

Evapotranspiration in a Prairie Ecosystem: Effects of Grazing by Cattle

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Accepted for publication in *Agronomy Journal*, 2001.

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ABSTRACT

Grazing by ungulates is common in grasslands and may influence evapotranspiration (ET). The Bowen ratio energy balance method was used to measure ET from grazed (GR) and ungrazed (UGR) tallgrass prairie in northeastern Kansas, USA. Yearling steers were stocked on the GR site from day of year (DOY) 128 to 202, 1999, and ET data were collected from DOY 141 to 295. Grazing reduced ET by 28% between DOY 179 and 207; mean ETs were 3.6 mm d⁻¹ (GR) and 5.0 mm d⁻¹ (UGR). During that period, leaf area index (LAI) averaged 78% lower on the GR site and below-normal precipitation kept soil dry near the surface; hence transpiration and evaporation of water from soil decreased. Lower ET during that period conserved soil water in the 0-0.30 m profile on the GR site. Prior to that (e.g., DOY 152 to 179), ET was similar between treatments despite an average 70% lower LAI on the GR compared with the UGR site. Above-normal precipitation during that period probably maintained high evaporation of water from soil, thereby compensating for reductions in transpiration (via LAI removal) on the GR site. Cumulative ETs during the 155-day study were estimated at 526 and 494 mm on the UGR and GR sites, respectively. Thus, grazing reduced seasonal ET by 6.1%. Late in the study, ET was higher on the GR site, despite a lower LAI compared with the UGR site. Younger leaves in regrowth after grazing resulted in delayed senescence, causing higher ET on the GR site.

Key words: Evapotranspiration; tallgrass prairie; grassland; energy balance; energy fluxes; Bowen ratio; latent heat flux;

Abbreviations: ET, evapotranspiration; PET, potential ET; DOY, day of year; GR, grazed; UGR, ungrazed; LAI, leaf area index; E, evaporation of water from the soil; T, transpiration; PAR, photosynthetically active radiation; R_n , net radiation; G , heat flux into the soil; LE , latent heat flux; H , sensible heat flux; BREB, Bowen ratio energy balance; β , Bowen ratio; θ_v , volumetric soil water content; γ , psychrometric constant; Δe , vapor pressure differential; ΔT , temperature differential; $R_{n,s}$, net radiation of soil; LE_s , latent heat flux of soil; H_s , sensible heat flux of soil; $R_{n,c}$, net radiation of canopy; LE_c , latent heat flux of canopy; H_c , sensible heat flux of canopy; β_s , β of soil component; β_c , β of canopy.

Predicting the impact of land management on the hydrology of agricultural and natural ecosystems will become essential as public demand for water increases (Reisner, 1993; Biswas, 1998). In native grasslands, evapotranspiration (ET) is the major form of water loss (Branson et al., 1981; Parton et al., 1981; Frank and Inouye, 1994). Grazing by cattle (*Bos taurus*), which is common in grasslands, may affect transpiration (T) and evaporation of water from soil (E) by removing significant amounts of vegetation and altering the microclimate of the surface (Whitman, 1971; Svejcar and Christiansen, 1987; Wraith et al., 1987). Therefore, land-management decisions about grazing potentially may affect the water balance of large areal regions.

In grasslands, the most important climatic variable in determining ecosystem structure, function, and productivity is the balance between precipitation and ET (Stephenson, 1990; Burke et al., 1991; Frank and Inouye, 1994). However, a recent review of ET from grasslands and forests found that few canopy-scale ET data were available from grasslands (Kelliher et al., 1993). Even fewer ET data are available from grazed prairies, despite the historical importance and widespread presence of grazing around the globe (Stebbins, 1981; Axelrod, 1985; Coughenour 1985; McNaughton, 1985).

In a grassland near the present study, during the First International Satellite Land Surface Climatology Project (ISLSCP) Field Experiment (FIFE), ET was found to be similar between grazed and ungrazed sites despite large differences in green leaf area index (LAI) (Stewart and Verma, 1992). Other studies during FIFE, although not necessarily comparisons between grazed and ungrazed prairie *per se*, reported that intersite differences in ET showed no significant correlation with LAI (Shuttleworth et al., 1989). However, a recent study at the same location used for FIFE reported that greater LAI caused higher ET rates from a burned site compared

with an unburned site (both ungrazed)(Bremer and Ham, 1999). In a grassland heavily grazed by prairie dogs, ET was lower than on an adjacent, lightly grazed area (Day and Detling, 1994). In the latter study, ET became higher on the heavily grazed site than on the lightly grazed site as soil water became limiting, suggesting that lower ET early in the season had conserved soil water on the heavily grazed site.

Grazing, via removal of green leaf area, affects ET by several mechanisms (Fig. 1). Defoliation reduces the amount of irradiance intercepted by the canopy, thereby decreasing the amount of energy partitioned to leaves and, hence, to transpiration (i.e., decreased T). Conversely, irradiance at the soil surface increases after grazing, thereby raising soil temperature (Whitman, 1971; Bremer et al., 1998) and increasing E. Therefore, grazing alters the partitioning of energy between the canopy and the soil, making less available for T and more available for E.

Other mechanisms affected by grazing include the aerodynamic resistance to water vapor transport from the soil, which likely is reduced by higher wind speeds at the soil surface (Ham and Heilman, 1991); this may cause E to increase. Also, canopy resistance to water vapor transport (r_c) generally has an inverse relationship with LAI (Kim and Verma, 1991; Loomis and Conner, 1992); therefore, grazing causes an increase in r_c . In smooth canopies, a reduction in canopy height (e.g., after grazing) also increases the aerodynamic resistance to water vapor transport from the canopy (r_a). However, in areas grazed by cattle and other large herbivores, vegetation is often patchy (Fahnestock and Knapp, 1993; Owensby, 1997), which may increase turbulence in the remaining canopy and offset the increase in r_a . Nevertheless, Stewart and Verma (1992) found r_a to be higher in a grazed prairie than in an ungrazed prairie.

Leaf age also may become more important as the growing season progresses. Younger leaves in regrowth of grazed prairie may have improved leaf water status; lower stomatal and

canopy resistances to water vapor transport; and, consequently, higher transpiration per unit leaf area (Coughenour, 1985; McNaughton, 1983, 1985; Archer and Detling, 1986; Svejcar and Christiansen, 1987; Wraith et al., 1987). The differences in effects of leaf age on canopy-scale ET between grazed and ungrazed prairies would likely become more pronounced late in the growing season.

The effects of grazing on E and T can impact soil water content and seasonal water use. In some instances, grazing has conserved soil water content (Svejcar and Christiansen, 1987; Wraith et al., 1987; Naeth and Chanasyk, 1995), although at other times, grazing had no effect (Coronato and Bertiller, 1996) and even caused reductions in soil water content (Whitman, 1971; Daddy et al., 1988; Naeth et al., 1991). Presumably, reductions in T after grazing can result in conservation of soil water (Parton and Risser, 1980; Day and Detling, 1994), although removal of vegetation can decrease infiltration and, consequently, reduce soil water content in some cases (Bohn and Buckhouse, 1985; Abdel-Magid et al., 1987; Thurow et al., 1988).

Grazing also can alter other variables that affect ET but are not listed in Fig. 1, such as precipitation intercepted by the canopy and dew formation (Couturier and Ripley, 1973; Dunin and Reyenga, 1978; Branson, et al., 1981). However, in the interest of simplicity, we included only the mechanisms that likely have the greatest impacts on ET in grasslands over the course of the growing season.

The objectives of this study were to measure the surface energy balance and ET and to estimate cumulative ET during the growing season from adjacent areas of grazed and ungrazed tallgrass prairie. Data were collected during a 155-day period that began shortly after cattle were stocked on the grazed site and continued past the vegetational regrowth stage, after the cattle were removed. Supporting measurements of green LAI, aboveground biomass, intercepted PAR,

soil temperature, soil water content, and reflected shortwave irradiance (albedo) were used to interpret seasonal trends in the energy balance.

MATERIALS AND METHODS

Study site

This study was conducted from May to October, 1999 on the Rannells Flint Hills Prairie Preserve (39° 08' N. 96° 32' W, ~340 m above mean sea level), 5 km south of Manhattan, KS, USA. Vegetation at the site was tallgrass prairie dominated by the C₄ grasses big bluestem (*Andropogon gerardii* Vitman), little bluestem (*A. scoparius* Michx.), and indiagrass (*Sorghastrum nutans* (L.) Nash). Soils were silty clay loams (Benfield series: Fine, mixed, mesic Udic Argiustolls), with depths to shale and limestone fragments ranging from 0 (surface) to 1.0 m. The upper 30 cm of the soil profile had a range of bulk densities from 1.0 to 1.27 g cm⁻³, which were determined from volumetric samples (4.8 cm dia x 5.0 cm). The 30-yr average annual precipitation was 859 mm.

Data were collected from two adjacent, expansive, upland watersheds, with one representing a grazed (GR) treatment and the other an ungrazed (UGR) treatment. Yearling steers (248 kg steer⁻¹) were placed on the GR site on 8 May (day of year [DOY] 128) and removed on 21 July (338 kg steer⁻¹; DOY 202) using an intensive-early stocking rate (0.81 ha steer⁻¹; Smith and Owensby, 1978). The UGR site had been ungrazed since 1997. Prior to that, both sites had been grazed since the mid 1800's. Both sites had been burned annually for several decades. In the year of this study, both watersheds were burned on 19 April (DOY 109). One flux-measurement tower was located on each watershed; the tower on the GR site was located approximately 450 m west of that on the UGR site.

Measurements of energy fluxes

The surface energy balance at each site was measured using the Bowen ratio energy balance (BREB) method (Tanner, 1960) following the technique of Cellier and Olioso (1993). Differences in air temperature between 1.5 and 2.5 m above ground level were measured using shielded, fan-aspirated, copper-constantan thermocouples wired as a thermopile. Vapor pressure differences (Δe) were determined at the same heights using a vacuum sampler described by Ham and Knapp (1998) and Bremer and Ham (1999). Air was sampled continuously from each height at 0.5 liters min^{-1} through Excelon Bev-a-line IV tubing (Thermoplastic Processes, Inc., Stirling, NJ) with a 6.4-mm i.d. The inlet of each tube was located inside the fan-aspirated radiation shield used for air temperature measurement. Air samples were filtered (1 μm , Arco50, Gelman Sciences, Ann Arbor, MI) and routed to an environmental enclosure. To prevent condensation in the sample lines, tubing was enclosed in foam pipe insulation with a heat tape, which maintained air in the sample lines at a temperature above the dewpoint. Once inside the environmental enclosure, air samples traveled through 0.5-liter ballast tanks to reduce high frequency fluctuations in pressure and temperature. A relative humidity and temperature probe (HMP35A, Vaisala, Helsinki, Finland) attached to a sample chamber and connected to an automated valve system (Numatics, Inc., Highland, MI) was used to alternately measure the 1.5- and 2.5-m samples; measurements of Δe were obtained every 3 min. Because humidity samples from each height were not sampled simultaneously, data were corrected for the time-rate change in vapor pressure (Cellier and Olioso, 1993).

Net radiation (R_n) at each site was measured with a net radiometer (Q7, Radiation Energy Balance Systems, Seattle, WA) 2 m above the soil surface; the net radiometers were cross-

calibrated immediately before the study. To protect the instruments from damage by cattle, an electric fence was placed around the masts on the GR site. However, the net radiometer on the GR site extended out beyond the fence and over a grazed area. Soil heat flux (G) was measured with the combination method (Kimball and Jackson, 1979). At each site, four heat flux plates (HFT-3, Radiation Energy Balance Systems) were positioned parallel to the surface at a depth of 0.10 m. Soil temperature and the volumetric water content (θ_v) of the soil at 0.05, 0.10, and 0.30 m were measured automatically with dual-probe heat capacity sensors (Campbell et al., 1991; Tarara and Ham, 1997). Measurements of soil temperature were logged every 60 s, then averaged and recorded every 30 min, and θ_v was estimated one to four times daily. Soil heat flux plates and dual-probe sensors were placed along a 6-m transect that was located within 20 m of the towers at both sites.

On the GR site, no significant changes in topography or vegetation were observed within 600 m of the tower in the direction of the prevailing winds (i.e., south-southwesterly). Although topography was more broken on the UGR site, a minimum of 50 to 370 m of uniform relief extended from the tower in the direction of prevailing winds. As on the GR site, no significant changes in vegetation were observed within 600 m of the tower in the direction of prevailing winds. The BREB method can be used successfully at fetch-to-height ratios as low as 20:1 when β is small (Heilman et al., 1989), and fetch was sufficient on both the GR and UGR sites when winds were from the south and west.

Supporting measurements and data acquisition

Air temperature and relative humidity were measured at 2.5 m in the upper aspirated radiation shield with a temperature and humidity probe (HMP35A, Vaisala, Helsinki, Finland).

Wind speed and direction at each site were measured with a wind monitor (R.M. Young, Model 05103, Traverse City, MI) at a height of 3 m above ground level. Global irradiance was measured with a pyranometer (LI-200S, Li-cor, Inc., Lincoln, NE). All data acquisition and control at each location were accomplished with two microloggers and accessories (CR10x, AM25T, AREL-12, Campbell Scientific, Logan, UT). All sensors were logged at 1 Hz; averages and the energy balance were computed and stored at 30-min intervals. Precipitation was measured with a rain gauge on the UGR site (Sierra-Misco model 2501, Nova Lynx Corp., Gross Valley, CA).

Green LAI and aboveground biomass were determined at 2-week intervals from 18 May (DOY 138) to 30 Sept. (DOY 273), 1999. On each measurement date and at each site (i.e., GR and UGR), four 0.25 m² areas were harvested within 100 m of the flux-measurement towers. Green leaf area was measured with an area meter (LI-3100, Li-Cor, Lincoln, NE), and total aboveground biomass was determined gravimetrically after samples had been dried in a forced-air oven for 72 h at 55°C.

Intercepted PAR was measured at 1- to 4-week intervals, using a ceptometer lightbar (Sunfleck Ceptometer, Decagon Devices, Inc., Pullman, WA). On each measurement date, PAR was measured sequentially above the canopy and then below the canopy at the soil surface at 6 locations along a 100 m transect in both treatments (GR and UGR). Data were collected between 1000 and 1400 CST on clear days.

Albedo was measured using a pyranometer (8-48, Eppley Laboratories, Newport, RI) on the same dates and transects as intercepted PAR. Incoming and reflected irradiances were measured sequentially at each location along the transects with the same pyranometer; the height of the pyranometer was 1.2 m above ground level during measurements of reflected irradiance.

Energy balance definitions, data processing, and computed parameters

The energy balance for a thin layer at the surface is:

$$R_n - G = H + LE \quad [1]$$

where R_n is the net incoming radiation at the surface, G is the heat flux into the soil, and H and LE are the sensible and latent heat fluxes, respectively, into the atmosphere. The energy balance of the surface can be divided into its soil and canopy components. For example, the energy balance of the soil component of the surface is:

$$R_{n,s} - G = H_s + LE_s \quad [2]$$

where $R_{n,s}$, H_s , and LE_s are the net radiation and sensible and latent heat fluxes, respectively, of the soil. The energy balance of the canopy component of the surface is:

$$R_{n,c} = H_c + LE_c \quad [3]$$

where $R_{n,c}$, H_c , and LE_c are the net radiation and sensible and latent heat fluxes, respectively, of the canopy. Note that the total energy balance (Eq. 1) is the sum of the energy balances of the soil (Eq. 2) and canopy (Eq. 3)(Chin Choy and Kanemasu, 1974; Shuttleworth and Wallace, 1985; Ham and Heilman, 1991).

The Bowen ratio, $\beta (H/LE)$, was calculated in the traditional manner as $\gamma(\Delta T/\Delta e)$, where γ is the psychrometric constant and ΔT and Δe are the air temperature and vapor pressure differentials, respectively, between 1.5 and 2.5 m above ground level. Available energy (R_n-G) is the amount of energy available at the surface either to evaporate water (LE) or to heat the air above the surface (H). The evaporative fraction is defined as the ratio of latent heat flux to available energy ($LE/(R_n-G)$).

Certain data from the BREB system were rejected based on criteria described by Ohmura (1982), including periods near sunset and sunrise or during rain. Also, an electric fence around the instrumentation on the GR site resulted in a small ungrazed area to the north and east of the tower, thus limiting fetch in that direction. The close proximity of environmental enclosures to the north and east of the sensors also may have affected air temperature and humidity gradients from those directions. Therefore, data were rejected when winds were from the north and east.

Daily and seasonal evaporations were calculated using data from the BREB system. Missing sections of data were reconstructed using the concept of self preservation of the evaporative fraction and β as described by Crago and Brutsaert (1996). Those authors developed this concept from measurements obtained during FIFE at a site near the present study. This method estimates LE by using the measured available energy at the surface (R_n-G) and the evaporative fraction from another nearby day with good β data and similar θ_v . This approach proved reliable in a study by Bremer and Ham (1999); a similar approach was used by Holscher et al. (1997) in eastern Amazonia. In the present study, β were rejected on 99 entire days out of the 155-day period. Although this may sound excessive, note that in estimating ET, the evaporative fraction method did not model R_n-G , but rather modeled how R_n-G was partitioned between H and LE on certain days. We had confidence in the daily accuracy of R_n-G , which was measured *every day* during the study, but elected to use β data only when we had high confidence in the results. The evaporative fraction was typically highest after rain, then decreased steadily during the following days or weeks as the surface dried. Therefore, the evaporative fraction was similar from day to day given similar θ_v and could be relied on to estimate LE on intermittent days when the β data were rejected.

Cumulative seasonal evaporation was calculated from measured daytime LE plus an estimated nighttime LE , which was assumed to be 10% of total daily evaporation (Brutsaert and Sugita, 1992). Daytime potential evapotranspiration (PET; when R_n was positive), or the maximal amount of ET given a wet surface, was calculated by the Penman equation (Penman, 1948) using data from the BREB system. Aerodynamic conductance was estimated by an empirical relationship suggested by Thom and Oliver (1977) that used windspeed at known height (e.g., 3 m in this study), zero-plane displacement (d), and roughness length (z_M). The latter were estimated from empirical equations based on canopy height ($d=0.65 \times$ canopy height; $z_M=0.13 \times$ canopy height). The canopy height was assumed to increase linearly from 0 m immediately following fire (DOY 109) to 0.5 m by DOY 228.

A note on micrometeorological tower studies

One limitation of nearly all tower studies (e.g., Dugas and Mayeux, Jr., 1991; Stewart and Verma, 1992; Wofsy et al., 1993, Bremer and Ham, 1999) such as ours is the possibility that confounding site effects other than the designated treatment (e.g., grazing) may influence energy fluxes and ET. For example, variations in slope and aspect; soil depth, which affects water availability; and species composition all may impact ET (Nie et al., 1992; Stewart and Verma, 1992). After much evaluation, our two sites were chosen because they were adjacent, expansive, upland watersheds with deep soils and similar slopes and aspects. Slight differences in species composition between treatments (e.g., more C_3 forbs on the UGR site) were results of grazing, and, therefore, represented a normal factor when comparing ET between grazed and ungrazed prairies.

RESULTS AND DISCUSSION

Meteorological Conditions

Precipitation from May through October was 524 mm, which was 80 mm less than the 30-yr average for the same period. The driest months were July and October, with only 32 mm received in July and 2 mm in October; normal precipitation amounts for July and October were 83 and 78 mm, respectively. The highest average daytime vapor pressure deficit (2.58 kPa), PET (11.8 mm d⁻¹), and maximum air temperature (36.5°C) all occurred during July (Table 1). Only one minor frost occurred during the study (DOY 277; -0.4°C). Meteorological conditions for the entire study are listed in Table 1.

Canopy size, intercepted photosynthetically active radiation, albedo, and soil temperature

Green LAI and aboveground biomass were not significantly different between treatments early in the study (DOY 138; Fig. 2a and 2b). During the following six weeks (DOY 138 to 179), LAI and biomass increased rapidly on the UGR site. However, grazing slowed the increase in LAI and biomass on the GR site. Differences in canopy size were largest toward the end of and just after the grazing period, from DOY 179 to 207. During that time, green LAIs averaged 3.3 m² m⁻² on the UGR site and 0.7 m² m⁻² on the GR site. After the cattle were removed (DOY 202), LAI and aboveground biomass increased on the GR site as the vegetation regrew. By DOY 238, LAI had doubled on the GR site (LAI=1.5 m² m⁻²). On the same date, peak biomass was measured on both the UGR (0.637 kg m⁻²) and GR (0.238 kg m⁻²) sites. Late in the growing season, senescence caused green LAI to decline rapidly on the UGR site.

The pattern of intercepted PAR followed that of green LAI and aboveground biomass and illustrates the differences in canopy sizes (Fig. 2c). Intercepted PAR was the same between

treatments early in the study but became greater on the UGR site as its canopy grew in relation to the GR site. On the GR site, the period of rapid regrowth after the cattle were removed resulted in an increase in intercepted PAR. Higher green LAI and intercepted PAR indicated the potential for higher T on the UGR site early in the season (Fig. 1). However, differing leaf ages between treatments may cause green LAI and intercepted PAR to be less indicative of T late in the season.

Early in the study, albedo was low following the spring burn that exposed the dark soil surfaces on both sites (DOY 130-145)(Fig. 2d). Albedo increased steadily on both sites during the following weeks as lighter-colored leaves emerged and began to cover the soil. However, albedo gradually became greater on the UGR site as differences in canopy sizes increased (Fig. 2a). This was similar to findings of other studies that reported higher albedo with increased vegetational cover (Ritchie, 1971; Rosset et al., 1997). Not surprisingly, the greatest differences in albedo occurred when differences in the canopies also were the greatest (UGR=20.8% and GR=15.3%; DOY 195). The higher amount of exposed soil surface on the GR site was probably the largest contributor to the lower albedo, because optical properties of the soil are different than those of the canopy. The disparity in albedo between treatments illustrates that energy flows were affected by grazing and suggests that other variables in the energy balance (e.g., *LE*) also may be affected. By DOY 288, both canopies had senesced, and albedo was once again the same between treatments.

Soil temperature also was affected by the removal of vegetation (Fig. 3). Daytime soil temperatures (averaged between 0800 and 1730 CST), were similar between treatments early in the study but increased on the GR site as vegetation was removed by grazing. Maximum differences occurred near the end of and just after the grazing period. For example, between

DOY 190 and 210, soil temperatures at 0.05 m averaged 3.8°C higher on the GR site (30.7°C) than on the UGR site (26.9°C). Thereafter, regrowth on the GR site began to moderate differences between treatments. However, soil temperature generally remained higher on the GR site throughout the remainder of the study.

Energy fluxes and the Bowen ratio

Net radiation was not substantially different between treatments (Fig. 4a) despite differing amounts of shortwave energy absorbed by the surfaces during much of the study (Fig. 2d). Higher soil temperatures in the 0.05 m layer on the GR site (Fig. 3) probably caused greater emissions of longwave energy by the surface, thus, offsetting the higher shortwave absorptance. Early in the study, G , LE , and H also were similar between treatments, suggesting that no inherent differences in the energy balance existed between sites (Figs. 4b-4d). Energy fluxes remained similar between treatments even after significant differences in canopy sizes had developed (i.e., DOY 150-175; Figs 2a and 2b). However, G , LE , and H eventually were affected by the large disparities in canopy size and, as we will see later, by drier soils near the surface. In general, the largest differences in G , LE , and H occurred toward the end of and just after the grazing period (i.e., July; DOY 180-210) when differences in canopy sizes were greatest between treatments. For example, between DOY 190 and 210, G and H averaged 84 and 95% higher, respectively, and LE averaged 29% lower on the GR site than on the UGR site.

Although no differences in total R_n occurred between treatments, grazing strongly affected how R_n was partitioned between the soil ($R_{n,s}$) and the canopy ($R_{n,c}$). Specifically, the removal of leaf area by grazing increased the fraction of R_n partitioned to $R_{n,s}$. For example, the radiation reaching the soil surface ($R_{n,s}$) can be calculated as:

$$\frac{R_{n,s}}{R_n} = \exp(-\kappa LAI) \quad [4]$$

where κ is the extinction coefficient of the vegetation (Massman, 1992). Assuming $\kappa \cong 0.6$ and using values of LAI from our study (e.g., LAI of $0.7 \text{ m}^2 \text{ m}^{-2}$ on the GR site and $3.3 \text{ m}^2 \text{ m}^{-2}$ on UGR site), the ratios of $R_{n,s}$ to R_n were 0.657 on the GR site compared with 0.138 on the UGR site. Differences in $R_{n,s}$ and $R_{n,c}$ between treatments had a noticeable impact on G (Fig. 4b). However, G was a small component of the overall energy budget, and differences in the total available energy ($R_n - G$) between sites were subtle (Fig. 5). Nevertheless, $R_n - G$ was always larger on the UGR site, with the biggest differences occurring between DOY 195 and 220 when a fourfold difference in LAI occurred between treatments. Over the entire study, available energy was 88.5 MJ m^{-2} more at the UGR site than at the GR site. This would be equivalent to 36 mm of ET.

Grazing also affected the partitioning of $R_n - G$ between H and LE (Fig. 6). Early in the study, β was the same between treatments even after significant differences in LAI had developed (Fig 2a). For example, between DOY 150 and 165, β averaged 0.42 on both sites despite LAI being more than doubled on the UGR site. However, after DOY 165, β became greater on the GR site. Near the end of and just after the grazing period (DOY 190 to 210), β averaged 0.54 on the GR site and 0.20 on the UGR site, indicating that a higher fraction of $R_n - G$ was partitioned to H on the GR site.

The partitioning of $R_n - G$ between H and LE was dependent on the energy budgets of the soil and canopy components (Eqs. 2 and 3) and on soil water content near the surface. For example, on the GR site, defoliation decreased the contributions of H_c and LE_c to total H and LE (Eqs. 1 and 3), while increasing the contributions of H_s and LE_s (Eq. 2). Therefore, the β of the

soil component ($\beta_s; H_s/LE_s$) became more influential on the GR site, whereas the β of the canopy ($\beta_c; H_c/LE_c$) remained dominant on the UGR site. As long as soil water content near the surface was nonlimiting, the contribution of LE_s to total LE apparently offset the reduction in LE_c after defoliation on the GR site. This may explain why β , H , and LE were not substantially different between DOY 150 and 165 despite large differences in LAI (Figs. 2a, 4c, 4d, and 6). During that period, precipitation was above normal (Table 1), which maintained high θ_v near the surface (Figs. 7a and 7b). Stewart and Verma (1992) also found no significant differences in ET between grazed and ungrazed prairie with large differences in LAI when soil water was nonlimiting. During our study, however, precipitation was below normal during July (DOY 182 to 212), and the upper part of the profile became dry (Fig. 7a and 7b). Thus, β_s increased as more energy was partitioned to H_s and less to LE_s . Because β_s was more dominant on the GR site, this increase in β_s caused the total β to increase on the GR site (Fig. 6). On the UGR site, where β_c was more dominant, the larger canopy probably had access to water lower in the profile. This caused LE_c to remain relatively high, which lowered β_c and, consequently, lowered the total β on the UGR compared with the GR site during July.

After the cattle were removed, regrowth of vegetation on the GR site generally moderated differences in G , LE , and β (Figs. 4b, 4c, and 6), although G remained higher on the GR site for the remainder of the study. The rapid increase in β late in the study illustrates the effect of senescence on the partitioning of energy (Fig. 6). During senescence, grasslands shift from an LE - to an H -dominated system (Ham and Knapp, 1998). Despite a decrease in R_n , H increased during this transition (Figs. 4a and 4d). On the GR site, the transition to an H -dominated system occurred later and was more gradual than that on the UGR site. This was likely an effect of delayed senescence on the GR site, resulting from the younger leaves during

the regrowth after cattle were removed. Younger leaves and the subsequent delayed senescence on the GR site likely contributed to the lower H , higher LE , and lower β compared with the UGR site (Figs. 4c, 4d, and 6) late in the study.

Values of R_n , G , LE , and H from the GR and UGR sites during the study are reported in Table 2, which is provided for those who are interested in modeling ET based on the meteorological data given in Table 1.

Evapotranspiration and soil water content

Grazing reduced ET by an average of 28% near the end of and just after the grazing period (e.g., DOY 179 to 207), with daily reductions in ET as great as 40% (e.g., $2.45 \text{ mm d}^{-1} < \text{ET}$ on the UGR site)(Fig. 8a). During that period, LAI was 78% lower on the GR site (Fig. 2a), and below-normal precipitation limited evaporation of water from the soil surface. This is similar to the findings of Bremer and Ham (1999), where ET also was reduced on an unburned site when precipitation was below normal and green LAI was less than on an adjacent burned site. In the present study, the large divergence in ET between treatments near the end of the grazing period (e.g., DOY 179 to 207) clearly illustrates the impact that grazing, via changing canopy size, can have on the water balance in prairie.

The ETs converged between treatments after cattle were removed and significant regrowth had occurred on the GR site (e.g., DOY 215; Figs. 8a and 2a). Several days of cool, cloudy weather and precipitation occurred between DOY 212 and 216, which also may have minimized differences in ET between treatments during that period. Interestingly, ET was slightly higher on the GR site during several periods thereafter, despite the significantly lower green LAI. These periods occurred after significant rain and also near the end of the study, when

precipitation and soil water were limited (Fig. 8b; Table 1). Higher ET on the GR site after DOY 215 was likely an effect of younger leaves with higher transpiration rates (i.e., lower stomatal resistance), although increased E also may have contributed to the elevations in ET on the GR site after rain. Younger leaves on the GR site also were slower to senesce, which likely caused ET to be higher than on the UGR site during the final month of the study (DOY 275 to 295).

Grazing conserved soil water in the 0-0.3 m profile throughout much of the study (Fig. 8b). This is consistent with other studies that reported higher soil water content under clipped or grazed prairie (Owensby et al., 1970; Buckhouse and Coltharp, 1976; Svejcar and Christiansen, 1987; Wraith et al., 1987). The largest differences in θ_v occurred toward the end of and just after the grazing period, when differences in the canopy size and ET also were maximal (Figs. 2a and 8a). For example, from DOY 190 to 215, θ_v averaged 0.41 on the GR site compared with 0.32 on the UGR site. Near the end of the study the trend reversed, and θ_v became higher on the UGR site. This illustrates the impact of delayed senescence, higher ET, and possibly reduced infiltration on θ_v in grazed prairie late in the growing season.

The θ_v on the UGR site was depleted faster early in the growing season (DOY 150-160, Fig. 8b), when basically no differences in ET existed between treatments (Fig. 8a). The reduction in θ_v during this period may have been specific to the small area where soil-moisture sensors were placed and not representative of the much larger area of ET measurement. At the beginning of the study, heavy rain occurred immediately after installation of the soil-moisture sensors on the GR site but before installation on the UGR site. The small trench on the GR site that was cut for installation of the sensors was filled with water. Thus, equilibration of the probes with the surrounding soil may have taken up to 2 weeks, during which the water in the trench artificially inflated θ_v . Compounding this was a higher fraction of limestone fragments in the surface layer

on the UGR site, which may have reduced the water holding capacity in its 0-0.3 m profile. Thus, soil water in this profile may have been depleted faster on the UGR site given similar ET rates between treatments. Lower water-holding capacity in the 0-0.3 m profile also may explain why θ_v was lower on the UGR site between DOY 235 and 275, when similar or even lower ET rates on the UGR site might have been expected to equilibrate or conserve θ_v compared with the GR site.

Although reduced water-holding capacity may have contributed to lower θ_v on the UGR site during July (DOY 182-212), the primary cause was likely higher ET. Evidence for this is that the magnitudes of the differences in both ET and θ_v between treatments were much greater during July than at any other time in the study (Fig. 8b). The reduced water-holding capacity in the surface layer of the UGR site apparently did not limit canopy-scale ET either, probably because of deep soils. This was evident during July, when ET remained higher on the UGR site despite the significant depletion of soil water in the 0-0.3 m profile compared with the GR site (Figs. 8a and 8b). Soil water was removed much faster from the lower profile of the UGR site than the GR site during July (e.g., 0.30 m, Figs. 7a and 7b), indicating that plants on the UGR site used water from lower depths as soil water was depleted in the surface layer (Anderson, 1965). Conversely, the decline in θ_v at 0.30 m was slow on the GR site.

Cumulative evapotranspiration

Cumulative estimates of ET during the 155-day study, which were adjusted for nighttime ET, were 526 mm on the UGR site and 494 mm on the GR site. Therefore, the removal of green LAI by grazing and its subsequent effects on energy partitioning at the surface caused seasonal ET to decline by 6.1%. Most of the decrease in ET occurred near the end of and just after the

grazing period (i.e., July), when large differences in LAI between treatments and dry soil surfaces strongly impacted energy fluxes.

Year-to-year variations in climate may affect differences in cumulative ET between grazed and ungrazed prairies. In wet years when soil water is nonlimiting, ET may be similar between treatments (Stewart and Verma, 1992), resulting in little net difference in cumulative ET. However, in years with periodic moisture stress, the reduction in ET on grazed prairie may result in substantial reductions in seasonal ET similar to the present study. In dry years, the reduction in ET under grazing may conserve soil water that would then be available later in the growing season (Day and Detling, 1994). The effects of grazing on ET also may have implications for the carbon balance of the prairie, because water conservation under grazed prairie coupled with younger leaves late in the growing season may extend the photosynthetically active period. This would be similar to the effects of elevated CO₂ on this grassland, where CO₂-induced reductions in transpiration resulted in increased productivity in years with frequent water stress (Owensby et al., 1993, 1997, 1999). Therefore, the decrease in photosynthetic rates after defoliation in grazed prairie may be offset by improved water relations during dry periods. In a mixed-grass prairie, grazing affected photosynthetic rates and also increased soil carbon and nitrogen (LeCain et al., 1999; Schuman et al., 1999), suggesting that other factors in that grassland, such as ET, also may have been impacted by grazing.

CONCLUSIONS

Grazing reduced daily ET by up to 40% (2.45 mm d⁻¹) near the end of and just after the grazing period (i.e., DOY 180 to 210), when differences in green LAI were large and soil surfaces were dry. Reductions in T by defoliation, combined with minimal contribution of E

from the soil, caused the significant reductions in ET on the GR site during that period. In contrast, ET was similar between treatments just prior to this period (i.e., DOY 150 to 180), when differences in LAI also were significant but θ_v was high from above normal precipitation, hence, E from the soil was increased. After cattle were removed and significant regrowth had occurred on the GR site, ET converged between treatments despite remaining and significant differences in green LAI. Younger leaves in regrowth on the GR site likely had lower stomatal resistance and, thus, higher transpiration per unit leaf area compared with their counterparts on the UGR site. Younger leaves on the GR site also senesced later, resulting in higher ET compared with the UGR site during the final month of the study (DOY 275 to 295). Cumulative ET during the study was reduced 6.1% by grazing. Lower ET under grazing may have implications for the hydrology of watersheds, although further research is required for longer time periods and measuring other components of the water balance besides ET (e.g., deep percolation, runoff, soil water storage) to determine the effect of grazing on hydrology. In addition, climate change may increase aridity in some areas (Chaves and Pereira, 1992), accentuating the need to accurately predict ET in grasslands under various forms of land management such as grazing.

ACKNOWLEDGEMENTS

Research was funded by the Kansas Agricultural Experiment Station and the Rannells Flint Hills Prairie Preserve. Salary for first author was provided by grants from the National Aeronautics and Space Administration's (NASA's) Land Cover Land Use Change (LCLUC) Program and the Long Term Ecological Research (LTER) Program of the National Science Foundation (NSF). The technical assistance of Fred Caldwell was appreciated.

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Figure 1. Conceptual model illustrating the effect of grazing on evapotranspiration.

Figure 2. Seasonal patterns in green leaf area index (LAI) (a), aboveground biomass production (b), intercepted photosynthetically active radiation (PAR)(c), and albedo (d) on grazed and ungrazed prairie sites. Vertical bars indicate ± 1 standard error (LAI and biomass: $n=4$; intercepted PAR and albedo: $n=6$). In some cases, error bars are smaller than symbols. Measurements of intercepted PAR and albedo were taken near midday. Data points are connected with lines to aid in interpreting the graphs and are not meant to represent values between observations.

Figure 3. Seasonal patterns of daytime soil temperature (averaged between 0800 to 1730 CST) at 0.05 m on grazed and ungrazed prairie sites. Data are presented in 5-day averages to show seasonal trends.

Figure 4. Seasonal patterns in net radiation (R_n ; a), heat flux into the soil (G ; b), latent heat flux into the atmosphere (LE ; c), and sensible heat flux into the atmosphere (H ; d) from grazed and ungrazed sites. Data are presented in 5-day averages to show seasonal trends. The scale of the y-axis is different for each figure.

Figure 5. Seasonal patterns in available energy at the surfaces (R_n+G) of grazed and ungrazed prairie sites. Data are presented in 5-day averages to show seasonal trends.

Figure 6. Seasonal patterns in the Bowen ratio on grazed and ungrazed prairie sites. Data are presented in 5-day averages to show seasonal trends.

Figure 7. Seasonal patterns in volumetric soil water content at 0.05, 0.10, and 0.30 m depths for grazed (a) and ungrazed (b) prairie sites. Data are presented in 5-day averages.

Figure 8. Seasonal patterns in daytime evapotranspiration (when net radiation was positive)(a) and in volumetric soil water content for the 0-0.30 m profile and precipitation (b) from grazed and ungrazed prairie sites. Data are presented in 5-day averages to show seasonal trends.

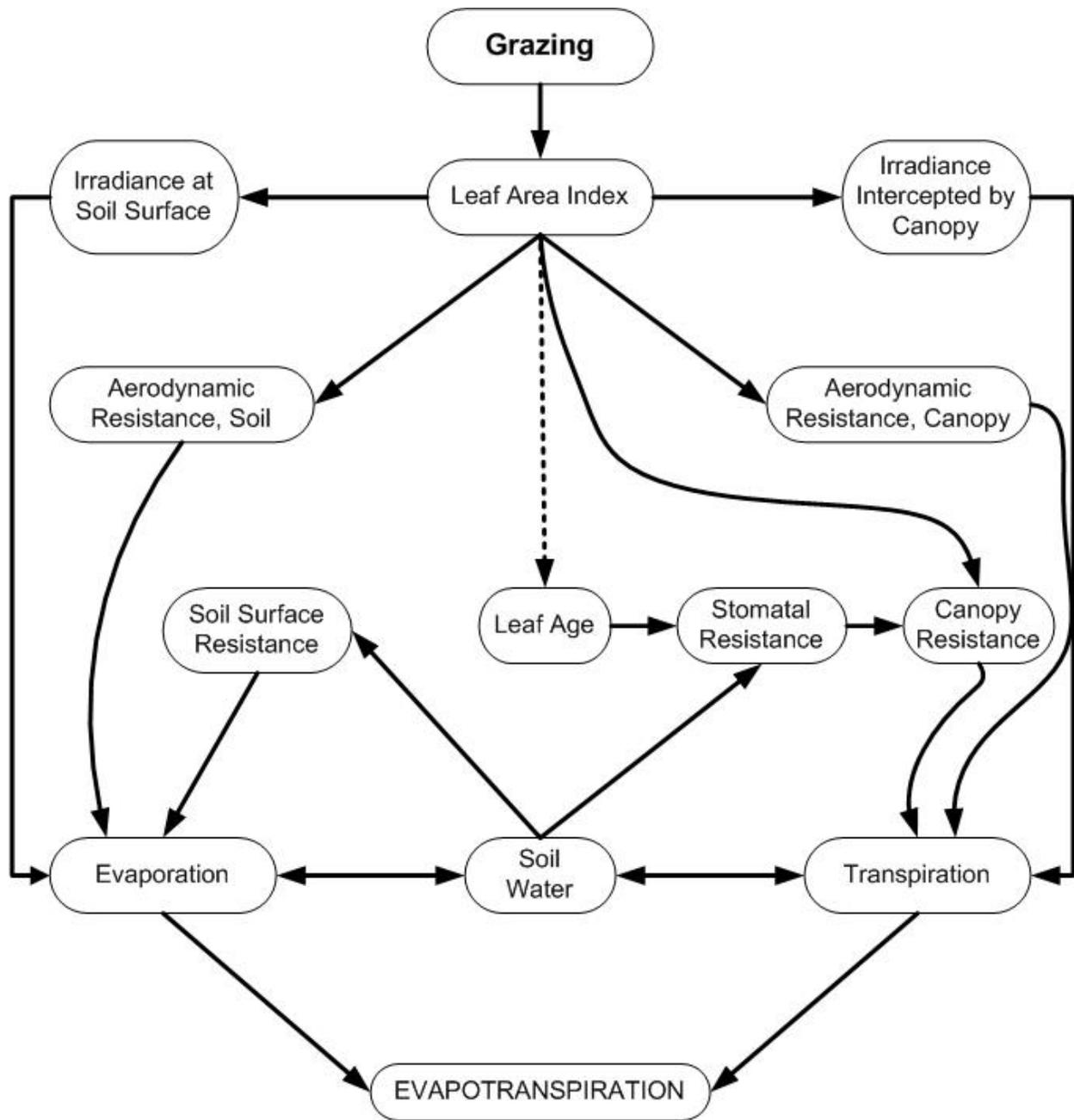


Figure 1

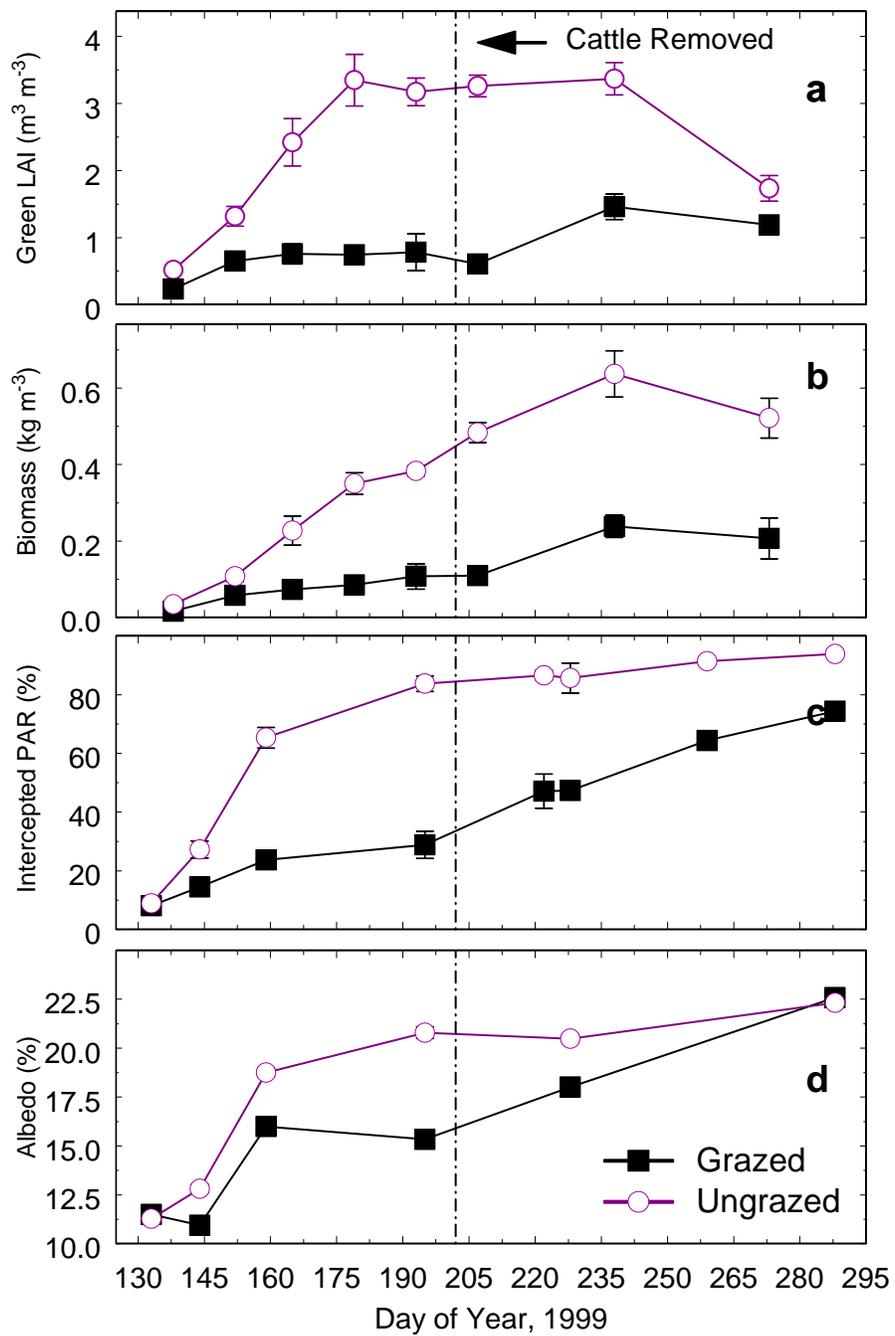


Figure 2

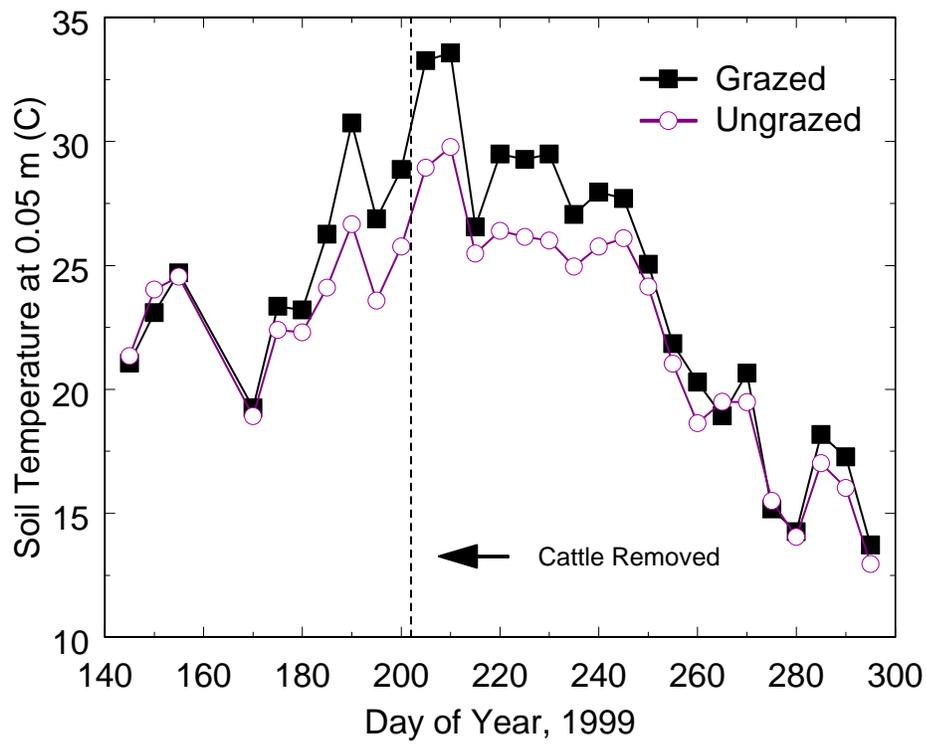


Figure 3

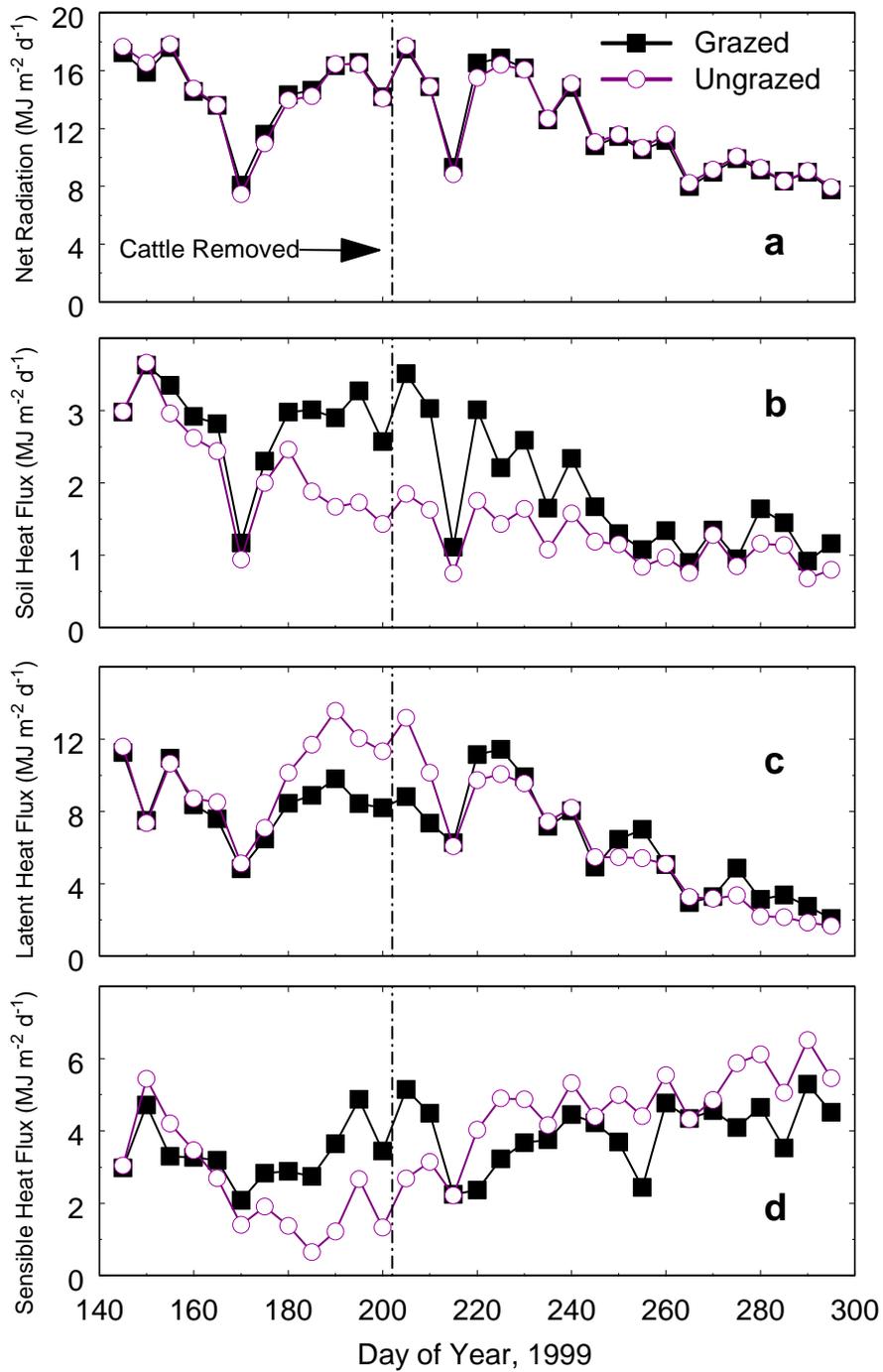


Figure 4

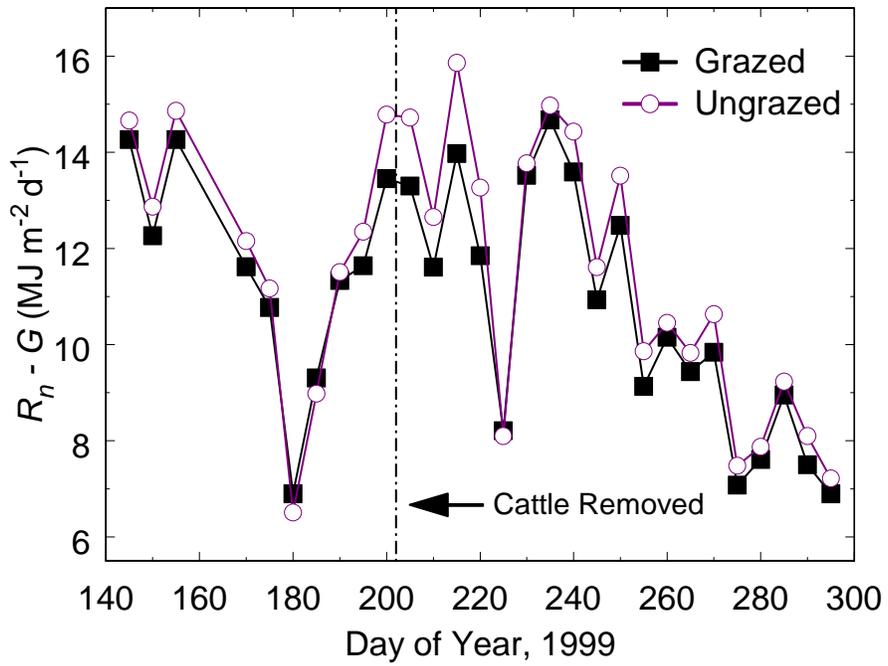


Figure 5

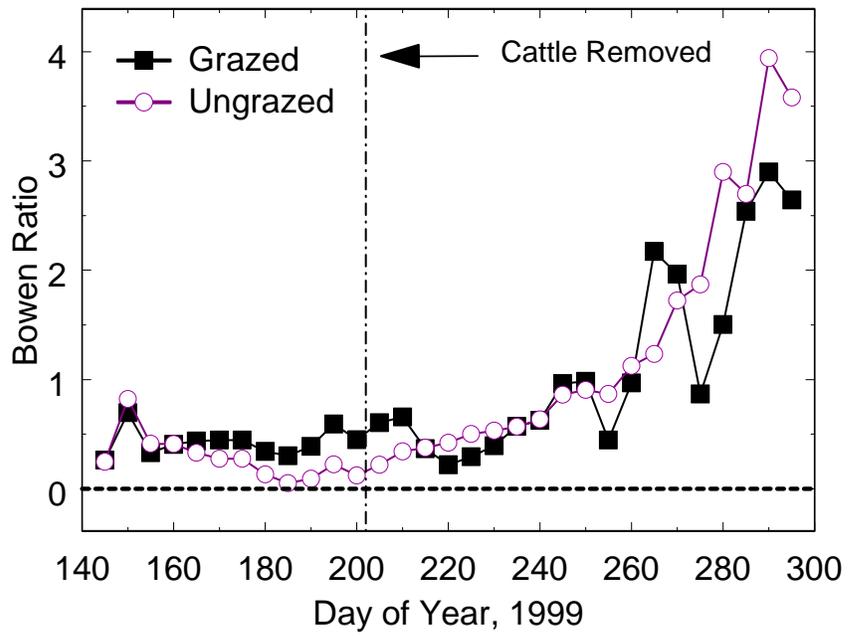


Figure 6

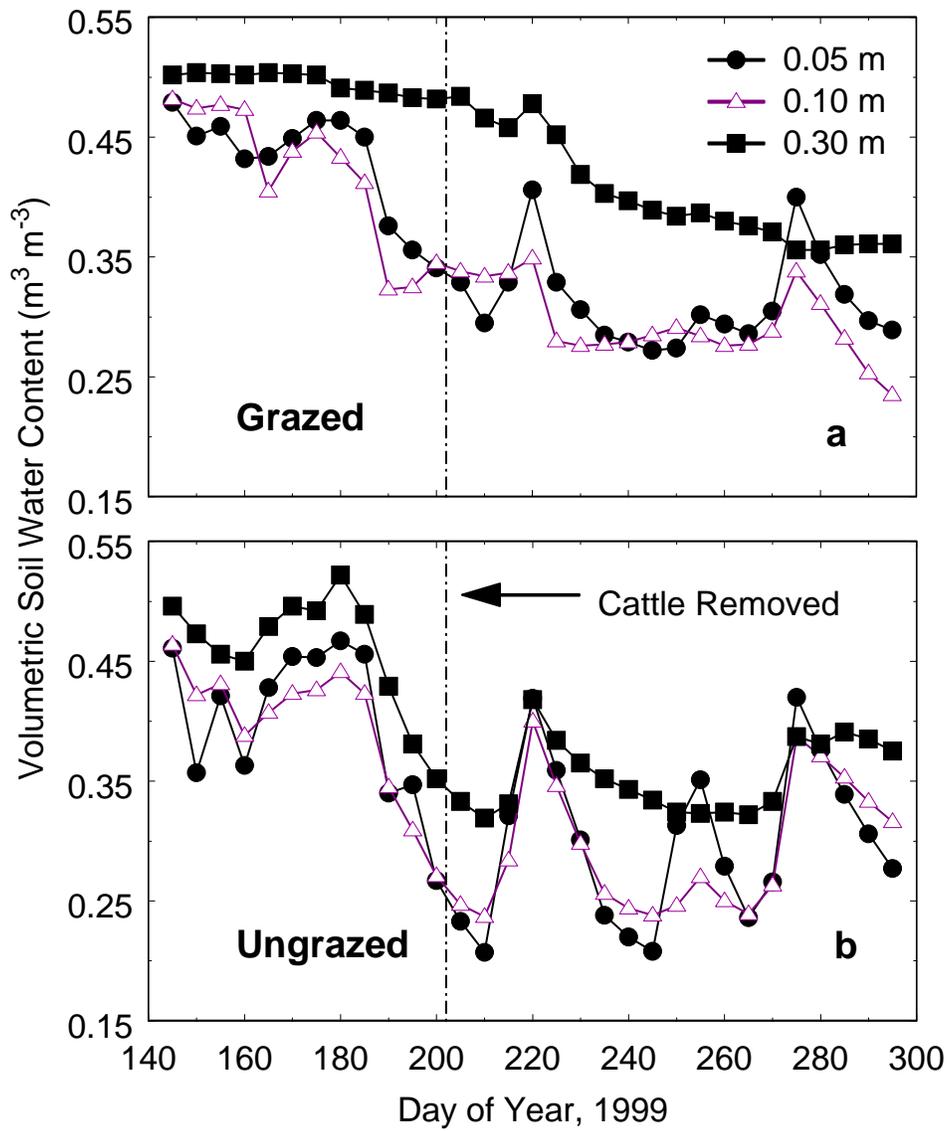


Figure 7

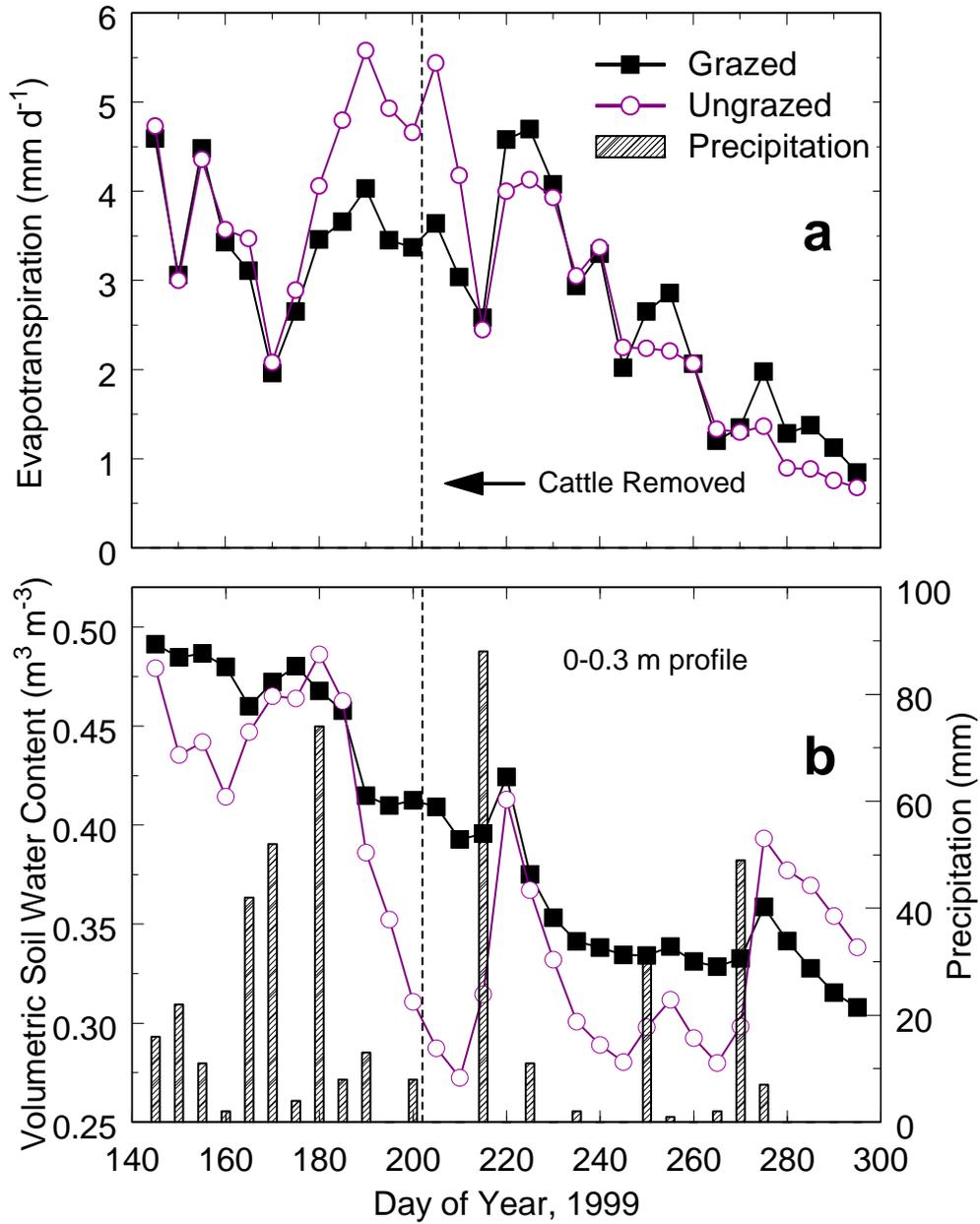


Figure 8

Table 1. Daily maximum and minimum air temperatures (T_{\max} and T_{\min} , respectively); average windspeed (wind; 24 h); total global irradiance (R_s); precipitation (precip; daily average); average vapor pressure deficit (VPD; when net radiation was positive); and potential evapotranspiration (PET; when net radiation was positive) during the study [day of year (DOY) 141 to 295, 1999]. Data are presented as 5-day averages.

DOY	T_{\max}	T_{\min}	wind	R_s	precip	VPD	PET
1999	———C———		m s^{-1}	$\text{MJ m}^{-2} \text{d}^{-1}$	mm	kPa	mm d^{-1}
145	22.6	14.2	3.97	25.67	3.2	1.01	7.21
150	24.6	13.5	3.16	25.81	4.4	1.22	6.53
155	26.1	16.5	4.63	25.97	2.2	0.73	6.67
160	29.0	20.9	6.98	22.45	0.4	1.00	7.64
165	25.1	16.9	3.29	20.76	8.4	0.75	5.48
170	19.5	12.3	3.71	12.06	10.4	0.42	3.23
175	25.9	18.6	3.72	15.84	0.8	0.50	4.38
180	26.2	17.7	4.13	20.27	14.8	0.65	5.76
185	28.6	20.4	6.02	20.62	1.6	0.81	7.68
190	30.4	20.3	4.85	23.65	2.6	1.17	8.88
195	26.5	16.3	3.87	24.46	0.0	1.17	8.74
200	30.5	22.1	5.40	18.65	1.6	1.22	9.06
205	34.3	24.6	4.99	22.80	0.0	2.05	11.80
210	36.5	24.8	4.36	20.21	0.0	2.58	11.69
215	27.4	20.6	4.67	11.81	17.6	0.86	5.48
220	29.9	20.2	3.28	21.00	0.0	1.18	8.06
225	30.0	19.9	4.42	22.24	2.2	1.42	9.78
230	32.0	19.8	3.90	22.08	0.0	1.73	10.47
235	28.1	17.1	2.82	17.83	0.4	1.24	7.58
240	31.5	17.8	3.09	20.77	0.0	1.78	9.66
245	32.1	20.7	3.71	15.34	0.0	1.90	9.36
250	29.2	17.8	3.78	15.75	6.4	1.13	7.18
255	23.9	13.5	2.91	14.75	0.2	1.02	6.49
260	21.7	10.7	2.59	16.46	0.0	1.16	7.27
265	20.0	9.5	3.36	11.80	0.4	0.65	4.73
270	24.6	12.7	4.96	12.91	9.8	1.26	7.16
275	18.5	7.4	4.19	14.56	1.4	0.63	5.87
280	20.1	6.4	4.31	13.75	0.0	0.99	7.02
285	25.2	12.8	3.86	12.76	0.0	1.34	7.17
290	21.3	8.6	5.25	14.16	0.0	1.39	9.67
295	19.1	4.8	3.90	13.17	0.0	1.27	8.31

Table 2. Average daytime [when net radiation (R_n) was positive] values of R_n , soil heat flux (G), latent heat flux (LE), and sensible heat flux (H) during the study [day of year (DOY) 141 to 295, 1999]. Data are presented as 5-d averages from grazed (GR) and ungrazed (UGR) prairie.

DOY	R_n		G		LE		H		
	GR	UGR	GR	UGR	GR	UGR	GR	UGR	
1999	MJ m ⁻² d ⁻¹								
145	17.24	17.64	2.98	2.99	11.26	11.59	2.98	3.04	
150	15.89	16.53	3.63	3.66	7.50	7.35	4.72	5.44	
155	17.61	17.82	3.35	2.96	10.94	10.65	3.30	4.20	
160	14.55	14.77	2.92	2.62	8.36	8.70	3.27	3.46	
165	13.59	13.62	2.82	2.44	7.60	8.50	3.19	2.69	
170	8.07	7.45	1.17	0.94	4.82	5.11	2.08	1.40	
175	11.61	10.97	2.30	2.00	6.48	7.07	2.83	1.91	
180	14.32	13.96	2.98	2.46	8.45	10.14	2.89	1.37	
185	14.65	14.23	3.01	1.88	8.90	11.70	2.74	0.65	
190	16.34	16.45	2.90	1.67	9.80	13.57	3.65	1.22	
195	16.58	16.44	3.27	1.73	8.44	12.04	4.87	2.67	
200	14.18	14.08	2.57	1.43	8.20	11.32	3.44	1.33	
205	17.48	17.71	3.51	1.85	8.82	13.18	5.15	2.68	
210	14.88	14.89	3.03	1.63	7.36	10.13	4.49	3.14	
215	9.32	8.84	1.11	0.75	6.28	6.08	2.24	2.22	
220	16.52	15.52	3.01	1.75	11.15	9.74	2.36	4.03	
225	16.87	16.40	2.21	1.43	11.44	10.07	3.22	4.90	
230	16.18	16.07	2.59	1.64	9.92	9.56	3.67	4.87	
235	12.58	12.69	1.65	1.08	7.17	7.45	3.76	4.16	
240	14.82	15.10	2.34	1.58	8.03	8.20	4.45	5.32	
245	10.79	11.05	1.67	1.19	4.91	5.46	4.22	4.40	
250	11.45	11.59	1.30	1.15	6.46	5.46	3.69	4.99	
255	10.52	10.67	1.08	0.84	7.00	5.42	2.44	4.41	
260	11.17	11.59	1.34	0.97	5.07	5.08	4.77	5.54	
265	7.98	8.24	0.90	0.76	2.95	3.27	4.34	4.32	
270	8.97	9.16	1.35	1.28	3.29	3.17	4.56	4.85	
275	9.91	10.08	0.95	0.85	4.87	3.36	4.09	5.87	
280	9.14	9.26	1.64	1.16	3.15	2.21	4.65	6.12	
285	8.36	8.36	1.45	1.14	3.37	2.16	3.53	5.06	
290	8.97	9.05	0.92	0.68	2.76	1.86	5.29	6.51	
295	7.76	7.93	1.16	0.80	2.08	1.67	4.52	5.46	