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Key Points:

- *Cornus drummondii*, the primary woody encroacher in this grassland, exhibited the greatest canopy-level water loss
- Nocturnal transpiration was a large component of the water lost in this ecosystem and was driven primarily by C_4 grasses and *C. drummondii*
- The sensitivity of canopy transpiration to environmental drivers varies among plant functional types and throughout a 24-hr period

Supporting Information:

- Supporting Information S1

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Bridging the Flux Gap: Sap Flow Measurements Reveal Species-Specific Patterns of Water Use in a Tallgrass Prairie

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Abstract Predicting the hydrological consequences following changes in grassland vegetation type (i.e., woody encroachment) requires an understanding of water flux dynamics at high spatiotemporal resolution for predominant species within grassland communities. However, grassland fluxes are typically measured at the leaf or landscape scale, which inhibits our ability to predict how individual species contribute to changing ecosystem fluxes. We used external heat balance sap flow sensors and a hierarchical Bayesian state-space modeling approach to bridge this “flux gap” and estimate continuous species-level water flux in common tallgrass prairie species. Specifically, we asked the following: (1) How do diurnal and nocturnal water fluxes differ among woody and herbaceous plants? (2) How sensitive are woody and herbaceous species to environmental drivers of diurnal and nocturnal water flux? We highlight three results: (1) *Cornus drummondii*, the primary woody encroacher in this grassland, exhibited the greatest canopy-level water loss; (2) nocturnal transpiration was a large component of the water lost in this ecosystem and was driven primarily by C_4 grasses and *C. drummondii*; and (3) the sensitivity of canopy transpiration to environmental drivers varies among plant functional types and throughout a 24-hr period. Our data reveal important insights regarding the water use strategies of woody versus herbaceous species in tallgrass prairies and about the potential hydrological consequences of ongoing woody encroachment. We suggest that the high, static flux rates observed in woody species will likely deplete deep water stores over time, potentially creating hydrological deficits in grasslands experiencing woody encroachment and concomitantly increasing the vulnerability of these ecosystems to drought.

Plain Language Summary Woody encroachment, the process through which woody plants (trees and shrubs) replace grasses and wildflowers in grassland ecosystems, is occurring globally. Because woody plants use water differently (e.g., rates, soil depths of uptake, and time periods of activity) than grasses, woody encroachment could potentially change the water cycle in grasslands. In order to understand how grassland water use might change with ongoing woody encroachment, we measured continuous rates of water loss in common plant species in a North American grassland. We found that the main encroaching shrub in this grassland used more water over time than grasses or wildflowers. Additionally, this shrub and grasses used a large amount of water at night compared to wildflowers. Finally, we found that different weather conditions had different impacts on how water was used by woody plants, grasses, and wildflowers. We suggest that woody encroachment might reduce the amount of water stored in grasslands, which could alter the composition of grassland plants in the future.

1. Introduction

Grasslands constitute a major portion of global vegetation, accounting for approximately 52.5×10^6 km² or 40% of the terrestrial biome (White et al., 2000). Due to their widespread cover, grasslands exert tremendous influence over local and global carbon and water cycling. For instance, grasslands account for an estimated 19–24% of global evapotranspiration (ET; Schlesinger & Jasechko, 2014), 30–35% of terrestrial net primary productivity (Field et al., 1998), and 30% of stored soil carbon (Jackson et al., 1997; Lal, 2004). Terrestrial carbon and water cycling are inherently linked through vegetation as plants balance carbon uptake with water loss via stomata. Thus, changes in the growth, distribution, or composition of grassland vegetation in response to a changing climate, shifting management regimes, or ecosystem state changes may have

profound implications for the mass and energy exchanged within the Earth-atmosphere system (Huxman et al., 2005; Jackson et al., 2002; Schlesinger & Jasechko, 2014).

Future grassland and global water fluxes will likely shift in response to the widespread occurrence of woody encroachment. Woody encroachment, or the increase in abundance and density of woody plants into historically herbaceous landscapes, has occurred globally over the past century with concomitant impacts on the hydrology of these ecosystems (Huxman et al., 2005). Previous studies show that woody encroachment can increase ET (Scott et al., 2006; Wang et al., 2018), reduce surface runoff and soil water recharge (Zou et al., 2018), and increase depletion of deep soil water (Acharya et al., 2017). These hydrological shifts occur because trees and shrubs often have drastically different water use strategies than their herbaceous neighbors; shrubs, for instance, rely on deeper water sources (Nippert & Knapp, 2007) and maintain more static leaf gas exchange rates (Muench et al., 2016) than co-occurring grasses or forbs, which can increase ET and alter other aspects of ecosystem functioning (Scott et al., 2014). Woody encroachment also increases aboveground productivity (Knapp et al., 2008), which may also increase ET. Understanding how grassland water fluxes will change due to woody encroachment will therefore require high spatial and temporal resolution information about the patterns and driving mechanisms of water use for both woody and herbaceous species within grassland communities.

Grassland water fluxes have been studied at the landscape or leaf scale, each of which have inherent trade-offs regarding spatial and temporal resolution. For instance, eddy covariance measurements are widely used to estimate net ecosystem exchange, ET, and ecosystem water use efficiency. While these large spatial scale and high temporal frequency data are invaluable for describing temporal flux dynamics across the landscape, eddy covariance measurements provide an integrated picture of Earth-atmosphere exchanges and cannot fully describe the mechanistic processes driving these fluxes for individual species. Nocturnal ET measurements made with eddy covariance techniques are also generally unreliable due to low turbulence that occurs at night (Baldocchi, 2003; Goulden et al., 1996), which limits their utility in describing diel patterns of water loss (but see Irmak, 2011, Novick et al., 2009, and Padrón et al., 2019). Conversely, leaf-level gas exchange measurements (e.g., instantaneous leaf photosynthetic and transpiration rates) are useful in describing the physiology of individual species across a heterogeneous landscape but only provide snapshots of temporally dynamic physiological processes. Leaf-level gas exchange is also time and labor intensive to measure on a wide range of species, and these measurements can be difficult to scale to the canopy level. Thus, we have limited understanding regarding the temporal patterns and environmental drivers of whole-plant water use for a wide range of herbaceous and woody grassland species. Without this information, robust predictions of water fluxes are lacking, for both modern and future climates as well as under conditions of changes in land cover arising from future woody encroachment.

Sap flow sensors offer a unique approach to quantify whole-plant water flux among coexisting species at fine temporal resolutions. Sap flow technology was first developed in the 1930s by Huber and colleagues (Huber, 1932; Huber & Schmidt, 1936) and has since become a standard approach utilized in many studies of plant-water relations (reviewed in Cermak et al., 2004). Although many sap flow methods now exist, most studies currently use thermodynamic methods to measure the rate of water ascent through plants. These techniques typically insert heater and thermocouple probes into the sapwood of trees (normally >10-cm stem diameter) and are therefore unsuitable for use on smaller-stemmed shrubs or herbaceous plants (Skelton et al., 2013). The external heat balance method was developed by Clearwater et al. (2009) to measure low sap flow rates on small stems, but these techniques have been primarily applied to crops such as maize (Gavloski et al., 1992), soybean, cotton (Cohen et al., 1990, 1993; Cohen & Li, 1996), and wheat (Langensiepen et al., 2014). With the exception of several studies conducted during the mid-1990s (Owensby et al., 1997; Senock & Ham, 1995), no work has investigated sap flux in small-stemmed, herbaceous plants growing within native ecosystems. However, sap flow measurements made on grassland species with small external heat balance sensors have the potential to bridge the gap between leaf gas exchange and eddy flux measurements, providing more robust estimates of water use in a heterogeneous and dynamic ecosystem. Furthermore, fine temporal-scale measurements of whole-plant water use can provide better insight into the role of nocturnal transpiration in grassland water budgets. Nocturnal transpiration has been shown to contribute substantially to the water budgets of forests (Dawson et al., 2007; Resco de Dios et al., 2015; Zeppel et al., 2014) and other ecosystems (Snyder et al., 2003; Bucci et al., 2004; Domec et al., 2006; Caird et al., 2007; Ogle et al., 2012;). Recent work has shown that nocturnal leaf transpiration rates can be high

in grassland plants as well (O'Keefe & Nippert, 2018), but no work has yet been able to quantify total daytime and nighttime water use for multiple species in a native grassland ecosystem.

We present here an assessment of whole-plant water use in herbaceous and woody species common throughout the tallgrass prairies of North America in order to better understand how grassland water budgets will change with ongoing woody encroachment. We used external heat balance sap flow microsenors to measure sap flow rates in small-stemmed plants (<7-mm diameter) in a tallgrass prairie that is currently experiencing extensive woody encroachment and then used a hierarchical Bayesian state-space modeling approach to scale stem sap flow to canopy transpiration and conductance. We then addressed the following questions: (1) How do diurnal and nocturnal water fluxes differ among woody and herbaceous plants in a tallgrass prairie? (2) How sensitive are woody and herbaceous species to environmental drivers of diurnal and nocturnal water flux? Given their access to deep, stable water sources (Nippert & Knapp, 2007), we hypothesize that woody species will have greater rates of canopy transpiration during the day and at night and will also be less sensitive to fluctuations in microclimate (e.g., shallow soil moisture content and vapor pressure deficit [VPD]) than herbaceous species.

2. Materials and Methods

2.1. Site Description

Research was conducted during May–September 2014 at the Konza Prairie Biological Station, a 3,487-ha area of native tallgrass prairie located in the Flint Hills region of northeastern Kansas, USA (39.1° N, 96.9° W). The Konza Prairie Biological Station is a long-term ecological research site that is divided into experimental watersheds, each of which receive varying combinations of prescribed fire (burned every 1, 2, 4, or 20 years) and grazing (grazed by *Bison bison*, cattle, or ungrazed) treatments. While these treatments alter vegetation diversity and productivity (Briggs & Knapp, 1995; Collins et al., 1998; Collins & Calabrese, 2012; Eby et al., 2014; Hartnett et al., 1996; Knapp et al., 1999; Veen et al., 2008), the landscape is generally dominated by a few perennial C₄ grass species along with numerous subdominant C₃ grass, forb, and woody species (Smith & Knapp, 2003). Long-term weathering at the site has created a topographically heterogeneous landscape, including shallow, rocky uplands, steep slopes, and deep, loess soiled lowlands.

The Flint Hills region of Kansas is characterized by a midcontinental climate with cool, wet winters and warm, dry summers. Long-term mean annual precipitation (1982–2014) at the Konza Prairie Biological Station is 829 mm, of which 79% occurs during the growing season (April–September). Precipitation was 706 mm in 2014, of which 68% occurred during the growing season. The warmest average month of the year (1982–2014) is July, with mean maximum and minimum air temperatures of 32.69 and 19.78 °C. The coldest average month (1982–2014) is January, with mean maximum and minimum air temperatures of 4.87 and –7.14 °C. Mean maximum and minimum air temperatures were 31.7 and 17.06 °C during July 2014.

This study was conducted in lowland prairie of a watershed that is burned every 4 years and was last burned in 2013 (Watershed 4B). This location was chosen because a 4-year fire interval is similar to the historic frequency of fire for the region (Frost, 1998) and because watersheds burned with this frequency have greater forb and shrub diversity than watersheds that are burned annually. We sampled commonly occurring herbaceous and woody species including two dominant C₄ grasses (*Andropogon gerardii* Vitman, big bluestem; *Panicum virgatum* L., switchgrass), two C₃ forbs (*Solidago canadensis* L., Canada goldenrod; *Vernonia baldwinii* Torr., Baldwin's ironweed), one leguminous C₃ subshrub (*Amorpha canescens* Pursh., leadplant), and two C₃ shrubs (*Rhus glabra* L., smooth sumac; *Cornus drummondii* C.A. Mey., roughleaf dogwood). *R. glabra* and *C. drummondii* are both rhizomatous shrubs that expand via the production of clonal stems (Benson & Hartnett, 2006). Of these two shrubs, *C. drummondii* is the primary shrub species expanding in the tallgrass prairies of Kansas. This species produces large clonal “shrub islands” that limit graminoid growth in their understory and prevent fire from carrying through the island (Ratajczak et al., 2011). Reduced fire frequency that enables the establishment of these clonal islands, as well as the reduced fuel load within established *C. drummondii* patches, has facilitated the extensive expansion of this shrub in native tallgrass prairie over the past several decades (Briggs et al., 2002). Previous studies at the Konza Prairie Biological Station have used the natural abundance of stable isotopes in soil and plant water to show that C₄ grasses primarily utilize shallow soil water through time, while clonal shrubs use shallow water when it is available and shift reliance to deeper soil water when shallow soils dry (Nippert & Knapp, 2007; Ratajczak et al., 2011).

2.2. Sap Flow Measurements

Stem sap flow was measured using the external heat balance method with commercially available sap flow sensors (SGA3 and SGA5 Dynagage Microsensors; Dynamax Inc., Houston, TX, USA) connected to a Flow32 sap flow system (Dynamax Inc., Houston, TX, USA). Briefly, a thermocouple sensor was attached to the circumference of a plant stem, heat was applied to the plant stem, and the flow of sap through the stem was estimated by measuring voltage outputs from the flux of heat through the heated stem section (Sakuratani, 1981; Smith & Allen, 1996). Sap flow was calculated as

$$Q = Q_r + Q_v + Q_f + S, \quad (1)$$

where Q is the total power, Q_r is the radial heat flux, Q_v is the axial heat flux, Q_f is the residual heat flux, and S is the rate of change in stem heat storage (see Senock & Ham, 1995, for detailed calculations of each heat flux component).

Sensors were installed on plants that fit within the stem diameter range of each sensor size (3–5 mm for SGA3 and 5–7 mm for SGA5). Prior to installation, dirt and debris were cleaned from stems, and a conducting gel was applied to the stem surface to facilitate heat transfer between the stem and the sensor (Dynamax, 2009). Each sensor was sealed with putty to prevent moisture damage to the sensor, and the stem and sensor were insulated with multiple layers of foam and bubble foil to reduce the impact of radiation on sensor measurements.

Eight sap flow sensors were installed during the growing season (DOY 140–260) on plants located within ~10 m of the central data logger and weather station. In order to alleviate potential stress associated with using sensors on small stems for prolonged periods of time, the sensors were rotated among all species throughout the growing season. The eight sensors were deployed on two individuals of four study species for a period of 10 days. Following the 10-day sampling period, all sensors were switched to a different set of four species. The species chosen for each 10-day period were randomly selected, but all species were sampled for approximately an equal amount of time across the growing season.

Measurements were sampled every 60 s, averaged, and logged every 30 min with a CR1000x data logger and an AM 16/32 multiplexer (Campbell Scientific, Logan, Utah). The data logger and sensors were powered with a 100-W solar panel, and sensor heat inputs were controlled with an AVR voltage regulator (v 3.1, Dynamax Inc., Houston, TX, USA) linked to the data logger.

2.3. Environmental Variables

Key environmental variables were measured, including air temperature (100-K thermistor; Betatherm, Hampton, VA, USA), volumetric soil moisture (v/v) at 10 cm (Hydramprobe II; Stevens Water Monitoring Systems, Portland, OR, USA), relative humidity (HM1500; Humierl, Hampton, VA, USA), wind speed (3-cup anemometer; Gill Instruments, Lymington, UK), and photosynthetically active radiation (LI200X-L Silicone Pyranometer; LI-COR, Inc., Lincoln, NE). A radiation shield (41003; RM Young, Traverse City, MI, USA) was used to protect the relative humidity sensor, and air temperature and relative humidity measurements were used to calculate VPD at the site. All measurements were logged every 10 s with a CR10X data logger (Campbell Scientific, Logan, UT, USA). Missing data due to inclement weather or equipment failure were gap filled using a moving diurnal mean (Falge et al., 2001).

2.4. Model Description

The hierarchical Bayesian State-Space Canopy Conductance (StaCC) model was used to gap fill missing sap flow data and to predict leaf transpiration, canopy conductance, and canopy transpiration for each species (Bell et al., 2015). The StaCC model was initially developed for modeling canopy conductance and transpiration in forests (Bell et al., 2015; Ward et al., 2013) and combines a sap flux data model with a canopy conductance model while applying prior knowledge of the model parameters and accounting for random error associated with individual sap flow sensors. The data model utilizes sap flow measurements made by a set of sensors to calculate average species sap flux across the time series. Sap flux of probe i at time t was modeled as

$$J_{it} \sim N(J_t a_i, S), \quad (2)$$

where J_t is the average sap flux at time t , a_i is the random effect associated with probe i , and S is the Gaussian observation variance. As opposed to the previous studies of trees using the StaCC model (Bell et al., 2015; Ward et al., 2013), we did not utilize a sapwood depth submodel due to the small sizes of stems (<7 mm) and a lack of information regarding radial reductions in sap flux. Similarly, because these small-stemmed plants do not likely store an appreciable amount of stem water (Nobel & Jordan, 1983), we also did not utilize the additional capacitance submodel described in Bell et al. (2015).

The canopy conductance process model was used to estimate canopy conductance (G_C), transpiration per m² leaf area (E_L), and canopy transpiration per m² ground area (E_C). First, steady-state canopy conductance at time t ($G_{s,t}$, mmol m⁻² s⁻¹) was modeled as a function of VPD (D_t), photosynthetically active radiation (Q_t), and volumetric soil moisture (M_t) according to Jarvis (1976):

$$G_{s,t} = f(D_t) g(Q_t) h(M_t). \quad (3)$$

Within this model, the effect of D_t on $G_{s,t}$ was calculated as

$$f(D_t) = G_{\text{ref}} - \lambda \ln(D_t), \quad (4)$$

where G_{ref} is the reference conductance ($G_{s,t}$ when $D_t = 1$ kPa) and λ is the stomatal sensitivity to D_t (Oren et al., 1999). Second, the effect of Q_t on $G_{s,t}$ was calculated as

$$g(Q_t) = 1 - \alpha_1 \exp(Q_t/\alpha_2), \quad (5)$$

where α_1 is the relative difference between diurnal and nocturnal stomatal conductance and α_2 is a parameter representing the sensitivity of G_s to Q_t . Third, the effect of M_t on $G_{s,t}$ was modeled as

$$h(M_t) = \exp(-0.5(M_t - \alpha_3)^2/\alpha_4^2) \text{ if } M_t \leq \alpha_3 \text{ or } h(M_t) = 1 \text{ if } M_t > \alpha_3, \quad (6)$$

where α_3 is the threshold below which M_t reduces $G_{s,t}$ and α_4 describes the sensitivity of the decline in $G_{s,t}$ with declines in M_t below that threshold. Next, $G_{s,t}$ was used to calculate actual canopy conductance (G_C), assuming that G_C is dependent on previous conductance and a time interval, d_t (Rayment et al., 2000; Ward et al., 2008):

$$G_C = G_{C-dt} + (G_{s,t} - G_{C-dt})V_t, \quad (7)$$

where $d_t = 30$ min and $V_t = 1 - \exp(-d_t/\tau)$ and τ is the stomatal lag in minutes. The V_t term accounts for stomatal lags using a stomatal time constant (τ), where $\tau = 10$ min, following Bell et al. (2015). Canopy conductance was then used to calculate $E_{L,t}$, (kg m⁻² s⁻¹) as

$$E_{L,t} = \frac{G_C D_t \left(\frac{T_t}{273} + 1 \right)}{44,600(115.8 + 0.4226T_t)}, \quad (8)$$

which includes air temperature (T_t), VPD, and several constant terms (Bell et al., 2015). Finally, E_L was scaled to E_C with the following equation:

$$E_C = E_L A_L A_s^{-1} \quad (9)$$

where A_L is the leaf area index (LAI) and A_s is the conducting tissue area index (CAI). LAI data for grasses, forbs, and small shrubs (*A. canescens* and *R. glabra*) were taken from previous work at this site (Klodd et al., 2016; J. Nippert, unpublished). LAI was measured in 2015 for *C. drummondii* with a LAI meter (LiCor, Inc, Lincoln, NE, USA). CAI is a proxy for sapwood area index, which is typically used to scale transpiration in trees and is calculated as the area of sapwood (m²) contained in a tree per m² ground area (Bell et al., 2015). Considering that many of the species in this study were small, herbaceous, and likely contain similar proportional conducting areas, we instead calculated CAI (in units of m² stem area per m² ground area) by multiplying the average stem cross-sectional area of each species measured during sensor installations

by the approximate stem density measured for each species at our study location (supporting information Table S1). Average stem density had been previously assessed visually using a 1-m² sampling frame for forbs and woody species and a 0.1-m² sampling frame for grasses (J. Nippert, unpublished). We assumed all stem cross-sectional area was functional for each species.

The final hierarchical Bayesian model is a joint distribution of sap flow data observations, canopy conductance latent states, and model parameters. When possible, priors for the data model and process model were utilized from Bell et al. (2015). Species specific inputs are described in Tables S1 and S2. See Bell et al. (2015) for a full description of prior distributions and the joint posterior distribution. A separate model analysis was implemented for each of the eight species. We ran the Gibbs sampler for 20,000 iterations and discarded the first 10,000 iterations as a burn-in and visually inspected output to ensure parameter convergence.

We used the estimated G_C , E_L , and E_C produced by the model to compare diurnal and nocturnal water fluxes among woody and herbaceous plants. First, “diurnal” and “nocturnal” classifications were assigned to each 30-min time step throughout a day based on daily sunrise and sunset times. We then calculated total daily (24-hr period), diurnal, and nocturnal E_L and E_C for each species and each day during the growing season, as well as mean daily, diurnal, and nocturnal G_C for each species and each day during the growing season. Although the StaCC model assumes functional relationships between modeled fluxes and environmental drivers, the model does not determine variation in the sensitivity of these relationships among species. As such, we also assessed potential differences in diel water flux sensitivity to environmental drivers among species. We evaluated the relationship of diurnal and nocturnal fluxes (E_C and G_C) with various environmental variables using log-linear and log-log transformed regression analyses. Specifically, we used separate regression analyses to assess the relationship between diurnal fluxes and VPD measured at average daily maximum (15:00 hr) conditions, nocturnal fluxes and VPD measured at average daily minimum (03:00 hr) conditions, diurnal fluxes and daily average soil moisture measured at 10 cm, and nocturnal fluxes and daily average soil moisture measured at 10 cm for each species. Due to the potential correlation between VPD and soil moisture, the relationships between E_C , G_C , and soil moisture were conducted separately for different VPD ranges determined by binning all diurnal and nocturnal VPD measurements into three equal groups for both diurnal and nocturnal analyses (“Low” < 1.50 kPa, “Mid” = 1.5–2.28 kPa, and “High” > 2.28 kPa for diurnal analyses; “Low” < 0.21 kPa, “Mid” = 0.21–0.45 kPa, and “High” > 0.45 kPa for nocturnal analyses). All analyses were performed using the statistical program R V3.1.0 (R Core Team, 2012) using a modified version of the StaCC model (<https://github.com/belland/StaCC-Model>).

3. Results

3.1. Environmental Data

Soil moisture measured at 10-cm depth declined over the growing season (Figure 1a) with highest values at DOY 161 and lowest soil moisture values at DOY 242. Air temperature was variable throughout the growing season and increased slightly as the growing season progressed (Figure 1b). The maximum air temperature during the day (15:00) was recorded on DOY 196, and the minimum air temperature at night (03:00) was recorded on DOY 236. VPD was also variable over time but was generally higher during the latter part of the growing season (Figure 1c), and this increase was largely driven by seasonal declines in relative humidity. Maximum VPD values measured during the day (15:00 hr) occurred on DOY 236, while minimum VPD values measured at night (03:00) occurred on DOY 219.

3.2. Model Performance

Model performance varied based on plant functional type. Generally, model convergence and model predictions were greatest in woody species, intermediate in forbs, and lowest in grasses (Figure S2 and Tables S3 and S4). Squared Pearson correlation coefficients (r^2) for each model were 0.98 for *C. drummondii*, 0.99 for *R. glabra*, 0.99 for *A. canescens*, 0.91 for *V. baldwinii*, 0.97 for *S. canadensis*, 0.69 for *A. gerardii*, and 0.93 for *P. virgatum*. Mean errors for each model were 0.02 for *C. drummondii*, 0.01 for *R. glabra*, 0.01 for *A. canescens*, 0.27 for *V. baldwinii*, −0.10 for *S. canadensis*, −6.09 for *A. gerardii*, and −1.28 for *P. virgatum*.

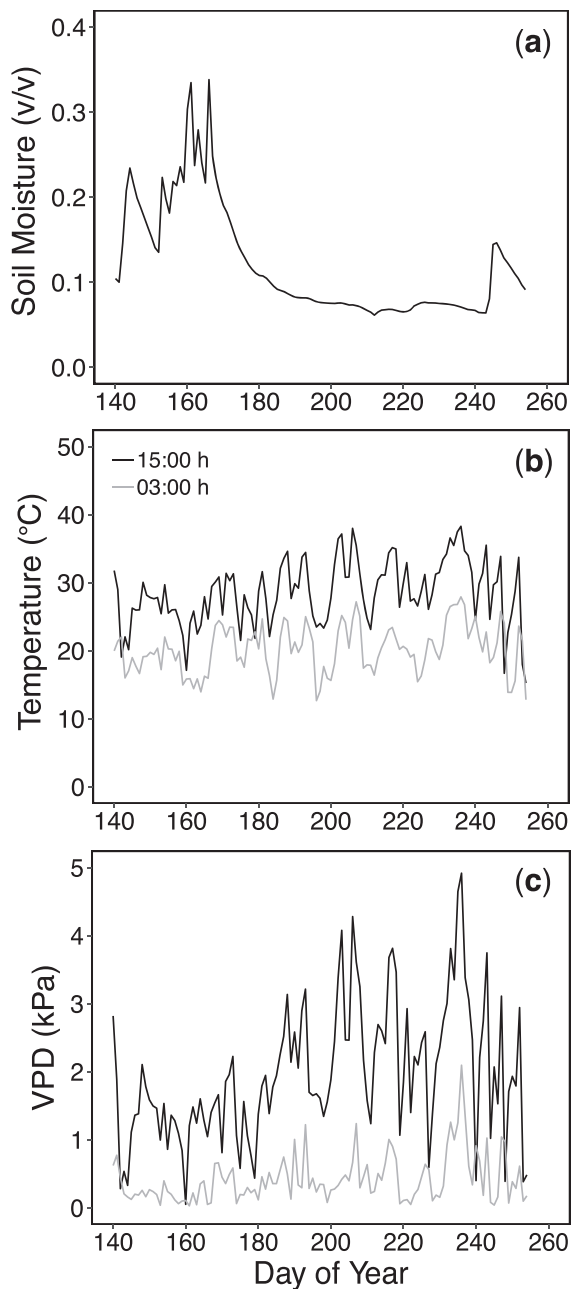


Figure 1. Environmental data measured between Day of Year 140 and 260 in 2014. Shown are daily averages of volumetric soil moisture (v/v) measured at 10 cm (a), air temperature measured at average daily maximum (15:00 hr) and minimum (03:00 hr) conditions (b), and vapor pressure deficit (VPD) measured at average daily maximum (15:00 hr) and minimum (03:00 hr) conditions (c).

Root mean squared errors for each model were 8.01 for *C. drummondii*, 9.81 for *R. glabra*, 9.82 for *A. canescens*, 12.79 for *V. baldwinii*, 11.93 for *S. canadensis*, 33.34 for *A. gerardii*, and 16.10 for *P. virgatum*.

3.3. Modeled Transpiration and Canopy Conductance

Canopy-level flux patterns varied among species and across the growing season (Figures 2–4 and S2). Diurnal E_C was greatest in the woody species, particularly in the clonal shrub *C. drummondii* and the nonclonal subshrub *A. canescens* (Figures 2a and 2c). The C_4 grass, *P. virgatum*, also exhibited high diurnal E_C (Figure 2g). Concomitantly, cumulative E_C over the measurement period (DOY 140–260) was greatest in *C. drummondii* (208.35 mm), followed by *P. virgatum* (114.10 mm) and *A. canescens* (112.07 mm) (Table 1). *R. glabra* and *V. baldwinii*, on the other hand, exhibited the lowest cumulative E_C throughout the measurement period (46.69 and 31.98 mm, respectively; Table 1).

Diurnal E_C varied among species within functional groups; for instance, diurnal E_C measured for *S. canadensis* was often twice as high as diurnal E_C measured in the co-occurring forb, *V. baldwinii* (Figures 2d and 2e). Diurnal E_C was also much lower in *R. glabra* compared to *C. drummondii* (Figures 2a and 2b), despite the two shrubs having similar leaf-level transpiration rates (Figures S2a and S2b). Additionally, temporal trends in diurnal E_C varied among species; diurnal E_C was fairly static through time for most species but declined substantially in *S. canadensis* toward the end of the growing season (Figure 2e). Diurnal E_C also peaked earlier in the season for certain species (e.g., *C. drummondii* and *S. canadensis*; Figures 2a and 2e) than others (e.g., *A. gerardii* and *P. virgatum*; Figures 2f and 2g). Finally, interspecific differences in transpiration varied between scales. At the leaf level, E_L was at least twice as high in the grasses and *A. canescens* as compared to the clonal shrubs and the C_3 forbs (Figure S2).

Nocturnal E_C was greatest in the C_4 grasses and *C. drummondii* (Figure 2) but constituted a much larger proportion of total daily E_C in the C_4 grasses compared to all other species (Figure 3). Nocturnal E_C increased over time in these species, despite static daytime E_C (Figure 2), resulting in nocturnal E_C values that were as much as 50% of daily E_C by the end of the growing season (Figure 3). As a result, nocturnal E_C represented 22–30% of the water used during the growing season by C_4 grasses, whereas nocturnal E_C ranged between 12% and 15% of the water used by shrubs and forbs (Table 1).

Canopy conductance also varied among species and through time (Figure 4). Grasses had greater G_C values than woody species or forbs, and all species exhibited a decline in G_C throughout the middle of the growing season before increasing again toward the end of the season. Nocturnal G_C was lower than daytime G_C for all species except the grasses, where night G_C was approximately equal to daytime G_C values throughout the growing season.

3.4. Response of Modeled Canopy Transpiration to Environmental Drivers

E_C increased and G_C decreased with increasing VPD, although the strength of these relationships varied among species (Figures 5 and 6 and Table S5). The C_4 grasses, *A. gerardii* and *P. virgatum*, as well as the nonclonal subshrub *A. canescens* exhibited the strongest relationships of E_C and G_C with VPD. These relationships varied throughout a 24-hr period; for instance, nocturnal E_C was more tightly related to VPD than

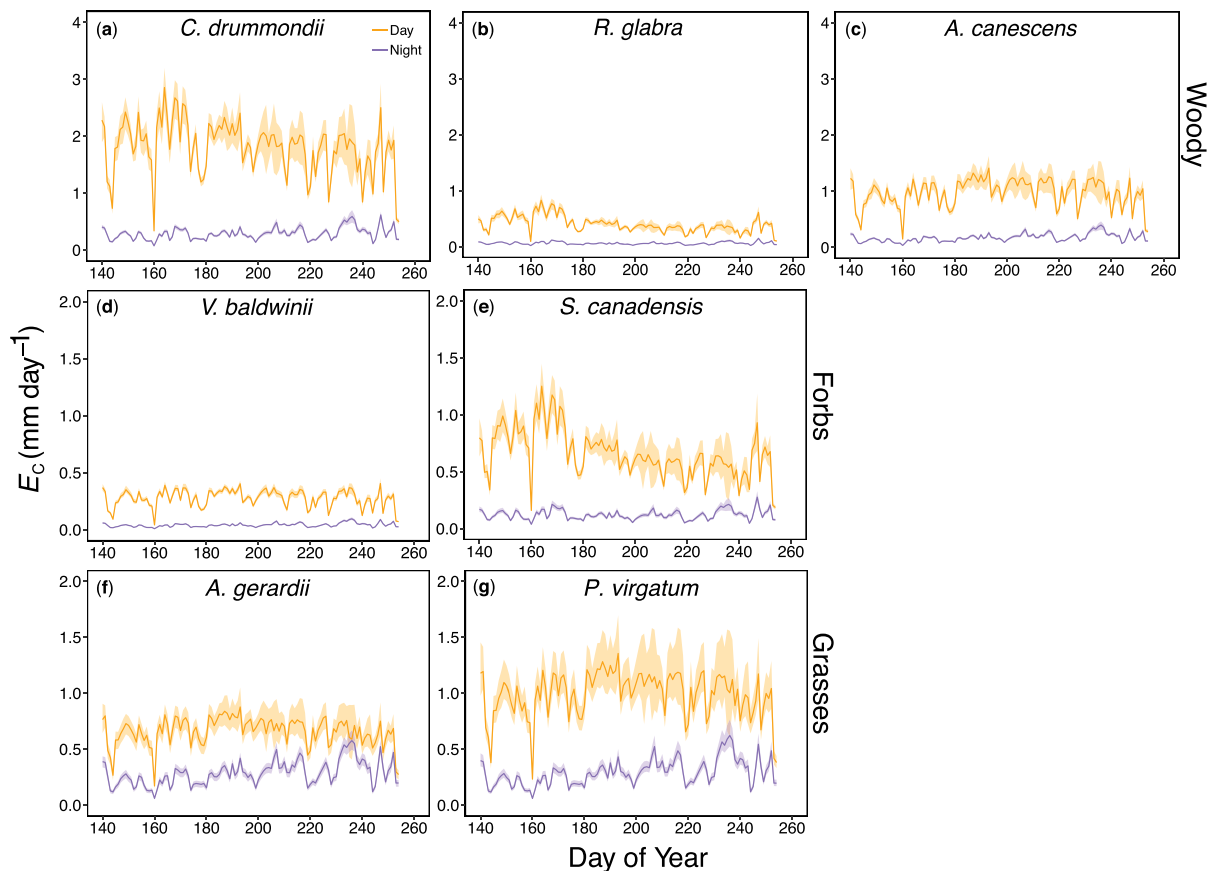


Figure 2. Modeled canopy transpiration (E_C) between DOY 140 and 260. Shown are total daily diurnal (yellow) and nocturnal (purple) values for woody species (a–c), forbs (d, e), and grasses (f, g). Shaded areas indicate 95% credible intervals.

diurnal E_C (Figure 5). Additionally, diurnal E_C increased asymptotically with VPD until reaching a threshold of ~ 1.5 kPa, whereas nocturnal E_C did not exhibit a saturating relationship with VPD (Figure 5). G_C did not exhibit similar diel trends with VPD (Figure 6).

Woody and forb E_C increased with greater soil moisture measured at 10 cm, primarily at “Mid” and “High” VPD ranges (Figures S3 and S4 and Table S6). Similarly, woody and forb G_C increased with greater soil moisture for all VPD ranges (Figures S6 and S7 and Table S7). The clonal shrubs (*C. drummondii* and *R. glabra*) and *S. canadensis* exhibited the strongest relationships with soil moisture, while the C_4 grasses exhibited the weakest relationships, and these trends did not vary between diurnal and nocturnal measurements (Figures S5 and S8).

4. Discussion

Although woody encroachment is occurring over much of the North American Great Plains, how this shift in land cover will alter the contribution of transpiration from woody and herbaceous species in grasslands is not well understood. We addressed this gap in knowledge by using external heat balance sap flow sensors to assess diel sap flow patterns within a tallgrass prairie currently experiencing extensive woody encroachment. We show that (1) *C. drummondii*, the primary woody encroacher in this grassland, exhibited the greatest canopy-level water loss, (2) nocturnal transpiration was a large component of the water lost in this ecosystem and was driven primarily by C_4 grasses and *C. drummondii*, and (3) the sensitivity of canopy transpiration and conductance to environmental drivers varied among woody and herbaceous species and throughout a 24-hr period.

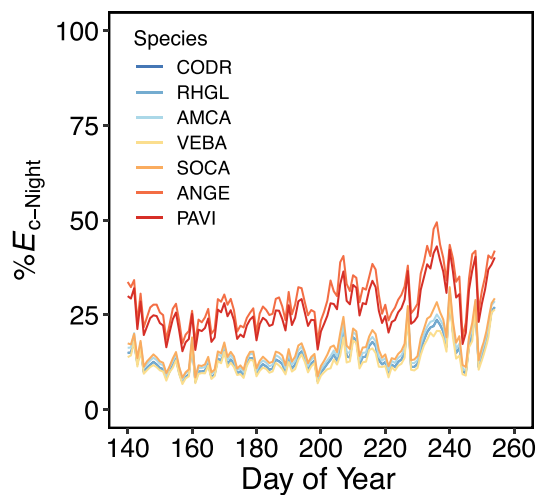


Figure 3. Percent nocturnal canopy transpiration of total daily canopy transpiration for *C. drummondii* (CODR), *R. glabra* (RHGL), *A. canescens* (AMCA), *V. baldwinii* (VEBA), *S. canadensis* (SOCA), *A. gerardii* (ANGE), and *P. virgatum* (PAVI).

4.1. *C. drummondii*, the Primary Woody Encroacher in This Grassland, Exhibited the Greatest Canopy-Level Water Loss

Our results support our hypothesis that woody species exhibit greater canopy water loss than herbaceous species. The highest daily E_C rates occurred in certain woody species (Figure 2), despite having much lower G_C values than the grasses (Figure 4). *C. drummondii* had particularly high E_C rates and consequently exhibited much greater cumulative diurnal and total E_C over the growing season than other species (Table 1). At the leaf level, however, grasses exhibited E_C rates that were approximately twice as high as *C. drummondii* and *R. glabra* (Figure S2). These findings reinforce the notion that leaf-level physiological patterns do not always translate to larger scales and that canopy flux measurements may not be easily predicted from leaf-level measurements (Ford et al., 2007; Granier et al., 2000; Medlyn et al., 2017). Thus, using whole-plant water flux will be critical for improving estimates of water use in heterogeneous ecosystems, particularly those undergoing extensive land cover change.

While the high daily E_C measured in *C. drummondii* is not surprising considering the high LAI of this shrub (Table S1), this result reveals important insights regarding the potential trajectory of grassland eco-

system hydrology given ongoing woody encroachment. Cumulative E_C exceeded annual precipitation for 2014, indicating that these species rely on water stored in the ecosystem, likely at deeper soil layers, to sustain transpiration throughout the growing season. Similarly, Logan and Brunsell (2015) reported landscape ET estimates using eddy-flux data that exceeded current cumulative precipitation during 2011. Considering that the primary woody encroacher in this grassland, *C. drummondii*, utilizes deep soil water (Ratajczak et al., 2011) and has the greatest cumulative E_C here (Table 1), continued exploitation of deep soil water at a rate greater than precipitation recharge is likely to create hydrological deficits for this ecosystem. Additionally, altered precipitation associated with climate change will likely reduce soil water content (Christensen et al., 2007), which may cause other deep-rooted species to increasingly rely on deep water (Asbjornsen et al., 2008; Nippert & Knapp, 2007). Deep water stores are typically recharged by winter precipitation (Nippert & Knapp, 2007; Ransom et al., 1998) and may consequently become depleted over time as woody cover increases (Vero et al., 2017). How this will impact the physiology and growth of deep-rooted species requires further investigation; however, more shallowly rooted grassland vegetation may become increasingly susceptible to drought (Pfisterer & Schmid, 2002; Verheyen et al., 2008).

Alternatively, if *C. drummondii* does not deplete deep water stores and is capable of hydraulic redistribution, encroachment by this species may increase shallow soil water content for species that do not have access to deeper soil water (Caldwell et al., 1998). Whether hydraulic redistribution is a biologically significant phenomenon in tallgrass prairie is unclear (O'Keefe & Nippert, 2017), as is whether hydraulic redistribution provides a functional benefit to grasses (Barron-Gafford et al., 2017; Ludwig et al., 2004). Regardless of the mechanism, the ongoing expansion of *C. drummondii* will likely alter soil moisture dynamics and have cascading impacts on biogeochemical cycling and productivity in grasslands (Hibbard et al., 2001; Lett et al., 2004).

4.2. Nocturnal Transpiration Was a Large Component of the Water Lost in This Ecosystem and Was Driven Primarily by C_4 Grasses and *C. drummondii*

ET measurements are difficult to make at night using eddy covariance techniques, and consequently, few studies have made continuous estimates of nocturnal transpiration in herbaceous ecosystems (Irmak, 2011; Novick et al., 2009; Padrón et al., 2019). By using an alternative approach, we were able to detect continuous rates of nocturnal transpiration in multiple grassland species (Figures 2 and S2). Nocturnal E_C constituted a large portion of the total water used by species throughout an entire day, especially for the C_4 grasses (Figure 3). Consequently, nocturnal E_C was a nonnegligible portion of the total water used by these species over the course of the growing season (Table 1). Our observation that grasses exhibited higher proportional nocturnal E_C than co-occurring forbs and shrubs validates previously reported patterns of leaf-

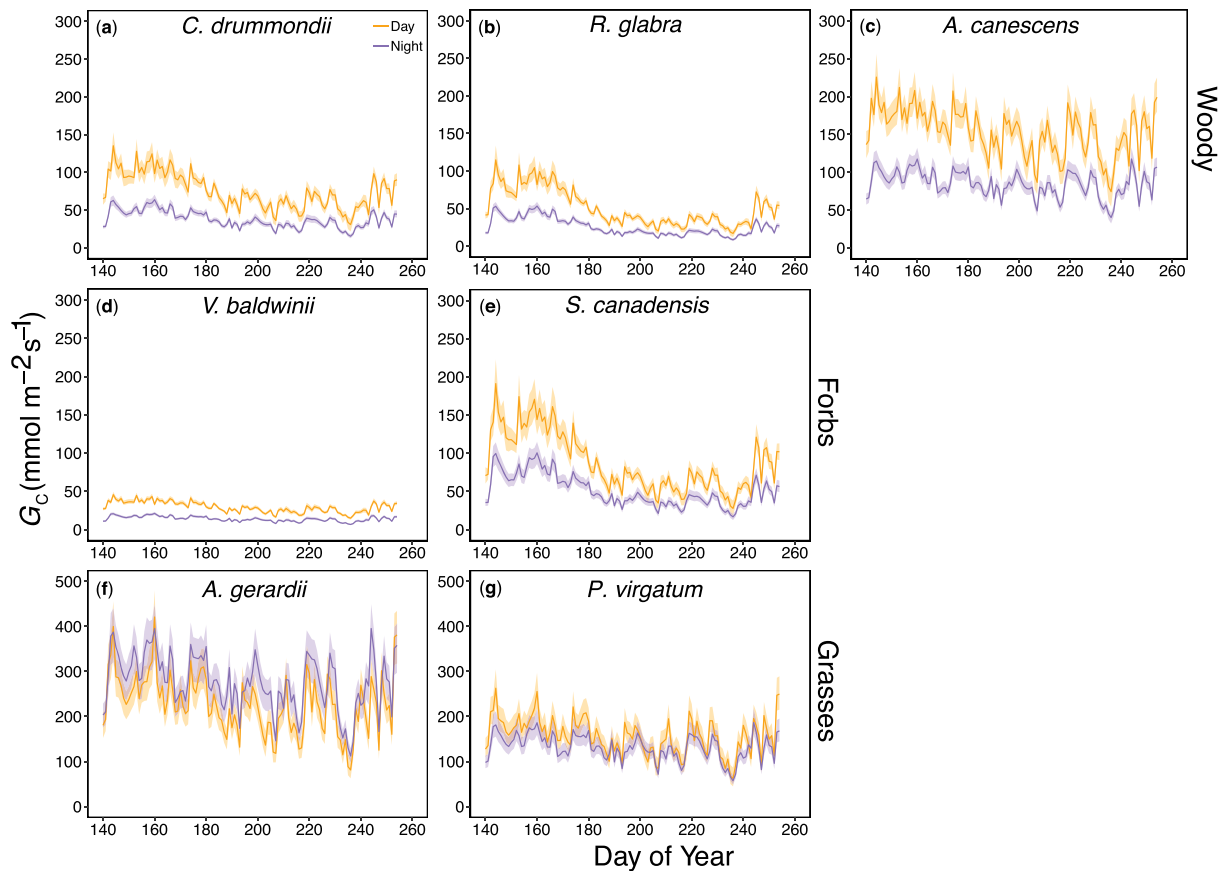


Figure 4. Modeled canopy conductance (G_C) between DOY 140 and 260. Shown are average daily diurnal (yellow) and nocturnal (purple) values for woody species (a–c), forbs (d, e), and grasses (f, g). Shaded areas indicate 95% credible intervals.

level nocturnal transpiration at this site and provides further evidence that nocturnal water loss is likely a substantial component of grassland water budgets (Muench et al., 2016; O’Keefe & Nippert, 2018). O’Keefe and Nippert (2018) measured diel leaf gas exchange on these same species and found that nocturnal transpiration was greatest in the C_4 grasses, reaching as much as 35.5% of daytime transpiration rates during wet periods. While several mechanisms have been proposed to explain nocturnal transpiration including enhanced nutrient acquisition (Scholz et al., 2007), increased carbohydrate export (Marks & Lechowicz, 2007), and circadian rhythm (Resco de Dios et al., 2016), O’Keefe and Nippert (2018)

suggested that nocturnal water loss may actually function as a competitive strategy in grasslands. They proposed that C_4 grasses, which are typically more physiologically tolerant to drought than co-occurring forbs and shrubs (Tucker et al., 2011), transpire at high rates during the day and at night to rapidly deplete surface soil water and negatively impact neighboring plants (O’Keefe & Nippert, 2018). These grasses have dense, fibrous root systems that are concentrated in the upper soil layers and can rapidly utilize limiting soil resources (Jackson et al., 1996; Nippert et al., 2012). We show that these grasses also maintain consistently high G_C regardless of seasonal changes in soil moisture (Figures 1, 4, and S8), which result in high nocturnal E_C , particularly during periods of higher nocturnal VPD (Figures 1–3). Thus, our ability to quantify whole-plant water use and link modeled nighttime fluxes with multiple environmental drivers not only validated the leaf-level measurements made by O’Keefe and Nippert (2018) but has

Table 1
Cumulative Canopy Transpiration

Species	$E_{C\text{-day}}$ (mm)	$E_{C\text{-night}}$ (mm)	$E_{C\text{-diel}}$ (mm)	% $E_{C\text{-night}}$
<i>C. drummondii</i>	208.35	33.10	241.45	13.71
<i>R. glabra</i>	46.69	7.21	53.90	13.38
<i>A. canescens</i>	112.07	19.90	131.97	15.08
<i>V. baldwinii</i>	31.98	4.71	36.69	12.84
<i>S. canadensis</i>	76.00	14.02	90.02	15.57
<i>A. gerardii</i>	75.95	32.85	108.80	30.19
<i>P. virgatum</i>	114.10	33.46	147.56	22.68

Note. Data include diurnal ($E_{C\text{-Day}}$), nocturnal ($E_{C\text{-Night}}$), and total ($E_{C\text{-diel}}$) canopy transpiration, as well as the percent nocturnal of total canopy transpiration (% $E_{C\text{-Night}}$) measured between Day of Year 140 and 260 for *C. drummondii*, *R. glabra*, *A. canescens*, *V. baldwinii*, *S. canadensis*, *A. gerardii*, and *P. virgatum*.

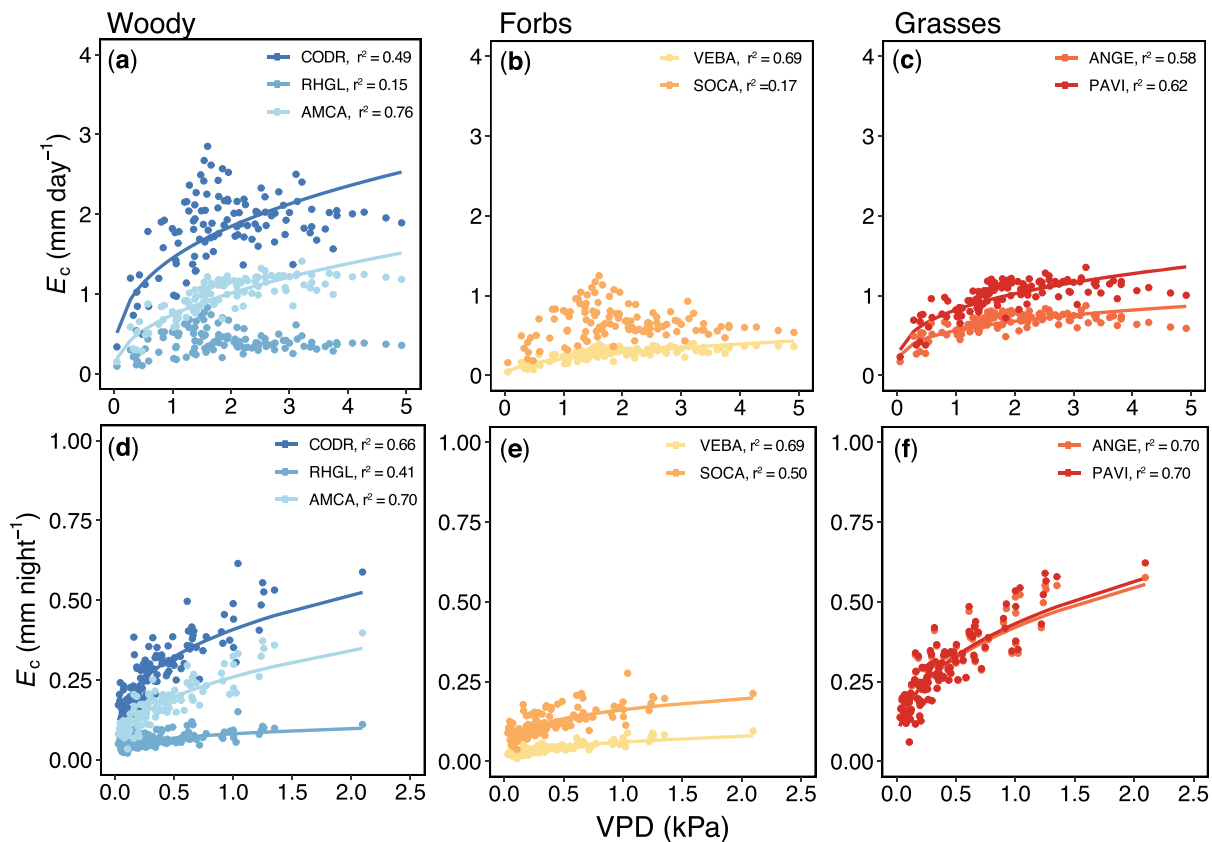


Figure 5. Relationships of total diurnal canopy transpiration with vapor pressure deficit measured at average daily maximum (15:00 hr) conditions (a–c) and total nocturnal canopy transpiration with vapor pressure deficit measured at average daily minimum (03:00 hr) conditions (d–f). Shown are regression curves for the corresponding log-log model for woody species (a, d) including *C. drummondii* (CODR), *R. glabra* (RHGL), and *A. canescens* (AMCA); forbs (b, e) including *V. baldwinii* (VEBA) and *S. canadensis* (SOCA); and grasses (c, f) including *A. gerardii* (ANGE) and *P. virgatum* (PAVI). r^2 values are provided for all species, but only relationships with $r^2 > 0.20$ are indicated with regression lines. Corresponding statistics are presented in Table S5.

also provided additional insight regarding the competitive role of nocturnal transpiration in grassland communities.

We also measured high nocturnal E_c in *C. drummondii*, which is likely related to the high LAI of this species as well as its access to stable, deep water sources. Given that the greatest cumulative nocturnal E_c occurred in grasses and *C. drummondii*, woody encroachment may not change the proportion of water lost from grasslands at night. Thus, Earth system models that estimate the impact of woody encroachment on carbon and water fluxes should still consider estimates of nocturnal transpiration for multiple functional groups. Nocturnal E_c was also greater on nights with higher VPD and may therefore constitute a larger than expected proportion of grassland water budgets in a warmer, drier climate, regardless of changes in woody cover. Previous studies show that a wide range of woody plants exhibit nocturnal water loss (Caird et al., 2007; Dawson et al., 2007), and models that assume zero-water loss at night can severely underestimate ET in ecosystems where this occurs (Zeppel et al., 2014).

4.3. The Sensitivity of Canopy Transpiration to Environmental Drivers Varied Among Woody and Herbaceous Species and Throughout a 24-hr Period

Because woody species rely on deep, stable water sources, we hypothesized that they would exhibit E_c rates that are less sensitive to fluctuations in microclimate than herbaceous species. In support of this hypothesis, we found that E_c and VPD, as well as G_c and VPD, were most strongly linked in grasses (*A. gerardii* and *P. virgatum*) and *A. canescens* (Figures 5 and 6) and were somewhat less tightly linked in the clonal shrubs *C. drummondii* and *R. glabra*. These results suggest that grasses and *A. canescens* experience tighter stomatal

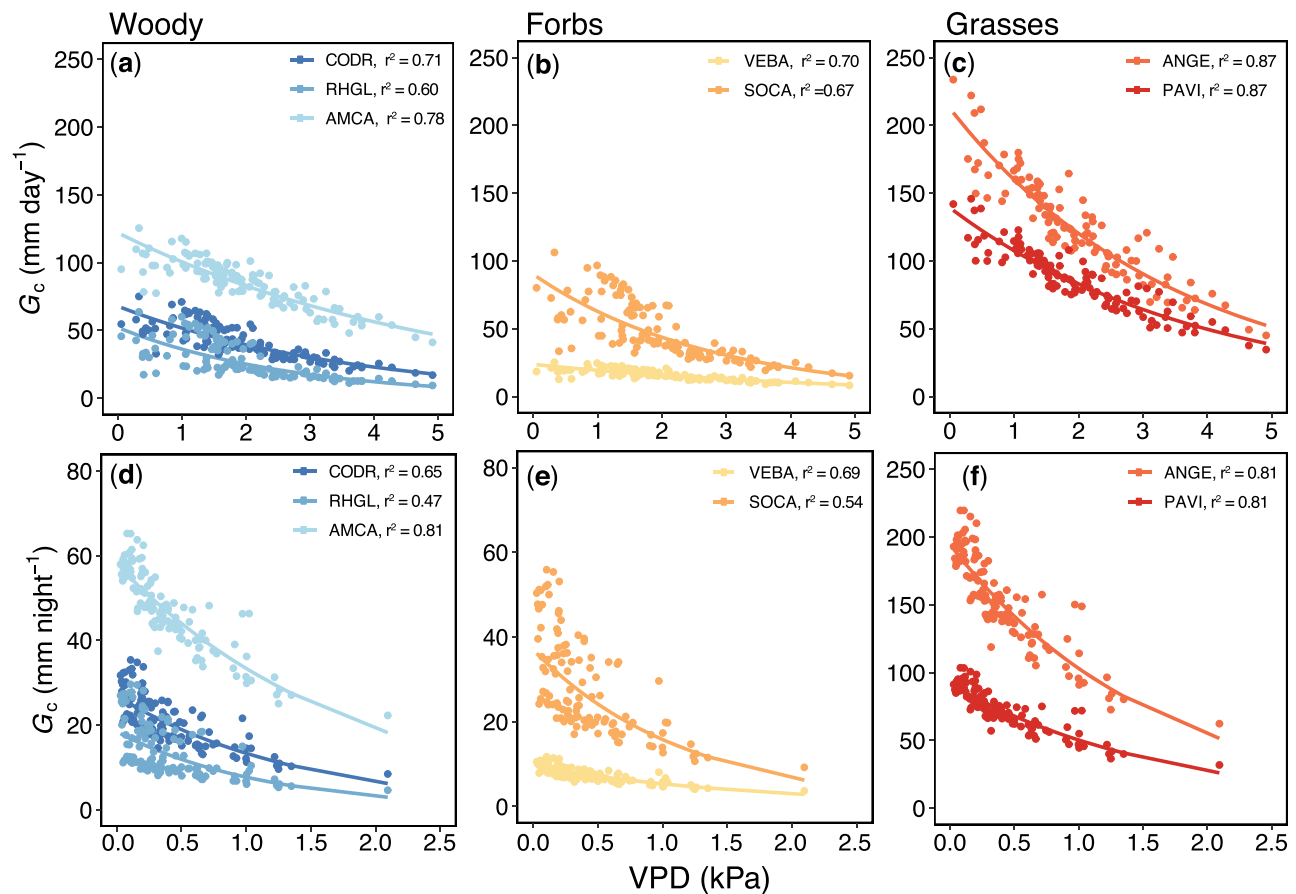


Figure 6. Relationships of mean diurnal canopy conductance with vapor pressure deficit measured at average daily maximum (15:00 hr) conditions (a–c) and mean nocturnal canopy conductance with vapor pressure deficit measured at average daily minimum (03:00 hr) conditions (d–f). Shown are regression curves for the corresponding log-linear model for woody species (a, d) including *C. drummondii* (CODR), *R. glabra* (RHGL), and *A. canescens* (AMCA); forbs (b, e) including *V. baldwinii* (VEBA) and *S. canadensis* (SOCA); and grasses (c, f) including *A. gerardii* (ANGE) and *P. virgatum* (PAVI). r^2 values are provided for all species, but only relationships with $r^2 > 0.20$ are indicated with regression lines. Corresponding statistics are presented in Table S5.

control over transpiration than the clonal shrubs. Tight stomatal control might be used to maintain the fairly static flux rates exhibited by these species (Figure 2), especially considering that grasses primarily utilize shallow soil water (Kulmatiski & Beard, 2013; Nippert & Knapp, 2007; Priyadarshini et al., 2015) that declines precipitously throughout the growing season (Figure 1a).

Conversely, *C. drummondii* and *R. glabra* are clonal shrubs that possess functional deep roots (Weaver, 1968; Weaver & Darland, 1949) and can shift reliance from shallow to deep water during dry periods (Ratajczak et al., 2011). As such, *C. drummondii* likely utilized shallow water during the early, wetter portion of the growing season, which would explain the high daily E_c exhibited by this species when VPD was lower (Figure 2a). If *C. drummondii* shifted reliance to deeper water as shallow soils dried, these shrubs would reduce competition with neighboring grasses and potentially allow grasses to increase E_c during the middle of the growing season (Figures 2f and 2g). This water use strategy also results in a physiological decoupling from climate fluctuations (Muench et al., 2016; Nippert et al., 2013), promotes clonal growth as water is transferred from deep roots to expanding clonal stems via rhizomes (Ratajczak et al., 2011), and likely allows these shrubs to maintain high, static flux rates over time (Figure 2). As such, these species will likely exhibit high E_c in the future, despite climate fluctuations, provided that deep water stores are available. *A. canescens*, which is a nonclonal subshrub, exhibited responses to environmental variables that were more similar to those of the C_4 grasses. Thus, difference in water use strategies of clonal versus nonclonal shrubs may contribute to the greater expansion rates of clonal shrubs compared to nonclonal shrubs in the Great Plains (Ratajczak et al., 2014).

Interestingly, we detected strong relationships between G_C and soil moisture and between E_C and soil moisture but only in forbs and woody species and primarily at higher VPD ranges (Figures S3–S8). Thus, the importance of soil moisture as a driver of plant water flux is likely dependent on a sufficient atmospheric driving gradient. The lack of a relationship between soil moisture and canopy-level fluxes for all species is somewhat unexpected and may have occurred because VPD increased throughout the growing season as shallow soil moisture decreased (Figure 1), weakening the relationship between E_C and soil moisture for species that rely on shallower soil water. Alternatively, most E_C measurements occurred over a rather narrow window of shallow soil moisture values (~ 0.10 – 0.20% ; Figures S3–S5), and E_C may simply be less sensitive to small changes in soil moisture than G_C in certain species. Of the species measured, G_C was least sensitive to soil moisture in grasses and was the most sensitive to soil moisture in *C. drummondii*, *R. glabra*, and *S. canadensis* (Figure S5). Grasses had consistently high G_C despite seasonal shifts in soil moisture, which is likely related to their competitive use of shallow water described above.

Finally, we found that the sensitivity of E_C to environmental drivers varied throughout a 24-hr period. Diurnal E_C exhibited a saturating relationship with VPD, where E_C increased with greater VPD until reaching a threshold at about 1.5 kPa (Figure 5). The threshold at which diurnal E_C no longer increased is likely related to the concomitant stomatal closure observed with increasing VPD (Figure 6). Interestingly, nocturnal E_C did not appear to experience the same VPD threshold even though stomatal closure also occurred with increasing VPD at night. This suggests that nocturnal E_C might be driven by a variety of factors in addition to VPD (e.g., wind speed, Karpul & West, 2016; and circadian rhythm, Resco de Dios et al., 2016). The strength of the relationship of E_C with VPD increased at night compared to during the day, particularly for grasses, which is consistent with the notion that atmospheric coupling is greater at night (Wullschlegel et al., 2000). Considering that air temperatures in this region will increase with future climate changes (Christensen et al., 2007; Zambreski et al., 2018) and will likely occur to a greater extent at night (Davy et al., 2017), concomitant increases in VPD may increase nocturnal E_C in grasses disproportionately over other species in tallgrass prairies. High rates of nocturnal E_C have the potential to create hydrological deficits and also reduce primary productivity in grasslands, as grasses deplete soil moisture without gaining carbon via photosynthesis.

4.4. Model Considerations

As with any model (Box et al., 1978), we made several simplifying assumptions when adapting the StaCC model for use in an herbaceous ecosystem. First, we assumed that water flux scales linearly with stem cross-sectional area and that stem capacitance is negligible. While previous research has shown that flux rates vary radially (Phillips et al., 1996) and with capacitance dynamics in tree stems (Phillips et al., 2003), radial patterns of sap flow and water storage are less likely to occur in small stems and herbaceous plants. Second, we assumed that functional xylem is contained within the entire cross section of each stem, which likely overestimated conducting area and did not account for potential variation in the proportion of functional xylem within the stem area between species or functional types. Thus, we likely overestimated E_C to a certain extent when scaling sap flux to the canopy level. Finally, we assumed that LAI and CAI were constant throughout the growing season. While these parameters likely increase with plant growth throughout the season (Klodd et al., 2016), we did not have continuous high temporal resolution estimates of LAI or CAI and instead used species-averaged estimates.

Despite these simplifications, we provided reasonable estimates of water flux across a range of herbaceous and woody species. For example, we estimated that daily maximum E_C varied between approximately 0.5 and 3.0 mm day^{−1} (Figure 2), which is comparable to eddy flux data that estimated maximum daily ET as 6 mm day^{−1} for this same watershed in 2014 (Brunsell et al., 2017). We also estimated that cumulative growing season E_C for these species was 732.5 and 171.5 mm during the day and at night, respectively. Considering that these species are among the most abundant at this site and the majority of their growth occurs between May and September, these estimates likely represent a large portion of the water used annually by this tallgrass prairie. Comparatively, Logan and Brunsell (2015) used eddy flux data to estimate that annual daytime ET at this same prairie varied between 600 and 700 mm over 3 years (2008–2009 and 2011). Our cumulative daytime E_C also falls within the range of ET estimates made for other tallgrass prairies (Bremer et al., 1996); annual ET estimates for other North American tallgrass prairies range anywhere

between 710–750 mm (Burba & Verma, 2005), 485–716 mm (Wagle et al., 2017), and 919 mm (Bajgain et al., 2018). Variation in precipitation, site characteristics, and management regimes likely explain the wide range of ET estimates described by these studies. Finally, we did estimate greater than expected G_C in grasses based on typical leaf gas exchange measurements (O’Keefe & Nippert, 2018), but this result likely occurs from high stem density and CAI for the grass species measured here (Table S1).

5. Conclusions

Overall, these observations have significant implications for understanding the consequences of woody encroachment in tallgrass prairies. We hypothesized that woody species would have greater rates of canopy transpiration during the day and at night and would also be less sensitive to fluctuations in microclimate than co-occurring herbaceous species. In support of this, we found that diel and cumulative E_C was greatest in *C. drummondii*, while nocturnal E_C was greatest in both grasses and *C. drummondii*. Therefore, nocturnal water loss may continue to account for a large amount of water lost from grasslands despite ongoing woody encroachment. Additionally, we found differing responses of woody and herbaceous functional types to different environmental drivers. Grasses exhibited greater stomatal control over transpiration than shrubs, which likely contributes to their static flux rates despite seasonal declines in shallow soil moisture. Woody species were less sensitive to changes in VPD but still exhibited high, static flux rates, which was likely facilitated by their use of soil moisture from deeper soil layers. If woody species continue to expand in this ecosystem, shallow water depletion might decrease following reductions in grass cover and abundance. However, if woody species continue to use deep water stores despite climate fluctuations, woody encroachment might create severe hydrological deficits for this ecosystem. Thus, shifts in the abundances of these species with future ecosystem state changes would not only impact tallgrass prairie diversity and productivity (Collins et al., 1998; Knapp et al., 2002; Smith & Knapp, 2003) but also ecosystem-level water fluxes (Logan & Brunsell, 2015; Scott et al., 2008; Wang et al., 2010). Future estimates of water balance in encroached grasslands would benefit from model parameterization with continuous measurements of species-specific, whole-plant water fluxes, particularly in different grasslands experiencing contrasting mechanisms of woody encroachment (Huxman et al., 2005).

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