten replicate pressure potential measurements were made weekly during the 1993 growing season. Water potential remained uniformly high and unchanged throughout the season at predawn for both species. Midday measurements were more variable and also more negative than at predawn on all but one sample date. Water potential deficit, defined as the difference between predawn and midday conditions, was larger for *B. inermis* (-1.56 MPa) than for *A. scoparius* (-0.68 MPa). Despite abnormally high rainfall (nearly 750 mm) in 1993, the data support the notion of tight coupling between *A. scoparius* and the water environment. The water potential deficit and extreme lows for *B. inermis* (-2.1 MPa) and *A. scoparius* (-1.4 MPa) indicate further that *B. inermis* may be less efficient yet more opportunistic in water use than *A. scoparius*. *A. scoparius*, by contrast, may be more efficient but also driven more by genetic cues.

† † †

The natural vegetation of central Nebraska is dominated by perennial grasses (Kaul and Rolfsmeier, 1993). Water stress is critical in directing plant growth and survival, particularly in regions subject to periodic drought (Svejcar and Christiansen, 1987). The erratic nature of precipitation in the mixed grass prairie complicates efforts at forecasting invasion or retreat of grasses. Timing of precipitation apparently is at least as important as amount in determining plant productivity.

Soil is a reservoir for water that is available to drive the transpirational stream in the plant. This reservoir permits transpiration to continue for several days without recharge by rainfall (Ritchie, 1981) in drought conditions. By contrast, an unusually wet year may lead to differential water use by grass plant species. Measurement of plant water status aids in quantifying the degree of stress to which a grass is subjected (Hsiao, 1973), water-use efficiency of grasses (Liang et al., 1989), and therefore overall productivity (Axelrod, 1985; Lauenroth, 1979).

Prominent among the grasses is *Andropogon scoparius* (little bluestem), a warm-season bunchgrass characterized by a tall (0.5–1.5 m) coarse seed culm and somewhat flattened and folded leaves (Stubbendieck et al., 1992). In the last century, a perennial cool-season species, *Bromus inermis* (smooth brome), has been introduced. A native of Europe, China, and Siberia (Phillips Petroleum, 1958), *B. inermis* is now naturalized in the northern two-thirds of the United States. *Bromus inermis* aggressively infiltrates the habitat of *A. scoparius* by vigorous rhizome growth (Johnson and Nichols, 1970). It is considered to be of good forage value early in the growing season, but palatability and forage quality drop sharply with plant maturity (Stubbendieck et al., 1986). *Andropogon scoparius* has been described as a xeric grass (Knapp, 1984) and has long been considered a key species in upland sites (Weaver and Fitzpatrick, 1934). By contrast, *B. inermis* was originally introduced in the Great Plains to retard soil erosion in watercourses.

Temporal separation of phenophases for the cool-season *B. inermis* and warm-season *A. scoparius* (Dickinson and Dodd, 1976; Martin et al., 1991; Weaver, 1954) may suggest reduced competition for water, despite the proximity of the grasses. Understanding patterns of response in *A. scoparius* and *B. inermis* to water has important theoretical implications for predicting the retreat of the former and the advance of the latter grass. There is economic significance as well since many ranchers depend on a reasonably predict-

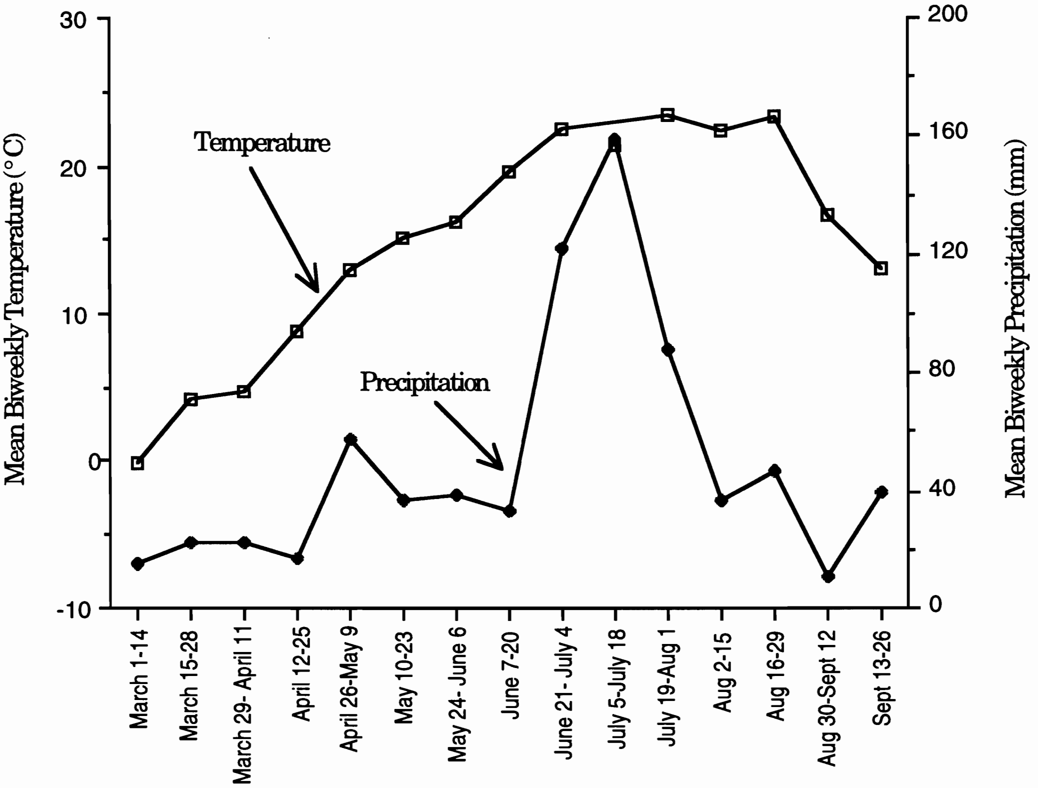

Figure 1. Climate diagram. Solid diamonds (◆) represent the pattern for precipitation and open squares (☐) the pattern for temperature during the growing season, 1993.

able mix of cool and warm season grasses to sustain grazing throughout the growing season.

This study was intended to improve the understanding of water status of two dominant grasses on the Oldfather Prairie, an area that has not previously been described in the literature. Our objective was to determine the diurnal and seasonal patterns of xylem pressure potential in *A. scoparius* and *B. inermis* under conditions of non-limiting water.

STUDY AREA

The study site was located on the Oldfather Prairie west of Kearney, Nebraska (41° 42' N, 99° 08' W), a mixed-grass prairie with rolling topography, elevation 600 meters above sea level. The soil is predominantly a Coly-Uly-Holdrege (Mollisols) association (Kuzila and Mack, 1988), the surface layer ranging from about 15 to 60 cm in depth. The soil was deposited as windblown loess and is typical for the region. The 16.0-ha study site has not been grazed since its establishment in 1987. There is no record of cultivation and the topography makes it highly unlikely the prairie had been plowed. The local climate is continental, characterized by distinct seasonality. Precipitation varies temporally, with most occurring during the April-to-October growing season.

The vegetation of the region is a mixed-grass prairie complex that includes both cool- and warm-season species. Short and mid-grasses such *Bouteloua gracilis*, *Bouteloua curtipendula*, and *Andropogon scoparius* tend to dominate drier areas. Moister locations are dominated by tallgrass species including *Andropogon gerardi*, and to a lesser extent, *Agropyron smithii*, a mid-grass species (Kaul and Rolfsmeier, 1993). While forbs are fewer than in the tallgrass prairie, several are highly visible, including *Ratibida columnifera, Psoralea tenuiflora*, and *Yucca glauca*. The landscape shows variation in communities in lowland and upland locations as well as in slope and aspect. Introduced *Bromus inermis* and *Poa pratensis* are present across most locations, with highly visible patches of *A. scoparius* interspersed with *B. inermis*.

METHODS

Xylem pressure potential of *Bromus inermis* and *Andropogon scoparius* was measured at predawn (0400–0600 hours) and midday (1230–1430 hours) weekly from June 11 to September 3, 1993. Those times of the day were selected because they correspond to periods of maximal and minimal water potential respectively in the plant tissue (Sala et al., 1981). The pressure-bomb technique (Scholander et al., 1965) was used (Soilmoisture Equipment, Inc. model 3005, Santa Bar-

bara, CA) and tillers were cut just above the crown and measured within thirty seconds. Ten replicates of each species were randomly selected at each sample time. All measurements were made on grasses from upper slopes and ridge tops. Relative humidity was determined using a sling psychrometer. Periodic light intensity measurements were made at midday through the growing season (General Electric, model 214, Cleveland, OH).

Significant differences in species and diurnal pressure potential were determined by assessing separation in 95% confidence intervals. Season-long trends were tracked using simple linear regression models.

RESULTS

Precipitation during the growing season ranged from 11.1 to 159.5 mm during the 16 biweekly intervals from March 1 to September 26, 1993 (Fig. 1). Total precipitation during the March-to-September growing season was 748 mm as compared to the yearly average of 580 mm.

Predawn pressure potential was higher (less negative) than at midday for both *A. scoparius* (Fig. 2a) and *B. inermis* (Fig. 2b) on all dates except 2 August 1993. It rained 12.0 mm between the predawn and midday measurements on this date. Linear regression analyses indicated no significant decline in plant pressure potential through the course of the growing season for *B. inermis* and a significant decline only at predawn for *A. scoparius* ($r^2 = 0.62, p = 0.01$).

Season-long mean pressure potential at predawn for *A. scoparius* was -0.29 ± 0.13 MPa. This was closely tracked by that for *B. inermis* with a mean of -0.27 ± 0.18 MPa. The most deviation occurred on the rain day 2 August 1993. Alternatively, while *A. scoparius* and *B. inermis* follow the same pattern at midday, *A. scoparius* showed a mean value of -0.86 ± 0.50 MPa, while that for *B. inermis* was -1.62 ± 0.70 MPa across the growing season. *Bromus inermis* had water-potential values that were nearly twice as dry (more negative) as *A. scoparius* yet *B. inermis* recovered to approximately the same predawn water level as *A. scoparius*.

The pressure potential deficit, defined as the range between predawn and midday measurements, was significantly less at -0.68 ± 0.37 MPa for *A. scoparius* than for *B. inermis* at -1.56 ± 0.51 MPa ($t = 4.2, p = 0.01$). In addition, the relative humidity at predawn averaged 88% ± 12% and 64% ± 19% at midday during the sampling period.

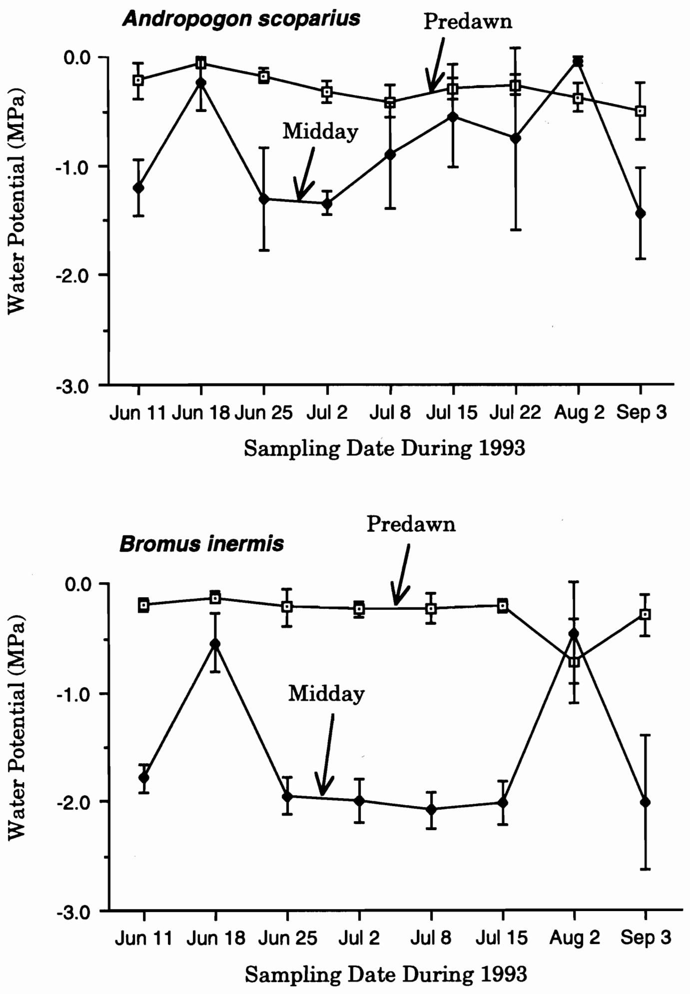

Figure 2. Water potential (MPa) at predawn (☐) and midday (◆) for *Andropogon scoparius* (Fig. 2a) and *Bromus inermis* (Fig. 2b). Vertical bars are 95% confidence intervals. Data are absent for *B. inermis* for July 22 because the O-rings on the pressure bomb leaked, causing us not to have a gas-tight system.

DISCUSSION

Pressure potential at predawn for both *A. scoparius* and *B. inermis* remained high and relatively unchanged during the growing season. The uniformly wet growing season appeared to prolong both the vegetative and flowering periods for both species. The classic temporal separation of cool and warm season species does not adequately describe plant growth and development during 1993. Dickinson and Dodd (1976) noted similar overlap in cool and warm season phenological scales with supplemental water in the shortgrass steppe of eastern Colorado.

Pressure potential at midday for both *A. scoparius* and *B. inermis* was lower and more variable than at predawn. This is likely a consequence of lower soil moisture, increased atmospheric demand, and variable wind speed and cloud cover at midday. *Bromus inermis* was nearly twice as dry as *A. scoparius* at midday in part because the C_3 *B. inermis* (Waller and Lewis, 1979) has lower water-use efficiency than the C_4 *A. scoparius* (Salisbury and Ross, 1992). In C_3 plants, transpiration rates are routinely highest after a rain (Barnes and Harrison, 1982) a typical occurrence during the 1993 growing season. Martin et al. (1991) found that even though both C_3 and C_4 plants exhibit significant increases in leaf water potential following rain, only C_3 species as a group showed significant increases in conductance and that changes in leaf water potential appeared greater in the C_3 species. *Bromus inermis* probably had a high transpiration rate and associated rapid growth in the spring, summer, and early fall as moisture was never a limiting factor in this aberrant growing season. As long as soil moisture is high, stomatal aperture also remains high (Barnes and Harrison, 1982) and the associated uptake of carbon dioxide in photosynthesis is maximized. *Bromus inermis* may be more opportunistic in wet years than dry. This may confer some competitive advantage for this grass in relation to *A. scoparius*.

Predawn pressure potentials are a reflection of the soil water (Slatyer, 1967) as shown by the wettest soil layer of the rooting zone (Sala et al., 1981). The average year has alternating periods of dry and wet surface soil which are likely stressful to the plants. The growing season of 1993 was uniformly wet and therefore less stressful to the plants. *Bromus inermis* was less efficient than *A. scoparius* in water use because it was drier in the afternoon, when atmospheric demand was at its maximum. The rate and total movement of water from the soil to the roots, culms, blades, and then to the atmosphere must have been greater for *B. inermis* than for *A. scoparius*. Water in the soil was not limiting during the 1993 growing season, so the less efficient *B. inermis* was not limited by water availability. Rapid and sustained growth in wet years, as signaled by xylem pressure-potential measurements, may explain, in part, the remarkable invasion of *B. inermis* in mixed grass prairies in Nebraska.

ACKNOWLEDGMENTS

We thank the Research Services Council in the University of Nebraska at Kearney for partial funding of this research and also Dusty Rodiek, manager of Cottonmill Park, for his assistance in access to the prairie sample sites.

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