

Soil water dynamics, transpiration, and water losses in a crested wheatgrass and native shortgrass ecosystem

M.J. TRLICA and M.E. BIONDINI

Range Science Department, Colorado State University, Fort Collins, CO 80523, USA Department of Animal and Range Sciences, North Dakota State University, Fargo, ND 58105, USA

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Abstract

The status of water in soil and vegetation was monitored in a stand of crested wheatgrass (*Agropyron cristatum*) and a nearby shortgrass steppe during a growing season. This was done to determine if water use and losses were similar among two very different communities in a similar climate. Precipitation was similar throughout the study period for both the crested wheatgrass and native shortgrass communities. However, the native shortgrass community with greater root biomass had consistently greater soil water depletion in the deeper soil horizons than was found in the crested wheatgrass community. Greater depletion of soil water by native shortgrass species suggests that they might be more competitive than crested wheatgrass in a water-limited environment.

Crested wheatgrass maintained high leaf water potential early in the season, but lower water potential during the latter part of the growing season as compared with the major species of the shortgrass steppe, blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*). Leaf conductance was lower for crested wheatgrass than for the native grasses during the later part of the growing season. Consequently, seasonal transpiration for crested wheatgrass was lower when compared with blue grama or western wheatgrass. Lower conductance allowed crested wheatgrass to maintain relatively high internal water potential and may have accounted for less soil water use at deeper soil depths during the latter part of the growing season.

Water loss through transpiration was less for western wheatgrass than for either blue grama or crested wheatgrass because western wheatgrass had less leaf area. However, western wheatgrass was as efficient as the other species in its use of water. Crested wheatgrass transpired more water than blue grama early in the growing season, but less than either native species for the remainder of the growing season. Estimated seasonal transpiration loss was greater in the shortgrass ecosystem than in the established crested wheatgrass stand.

Introduction

Numerous crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] communities have been established in the western USA and Canada during the past 50 years (Rogler and Lorenz, 1983; Smoliak and Dormar, 1985; Woolfolk, 1951). A number of these communities have remained

virtual monocultures with little or no apparent succession for more than 40 years (Vallentine, 1980). A great deal of information is available concerning differences in the standing crop biomass, net primary production, and carbon and nutrient allocation in crested wheatgrass and important species of shortgrass steppe communities. However, few studies have elucidated

differences in soil water losses, transpiration, and water use efficiency in these communities (Caldwell *et al.*, 1983; Fairbourn, 1982; Power, 1980; Wight and Black, 1972). Field studies of soil-plant water relations and water use patterns in these two communities in a similar environment are completely lacking.

This study was designed to determine if differences in soil-plant water relations existed between crested wheatgrass and native shortgrass communities. These differences might then result in differential resource allocation and utilization through space and time. We hypothesize that functional differences between crested wheatgrass and native shortgrass communities will be reflected in soil water use patterns and water use efficiency of the dominant grasses. Different water use patterns in these two communities through the growing season might, in turn, affect other ecosystem components and functions (*i.e.*, belowground herbivory, decomposition, exudation, mineralization, *etc.*). This might also help to explain the persistence of crested wheatgrass communities in the shortgrass steppe environment.

Study area

This study was conducted at the High Plains Grasslands Research Station (HPGRS), approximately 7 km west of Cheyenne, Wyoming. Topography of the area is nearly level to undulating at an elevation of about 1900 m. The climate at the HPGRS is semiarid-temperate. Wind is common and velocity averages from 5 to 10 km hr⁻¹. The average growing season is 132 days, and the average date for the last and first freeze are May 19 and September 28, respectively. Annual temperatures average 7°C, with extremes ranging from -36°C to 42°C. Temperatures average -3°C in January and 20°C in July. Annual precipitation at the HPGRS averages 365 mm with recorded extremes of 159 and 610 mm. Approximately 78% of the precipitation occurs between April 1 and September 30.

The soil of the two study sites is an Ascalon fine, loamy, mixed mesic Aridic Anguistol (Young and Singleton, 1977). This soil is found on nearly level to gently sloping alluvial fans and

terraces of granitic parent material. The soil contains about 13 cm of water in the surface 120-cm at field capacity (water content at saturation after gravitational water has percolated through). Native vegetation of the area is characteristic of the shortgrass steppe. Blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths] is the dominant warm-season species. Western wheatgrass (*Agropyron smithii* Rydb.), needlethread (*Stipa comata* Trin. and Rupr.), junegrass [*Koeleria cristata* (L.) Pers.], and sandberg bluegrass (*Poa secunda* Presl.) are the principal cool-season grasses. Sedges (*Carex* spp.), annual grasses, and annual and perennial broad-leaf species (forbs) make up a minor part of the vegetation.

The shortgrass prairie research site has never been plowed or tilled. The crested wheatgrass site was plowed and used for research plots for many years, then it was seeded to crested wheatgrass in the early 1950's and has not been tilled since then. Crested wheatgrass remains as a virtual monoculture with a limited amount of smooth brome (*Bromus inermis* Leyss.) and annual and perennial forbs. Some topsoil was lost through wind and water erosion from the crested wheatgrass site while the site was tilled. Both sites were grazed by cattle at a moderate level in the past, but have now been fenced to exclude domestic livestock. The two sites were separated by a distance of about 1 km.

Methods

Experimental design

The total size of each research area was about 0.3 ha. Four adjacent blocks were established in both the native shortgrass and nearby crested wheatgrass communities in October, 1984. Rectangular (1.5 × 32-m) plots within each block served as basic experimental units for various studies. The study was conducted as a randomized complete block design with four replications in each community.

Soil water

Water input to both sites was determined from

daily precipitation values recorded from 6.4 × 5.7-cm, wedge-shaped plastic gauges installed at each site. Soil samples for determination of gravimetric and volumetric water content were obtained from the native shortgrass and crested wheatgrass communities at approximately one-week intervals from late April through mid September, 1985. Duplicate samples were taken in each block, using a soil core with a diameter of 2 cm. Each core was sectioned into 3–7, 8–12, 18–22, and 58–62-cm soil depths, which were dried at 105°C to determine gravimetric soil water content. Bulk density samples were taken at the same depths from a soil pit in each community.

In addition to soil water content, soil water potential (Ψ_s , where $\Psi_s = \Psi_{\text{osmotic}} + \Psi_{\text{matrix}} + \Psi_{\text{pressure}}$) of both systems was measured at 5, 10, 20, and 60 cm, corresponding to the gravimetric sampling depths. Individually calibrated, screen-caged, single-junction, Peltier thermocouple psychrometers for measuring total water potential were installed in each block in a manner similar to that described by Fonteyn *et al.* (1987). Soil water potentials were recorded weekly from June through mid September.

Plant and water dynamics

Individual plants growing within plots near the thermocouple psychrometers were sampled for stomatal conductance, transpiration, and leaf water potential. Measurements were performed on dominant species (crested wheatgrass, blue grama, and western wheatgrass) from each community. The most recent fully-expanded leaves were used. A total of three leaves from each species in each block at one sampling date and time was used as a sample. Sampling of both communities was conducted at midday (10:00–14:00 h) at approximately one-week intervals from late May through mid September. In addition to the midday values, diurnal measurements were taken every other week at approximately three-h intervals throughout the daylight period. Diurnal transpiration rates were integrated to estimate total daily transpiration for each species.

Transpiration and leaf conductance were measured for the abaxial leaf surface with a

steady state diffusion porometer (Model LI-1600, LI-COR Inc., Lincoln, Nebraska). Leaf water potential was measured on these same leaves using a pressure chamber (Scholander *et al.*, 1965). The individually measured leaves were clipped, placed in humid plastic bags, and then placed in the pressure chamber to determine xylem pressure potential (leaf water potential).

Leaf area of grass species was determined on six different dates throughout the growing season utilizing a portable leaf area meter (LI-3000, LI-COR, Inc.). Individual grass species were clipped to ground level from 0.25-m² circular plots randomly located in each block. A total of two plots was clipped in each block, for a total of eight samples in each plant community on each sampling date. Integrated transpiration values for individual species were multiplied by their respective leaf area index to calculate water loss per m² ground area for the two communities. Seasonal water loss through transpiration from the two systems was estimated from integration of daily transpiration values for the entire growing season for crested wheatgrass, blue grama, and western wheatgrass. Integrated transpiration for the species may be overestimated, as these values were based on water flux from leaves that were not in their natural orientation and, therefore, did not include boundary layer resistance associated with canopy architecture. In addition, ignoring the boundary layer resistance of the bunchgrass morphology of crested wheatgrass could have led to a sizeable overestimate of seasonal transpiration and an underestimate of water use efficiency (WUE) for this species. These problems are inherent when one scales up from leaf responses to estimate community differences (Massman and VanDijken, 1989).

Data for net primary production (NPP) for both communities were obtained from Redente *et al.* (1989). Above- and below-ground plant biomass was sampled on four different dates during the growing season from both the crested wheatgrass and native shortgrass communities to estimate total NPP. Water loss through transpiration, leaf area index, and water use efficiency for representative species of both communities were estimated for each of the three periods within the four harvest dates. Water use efficiency

(WUE) was determined as total NPP/transpiration water loss for each species.

Data analysis

Analysis of variance and Tukey's Test were used to analyze all soil and plant water data. Significant differences were accepted at $P \leq 0.05$. In addition, transpiration data were subjected to forward stepwise multiple regression analysis, using leaf to air vapor pressure deficit, leaf water potential, and quantum flux density as independent variables.

Results

Precipitation and soil water

The weekly precipitation distributions for the crested wheatgrass and native shortgrass ex-

perimental sites are illustrated in Figure 1. Precipitation throughout the 1985 growing season was similar in both the crested wheatgrass and the native shortgrass experimental plots. The total amount of precipitation recorded for the 1985 growing season (April through September) was 340 and 350 mm for the crested wheatgrass and native shortgrass sites, respectively. Precipitation was, therefore, well above the average of about 285 mm for this period. Monthly distribution varied from an average low of 30 mm in June to an average high of 110 mm in July, on both sites. Approximately 50% of the precipitation in the growing season occurred during the warmest period between 15 July and 26 August.

Gravimetric water contents for four soil depths from both the crested wheatgrass and native shortgrass sites are presented in Figures 2 and 3, respectively. Soil water at the 5- and 10-cm soil depths at both sites was high at about 12 to 15% early in the growing season (mid April to mid

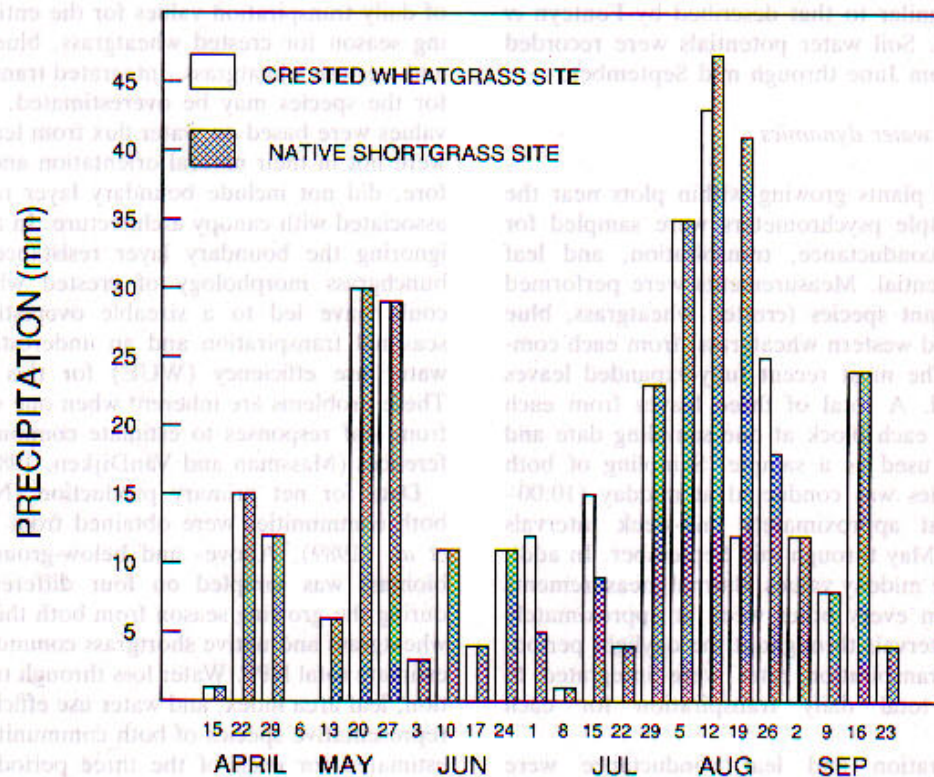


Fig. 1. Weekly precipitation during the 1985 growing season at the crested wheatgrass and native shortgrass experimental areas.

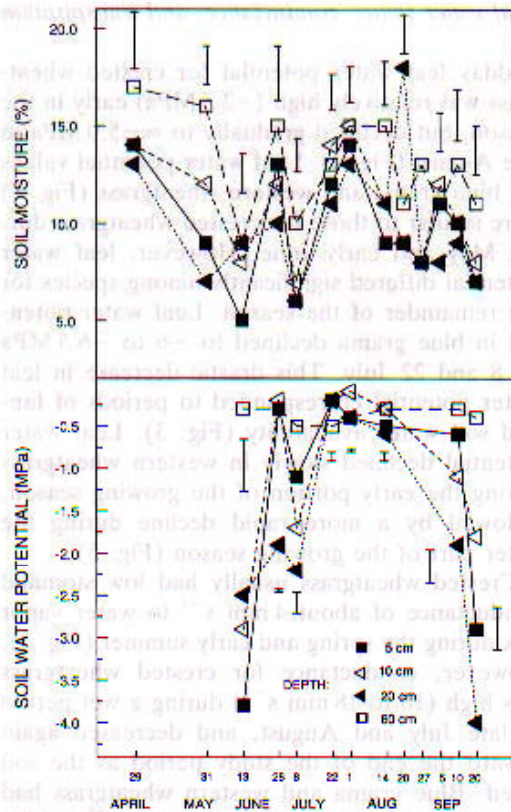


Fig. 2. Soil water (gravimetric) percentage at 5, 10, 20, and 60-cm soil depths for the crested wheatgrass site; and soil water potential at 5, 10, 20, and 60-cm soil depths for this same site. Bars adjacent to means represent the maximum standard error for means on that date.

May), but varied considerably among dates. Soil water at these shallow depths depended on the amount of precipitation that was received between consecutive sampling dates. Soil water at the 20-cm soil depth in the crested wheatgrass community was often lower than that for any other soil depth (Fig. 2). The deeper soil depth (60 cm) was consistently wetter in the crested wheatgrass system than the more shallow depths, and less live root biomass was found at deeper depths in the crested wheatgrass community (Re-dente *et al.*, 1989).

The trend in soil water levels at the 5- and 10-cm depths in the native shortgrass community (Fig. 3) was similar to that found at the crested wheatgrass site (Fig. 2) throughout the study period, except for a few sampling dates. Soil at

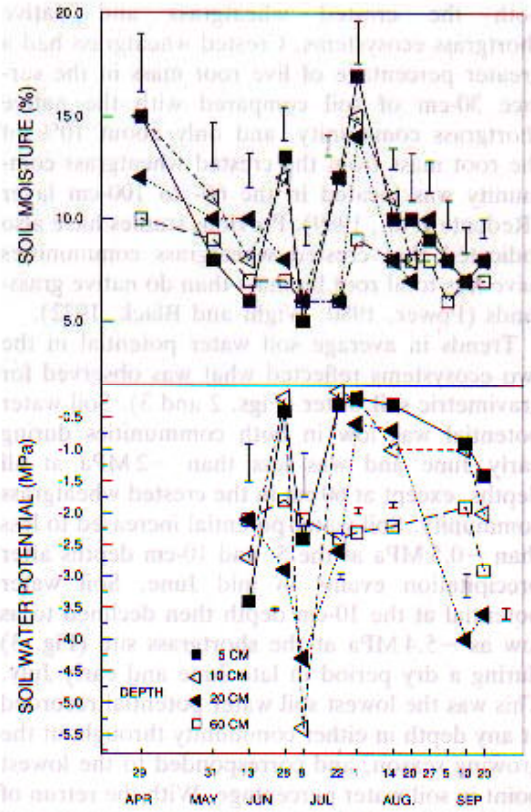


Fig. 3. Soil water (gravimetric) percentage at 5, 10, 20, and 60-cm soil depths for the native shortgrass site; and soil water potential at 5, 10, 20, and 60-cm soil depths for this same site. Bars adjacent to means represent the maximum standard error for means on that date.

the 20-cm depth was usually dryer than at shallower depths. Soil water at the 60-cm soil depth was often lower and less variable throughout most of the growing season as compared with shallower depths. This small amount of soil water at the 60-cm depth (6 to 10%) in the shortgrass community during the growing season is contrasted with the wet 60-cm depth (9 to 17%) in the crested wheatgrass community.

The average soil water percentage throughout the growing season was similar for both the crested wheatgrass and native shortgrass sites at the 5-, 10-, and 20-cm depths. However, the crested wheatgrass site had consistently higher ($P \leq 0.05$) soil water (13%) than did the native shortgrass site (7.5%) at the 60-cm soil depth. Soil texture at the 60-cm depth was similar for

both the crested wheatgrass and native shortgrass ecosystems. Crested wheatgrass had a greater percentage of live root mass in the surface 30-cm of soil compared with the native shortgrass community, and only about 10% of the root mass from the crested wheatgrass community was located in the 60- to 100-cm layer (Redente *et al.*, 1989). Previous studies have also indicated that crested wheatgrass communities have less total root biomass than do native grasslands (Power, 1980; Wight and Black, 1972).

Trends in average soil water potential in the two ecosystems reflected what was observed for gravimetric soil water (Figs. 2 and 3). Soil water potential was low in both communities during early June and was less than -2 MPa at all depths, except at 60 cm in the crested wheatgrass community. Soil water potential increased to less than -0.5 MPa at the 5- and 10-cm depths after precipitation events in mid June. Soil water potential at the 10-cm depth then declined to as low as -5.4 MPa at the shortgrass site (Fig. 3) during a dry period in late June and early July. This was the lowest soil water potential recorded at any depth in either community throughout the growing season, and corresponded to the lowest point in soil water percentage. With the return of significant rainfall in mid July and August, soil water potential at 5-, 10-, and 20-cm depths increased again to less than -1 MPa in both communities. Soil water potential at 60-cm in the crested wheatgrass community never dropped lower than -0.75 MPa throughout the entire growing season; whereas, in the shortgrass community, it was always less than -1.75 MPa. Soil water potential fluctuations were also less extreme in the crested wheatgrass community than in the native shortgrass community.

The seasonal averages for soil water potential at the 5- and 10-cm soil depths were similar in both the crested wheatgrass and native shortgrass ecosystems. However, soil water potential in the native shortgrass community was significantly lower than in the crested wheatgrass community at the 20-cm (-2.6 vs -1.6 MPa) and 60-cm (-2.2 vs -0.4 MPa) soil depths. The average seasonal soil water potential at the crested wheatgrass site was greater at 60-cm than near the surface.

Leaf water status, conductance, and transpiration

Midday leaf water potential for crested wheatgrass was relatively high (-2.5 MPa) early in the season, but declined gradually to ≈ -5.0 MPa in late August (Fig. 4). Leaf water potential values for blue grama and western wheatgrass (Fig. 5) were similar to those for crested wheatgrass during May and early June. However, leaf water potential differed significantly among species for the remainder of the season. Leaf water potential in blue grama declined to -6 to -6.5 MPa on 8 and 22 July. This drastic decrease in leaf water potential corresponded to periods of limited soil water availability (Fig. 3). Leaf water potential declined slowly in western wheatgrass during the early portion of the growing season, followed by a more rapid decline during the latter part of the growing season (Fig. 5).

Crested wheatgrass usually had low stomatal conductance of about 4 mm s^{-1} to water vapor flux during the spring and early summer (Fig. 3). However, conductance for crested wheatgrass was high (10 to 18 mm s^{-1}) during a wet period in late July and August, and decreased again toward the end of the study period as the soil dried. Blue grama and western wheatgrass had stomatal conductances of 4 to 12 mm s^{-1} in May and June, but conductance for both species increased to very high levels of 24 to 52 mm s^{-1} during the wet period in July and August (Fig. 5). These rates then declined to about 4 to 8 mm s^{-1} during the remainder of the growing seasons as soil water became more limiting.

The higher stomatal conductances measured for all species in late July through August corresponded to a period of higher soil water availability (Figs. 2 and 3). These rainfall events, however, had little effect on midday leaf water potential. Consequently, transpiration for all three species was not highly correlated with midday leaf water potential. It is possible, however, that transpiration and leaf water potential would be more highly correlated under conditions of greater water stress. Water stress during the 1985 growing season was not severe, as summer precipitation was above normal. It is also probable that predawn leaf water potentials would have been better correlated with maximum leaf con-

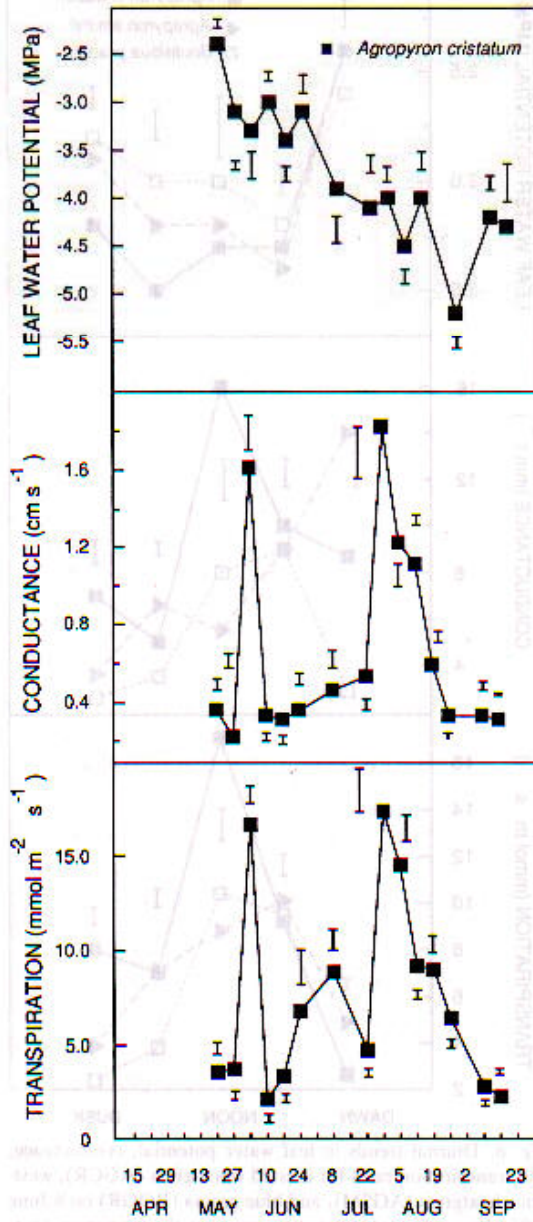


Fig. 4. Midday leaf water potential, midday leaf conductance, and midday transpiration rate for crested wheatgrass (*Agropyron cristatum*) during the 1985 growing season. Bars adjacent to means represent the maximum standard error for means on that date.

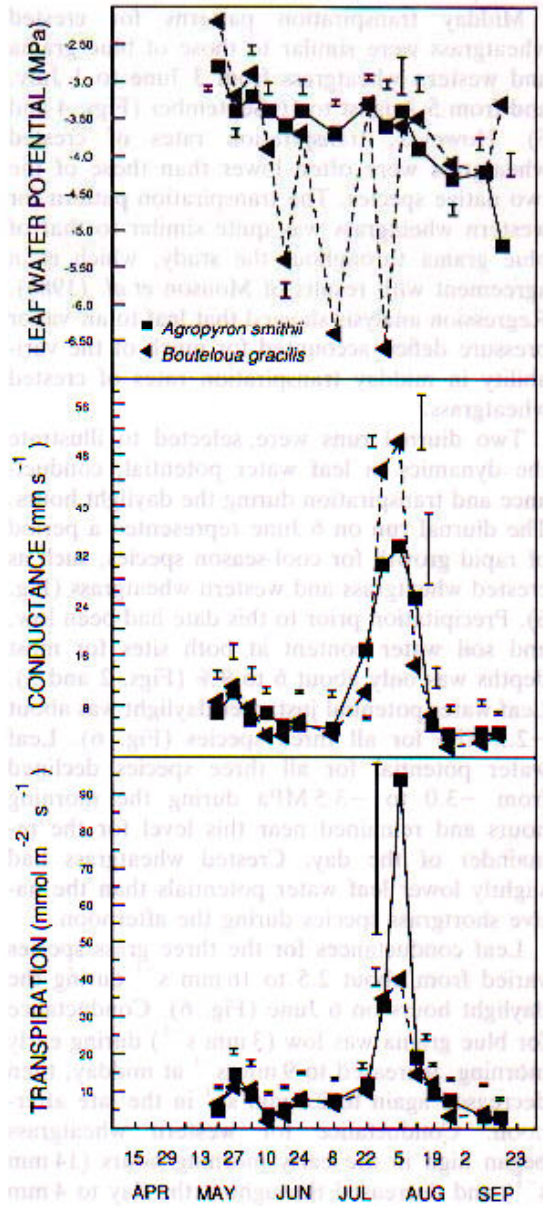


Fig. 5. Midday leaf water potential, midday leaf conductance, and midday transpiration rates for blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*) during the 1985 growing season. Bars adjacent to means represent the maximum standard error for means on that date.

ductances or transpiration than were midday leaf water potentials (DeLucia *et al.*, 1988).

Midday transpiration patterns for crested wheatgrass were similar to those of blue grama and western wheatgrass from 3 June to 1 July, and from 5 August to 16 September (Figs. 4 and 5). However, transpiration rates of crested wheatgrass were often lower than those of the two native species. The transpiration pattern for western wheatgrass was quite similar to that of blue grama throughout the study, which is in agreement with results of Monson *et al.* (1986). Regression analysis showed that leaf to air vapor pressure deficit accounted for much of the variability in midday transpiration rates of crested wheatgrass.

Two diurnal runs were selected to illustrate the dynamics in leaf water potential, conductance and transpiration during the daylight hours. The diurnal run on 6 June represented a period of rapid growth for cool-season species, such as crested wheatgrass and western wheatgrass (Fig. 6). Precipitation prior to this date had been low, and soil water content at both sites for most depths was only about 6 to 9% (Figs. 2 and 3). Leaf water potential just after daylight was about -2.5 MPa for all three species (Fig. 6). Leaf water potential for all three species declined from -3.0 to -3.5 MPa during the morning hours and remained near this level for the remainder of the day. Crested wheatgrass had slightly lower leaf water potentials than the native shortgrass species during the afternoon.

Leaf conductances for the three grass species varied from about 2.5 to 16 mm s^{-1} during the daylight hours on 6 June (Fig. 6). Conductance for blue grama was low (3 mm s^{-1}) during early morning, increased to 9 mm s^{-1} at midday, then decreased again to 2.5 mm s^{-1} in the late afternoon. Conductance for western wheatgrass began high in the early morning hours (14 mm s^{-1}) and decreased throughout the day to 4 mm s^{-1} by late afternoon. Crested wheatgrass had leaf conductance values from 9 to 16 mm s^{-1} from daylight until noon; then conductance declined to 5 to 7 mm s^{-1} during the afternoon.

Diurnal transpiration rates of the three grass species were fairly similar (2.5 to 10 $\text{mmol m}^{-2} \text{s}^{-1}$) during the morning hours, but crested wheatgrass transpiration rate increased to

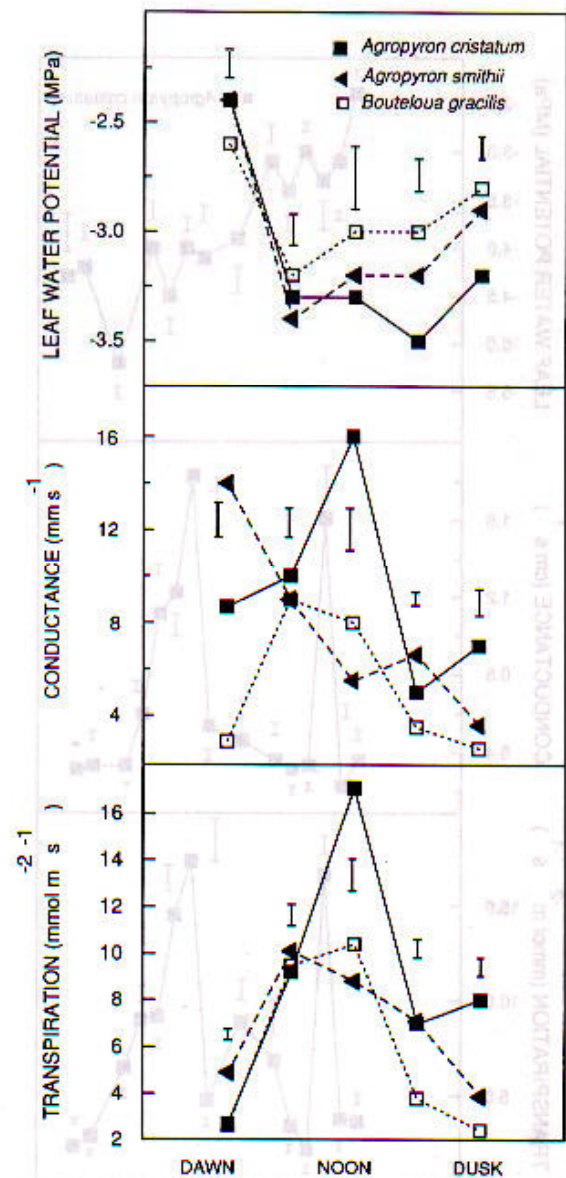


Fig. 6. Diurnal trends in leaf water potential, conductance, and transpiration rates for crested wheatgrass (AGCR), western wheatgrass (AGSM), and blue grama (BOGR) on 6 June 1985. Bars adjacent to means represent the maximum standard error for means at that time.

17 $\text{mmol m}^{-2} \text{s}^{-1}$ by noon (Fig. 6). By midday, transpiration rates for blue grama and western wheatgrass had leveled off at about 9 to 10 $\text{mmol m}^{-2} \text{s}^{-1}$. Transpiration rates for crested wheat-

grass remained higher than those of blue grama during the afternoon.

The diurnal run of 13 August (Fig. 7) was a time of warm and moist condition for plant growth. Air temperatures were high, but signifi-

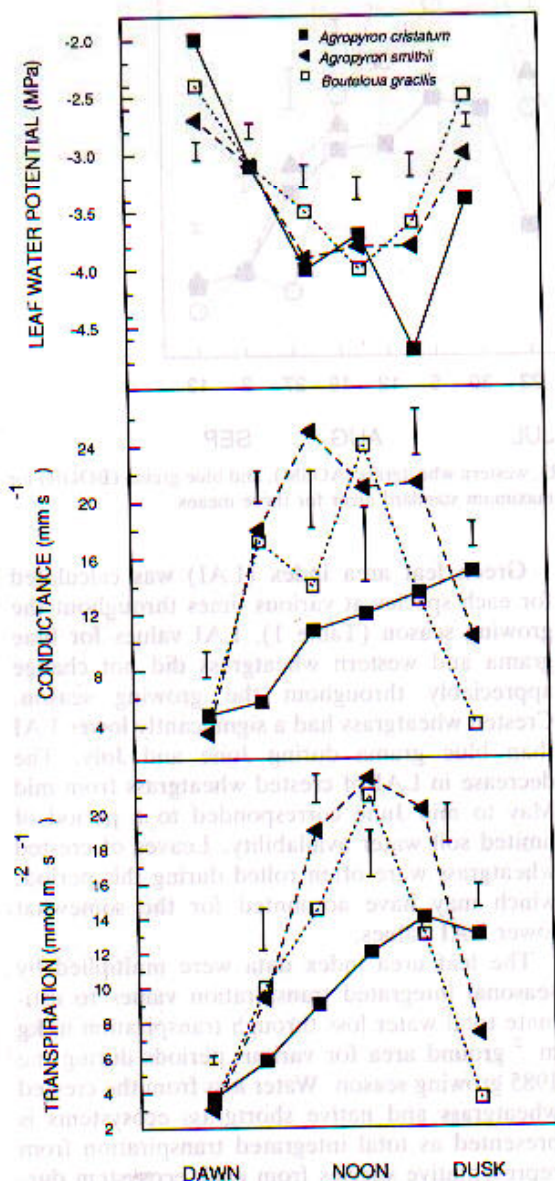


Fig. 7. Diurnal trends in leaf water potential, conductance, and transpiration rates for crested wheatgrass (AGCR), western wheatgrass (AGSM), and blue grama (BOGR) on 13 August 1985. Bars adjacent to means represent the maximum standard error for means at that time.

cant rainfall in late July and August had re-wetted the 0- to 20-cm soil depth. Leaf water potentials for all three grasses were about -2.0 to -2.8 MPa at daylight (Fig. 7). The leaf water potentials declined to about -4.0 MPa at mid-day. Thereafter, the native species (blue grama and western wheatgrass) exhibited some recovery in leaf water potential during late afternoon. However, leaf water potential remained low (-3.6 to -4.7 MPa) for crested wheatgrass throughout the afternoon.

Leaf conductance for the three grasses was about 44 mm s^{-1} in the early morning hours of 13 August (Fig. 7). These conductances increased to about 24 mm s^{-1} during the middle of the day for the two native grasses. Leaf conductance of blue grama and western wheatgrass then decreased during the late afternoon hours. Conductance for crested wheatgrass remained slightly lower than that of the two native species during the middle part of the daylight period.

Transpiration rates for all three grasses during early morning hours on 13 August were quite similar to those observed on 6 June, about 3 to $5 \text{ mmol m}^{-2} \text{ s}^{-1}$. Transpiration rates of blue grama and western wheatgrass increased to 20 – $22 \text{ mmol m}^{-2} \text{ s}^{-1}$ by early afternoon (Fig. 7). Although transpiration rates for crested wheatgrass also increased throughout the period, these rates were only about 30 to 60% of those of the native grasses during the mid morning to mid afternoon period. Leaf conductances for the native species decreased in the late afternoon, and transpiration rates declined; but conductance for crested wheatgrass remained high, and transpiration rates remained higher in the late afternoon.

Diurnal transpiration rates

Stepwise multiple regression analysis was used to determine importance of three independent variables associated with diurnal transpiration rates of each species throughout the 1985 growing season. Data were taken on seven days between 22 May and 3 September when transpiration was measured at four or more times throughout the daylight period. Leaf to air vapor pressure deficit was the most important variable accounting for variation in diurnal transpiration rates of the grasses. As expected, quantum flux density and

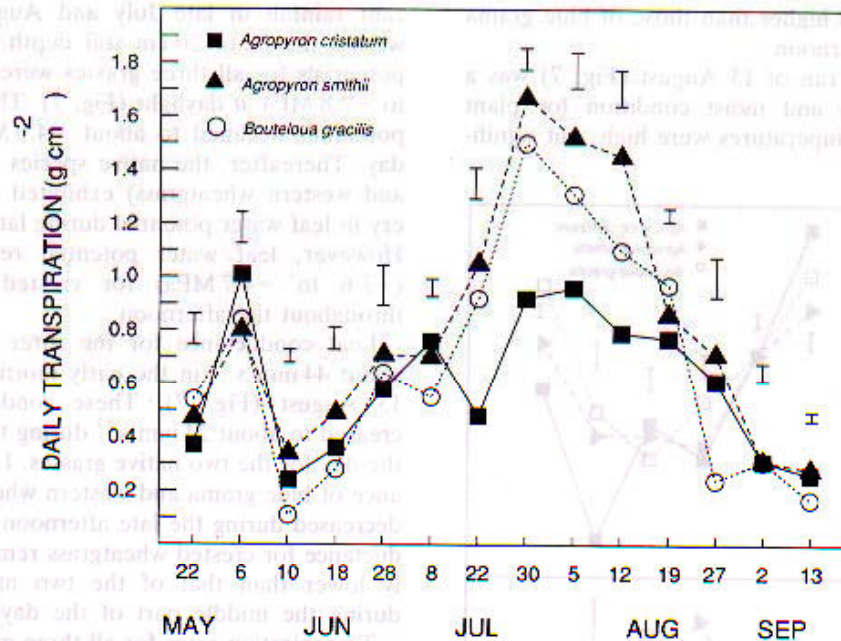


Fig. 8. Daily integrated transpiration for crested wheatgrass (AGCR), western wheatgrass (AGSM), and blue grama (BOGR) for the 1985 growing season. The bar above each set of means is the maximum standard error for those means.

midday leaf water potential usually only accounted for a small amount of the diurnal variation in transpiration rates of these grasses.

Integrated transpiration, water loss, and water use efficiency

We found that midday transpiration rates could be used as good predictors for total daily integrated transpiration throughout the daylight period ($r^2 = .74$ to $.89$). We then utilized our complete data set of midday transpiration rates for each species to estimate daily integrated transpiration throughout the 1985 growing season (Fig. 8). These data indicated that all three grasses lost similar quantities of water per cm^2 of leaf area during the spring and early summer. By late July, however, transpirational losses for crested wheatgrass leveled off; whereas, those for blue grama and western wheatgrass continued to increase to 1.5 to 1.7 g cm^{-2} or almost twice that of crested wheatgrass. These levels of water loss remained higher than that for crested wheatgrass until 19 August, at which time rates among the three species became similar again.

Green leaf area index (LAI) was calculated for each species at various times throughout the growing season (Table 1). LAI values for blue grama and western wheatgrass did not change appreciably throughout the growing season. Crested wheatgrass had a significantly lower LAI than blue grama during June and July. The decrease in LAI of crested wheatgrass from mid May to mid June corresponded to a period of limited soil water availability. Leaves of crested wheatgrass were often rolled during this period, which may have accounted for the somewhat lower LAI values.

The leaf area index data were multiplied by seasonal integrated transpiration values to estimate total water loss through transpiration in kg m^{-2} ground area for various periods during the 1985 growing season. Water loss from the crested wheatgrass and native shortgrass ecosystems is presented as total integrated transpiration from representative species from each ecosystem during consecutive harvest periods (Table 2). Blue grama showed a significant increase in transpiration during each consecutive time interval in the growing season. However, the two wheatgrasses

Table 1. Leaf area index for crested wheatgrass, blue grama, and western wheatgrass during the 1985 growing season

Species	Sampling period			Mean
	16 May– 11 June	12 June– 9 July	10 July– 13 Sept.	
Crested wheatgrass	0.23a ^a	0.16b	0.19ab	0.19
Blue grama	0.19ab	0.22a	0.24a	0.22
Western wheatgrass	0.04c	0.03c	0.01c	0.03

^a Means in a row or column followed by a similar letter are not significantly different ($P > 0.05$).

showed increased transpiration only from the second to the third harvest period. Transpiration per unit of leaf area was found to be similar for blue grama and western wheatgrass throughout most of the study period (Fig. 8). Western wheatgrass had significantly less transpiring leaf surface (Table 1) and lower total water loss through transpiration than did the other two species.

Active growth takes place in the spring and early summer for many cool season (C_3) plants, and during the summer for warm season or C_4 species (Ode *et al.*, 1980). Phenological development of crested wheatgrass (C_3) was approximately three weeks ahead of development of most native C_4 grasses. Consequently, differences in water loss between blue grama (C_4) and crested wheatgrass observed during the first sampling period were a function of temporal differences in development of the two species (Table 2). Transpirational losses of water by blue grama during the remainder of the season equalled or exceeded that of crested wheatgrass (Fig. 8 and Table 2).

We assumed that actual evapotranspiration (AET) was approximately equal to precipitation

received during the growing season (Parton *et al.*, 1981) of 340 mm. Potential evapotranspiration of 670 mm for this area should be quite similar to that of shortgrass steppe in northeastern Colorado determined by Parton *et al.* (1981). The calculated AET to PET ratio of about 0.5 for our research area was, therefore, much greater than the 0.25 to 0.30 range calculated by Parton *et al.* (1981) for their shortgrass steppe study. This difference was caused largely by the greater amount of precipitation received in 1985 at the HPGRS site. Only about 45% of the growing season precipitation was lost through transpiration of crested wheatgrass in the introduced community; whereas, 65% of the precipitation was lost through transpiration of blue grama and western wheatgrass in the shortgrass community.

Total aboveground net primary production in 1985 was greater in the crested wheatgrass ecosystem than in the shortgrass steppe (Redente *et al.*, 1989). While the amount of water transpired showed an upward trend in both systems through the growing season, total net primary production decreased significantly through the later part of the growing season for

Table 2. Seasonal integrated transpiration (Kg m^{-2}) for crested wheatgrass, blue grama, and western wheatgrass during the 1985 growing season

Species	Sampling period			Mean
	16 May– 11 June	12 June– 9 July	10 July– 13 Sept.	
Crested wheatgrass	30.3b ^a	23.1b	101.7a	155.1
Blue grama	22.0c	27.5b	158.4a	207.9
Western wheatgrass	4.8b	5.2b	8.1a	18.1

^a Means in a row followed by the same letter are not significantly different ($P > 0.05$).

Table 3. Water-use efficiency (NPP/Transpiration) for crested wheatgrass, blue grama, and western wheatgrass during the 1985 growing season

Species	Sampling period			Mean
	16 May– 11 June	12 June– 9 July	10 July– 13 Sept.	
Crested wheatgrass	0.02a [*]	0.02a	0.0002b	0.008
Blue grama	0.03a	0.01a	0.0001b	0.004
Western wheatgrass	0.02a	0.01a	0.0001b	0.008

^{*} Means in a row or column followed by a similar letter are not significantly different ($P > 0.05$).

all species. Our results indicated that WUE was similar for all three species across the growing season, and decreased significantly from the second to the third harvest periods (Table 3). The general downward trend in WUE is explained by a decrease in total NPP (attributed to senescence) and an increase in rate of transpirational water loss as the growing season progressed. It is important to note that western wheatgrass was as efficient in water use as was crested wheatgrass, although western wheatgrass did not produce as much biomass.

Discussion

Plant productivity in semiarid grasslands largely depends on seasonal and yearly variations in water availability, which also affect the overall structure and function of ecosystems (Hyder *et al.*, 1975; Lauenroth *et al.*, 1978). When water is deficient, plant productivity and leaf persistence may depend upon the extensive root systems, water use efficiency, and survival of dehydration (Briske and Wilson, 1980; Clarke and Durley, 1981; Nobel, 1980). Changes in soil water provide indices of water use by vegetation (Eissenstat and Caldwell, 1988; Schlesinger *et al.*, 1987). Soil water reservoirs for plants vary with individual species according to their rooting patterns and mass (Caldwell, 1979; Caldwell and Richards, 1986). Soil water use near the plant normally shifts outward and downward as the season advances, and water use decreases sharply after vegetative growth is completed (Hainsworth and Aylmore, 1989; Sala *et al.*, 1981).

We found that seasonal integrated transpiration losses of water accounted for approximately

45% of the growing season precipitation in the crested wheatgrass ecosystem. In contrast, transpiration losses from the dominant two grasses in the native shortgrass steppe accounted for about 65% of the precipitation. These differences partially explain why more water was available at deeper soil depths in the crested wheatgrass community. Greater root mass at deeper soil depths in the native shortgrass community resulted in more complete soil water use. Crested wheatgrass had less live root biomass at deeper soil depths than did native shortgrass species (Redente *et al.*, 1989). Observed differences in soil water losses during the growing season in the crested wheatgrass and native shortgrass ecosystems were also expected because of phenological and morphological differences among major species of each system (DeLucia, 1988; Eissenstat and Caldwell, 1988; Houérou, 1984). Most active growth of crested wheatgrass occurs during the spring and fall when evaporative demand is minimal. Frank *et al.* (1985) found that earlier morphological development of crested wheatgrass resulted in higher WUE.

Estimates of community transpiration losses of water by scaling up from single-leaf measurements made with a porometer are often inaccurate (Idso *et al.*, 1988; Jarvis and McNaughton, 1986). Transpiration rates may be overestimated by this method. However, in our grassland ecosystems, leaf area indices were always less than one, individual grass leaves were small, and wind velocities were usually greater than 2 m s^{-1} . Canopy resistance under these conditions should be very small. Therefore, leaf conductance becomes of paramount importance in estimating water vapor flux from the community (Massman and VanDijken, 1989). We believe that errors in

measurement of leaf conductance and transpiration (as indicated by the standard errors) were relatively small; whereas, those for LAI were much more important. Improvements in estimates of water vapor flux from semiarid grassland communities might best be accomplished by more frequent and accurate estimates of LAI.

Species with the C_4 photosynthetic pathway are often more efficient in the use of water than are C_3 species (Björkman, 1975; Hatch and Osmond, 1976). Fairbourn (1982) reported that blue grama had a higher water use efficiency (WUE) compared to western wheatgrass or to crested wheatgrass. Monson *et al.* (1986) also found a higher WUE for blue grama than western wheatgrass. Frank *et al.* (1985) found WUE was greater for crested wheatgrass than for western wheatgrass. However, water use efficiency was similar among all three species in our study, regardless of pathway type. This may have been caused by above normal precipitation during the latter part of the growing season and somewhat cooler temperatures.

Kramer (1983) suggested that the degree of plant water stress is probably best expressed in terms of water potential, as physiological and biochemical processes that control growth are often affected by plant water status. When adequate soil water is available and transpiration is retarded, the leaf, shoot, and soil water potential may reach an equilibrium with a small differential among the components (Caldwell and Richards, 1986; Ritchie and Hinkley, 1975). Thus, predawn xylem water potential can be related to the effective soil water potential (Fonteyn *et al.*, 1987). Sala *et al.* (1981) found a good correlation between predawn leaf water potential of blue grama with soil water potential of the wettest layer. As soils dried, predawn xylem water potential became less indicative of soil water potential, but did indicate the level of water stress at which the plant began each day. Leaf rolling in crested wheatgrass and lower transpiration rates indicated plant water stress during the droughty period in June when available soil water had largely been depleted. Both data from Sala *et al.* (1981) and our study indicated that leaf water potential of blue grama was related to effective soil water potential, which underscores the importance of root absorption

area. This present study indicated the importance of root biomass distribution to the availability of soil water in the profile.

Stomatal behavior and the related diffusion processes are important physiological factors that differ among various plant species. Kemp and Williams (1980) reported that rates of net photosynthesis of blue grama and western wheatgrass decreased exponentially with decreasing leaf water potential. Furthermore, they indicated that seasonal soil water gradients were not as important as seasonal air temperature gradients in niche separation between the two species. Sala *et al.* (1982) asserted that leaf water potential of blue grama was independent of leaf conductance, and closely followed the pattern of atmospheric water demand, while both leaf conductance and atmospheric water demand exerted control upon leaf water potential of western wheatgrass. In addition, blue grama was adapted to a scarce and highly variable water supply, and to a precipitation pattern in which small rainfall events constituted a large portion of total water input into the system. Western wheatgrass was adapted to frequent recharge of water in the soil profile, or to a less variable and more predictable water supply. In our study, midday transpiration for both crested wheatgrass and western wheatgrass was dependent upon leaf diffusive resistance and atmospheric water demand.

Leaves of crested wheatgrass rolled readily during periods of limited soil water availability, while blue grama leaves did not. Western wheatgrass showed limited leaf rolling caused by water stress throughout the study period. Leaf rolling is generally viewed as a measure to reduce radiation load and transpiration losses of water (Barnes, 1985; Parker, 1968; Redmann, 1985; Turner and Kramer, 1980). Morphological (Caldwell, 1987; Nobel, 1980; Yun and Taylor, 1986) and physiological characteristics (Schulze *et al.*, 1987) that maintain high internal water potential, lower transpirational losses, and greater allocation of carbon to aboveground components (Percy *et al.*, 1987) may give crested wheatgrass a competitive advantage over other species that show reduced allocation to aboveground structures, slower growth rates, and high transpirational losses of water. This helps to explain how monocultures of the highly competitive crested

wheatgrass have persisted within the shortgrass steppe environment. However, crested wheatgrass may not be as persistent in more arid areas of the shortgrass steppe because it cannot effectively use water resources available in the deeper soil profile. Native shortgrasses should be more competitive under these conditions.

Since crested wheatgrass completes its vegetative growth cycle by mid summer, we suggest that this species relies heavily upon soil profile recharge from winter and early spring precipitation for its growth. This, coupled with greater control of transpirational losses by crested wheatgrasses during the summer and less root mass in the deeper soil horizons, probably accounted for greater soil water reserves at deeper soil depths in the crested wheatgrass community. This reserve of soil water might then be available for fall regrowth of crested wheatgrass, given favorable environmental conditions and sufficient root growth at deep soil depths.

Different water use patterns by dominant species in the crested wheatgrass and native shortgrass communities imply different ecological strategies and suggest conditions that might favor one or another species. Wet, cool springs should favor crested wheatgrass; whereas, summertime thunderstorms might be more effectively used by native shortgrass species. This is probably reflected in the ease of establishment of crested wheatgrass in the northern portion of the shortgrass steppe, while crested wheatgrass stands in the southern portion of the shortgrass are not nearly as persistent (Hyder, Personal Communication, 1986). Spring use of surface soil water in the crested wheatgrass community should stress invading shortgrass species and increase the time required for succession to a shortgrass community.

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