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Comparative ecohydrology between *Cornus drummondii* and *Solidago canadensis* in upland tallgrass prairie

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Abstract Woody species expansion threatens to transform mesic North American grasslands. In many tallgrass prairies of the central Great Plains with deep soil, *Cornus drummondii* develops large shrub islands that exhibit non-linear increases in cover through time. Reliance on soil moisture from deeper soil depths facilitates constant gas exchange rates and minimizes competition with coexisting herbaceous species. Conversely, *C. drummondii* growth and expansion in thin-soil locations is stochastic and these locations are typically free of large shrub islands. At the Konza Prairie in northeast Kansas, USA, we compared the ecohydrology of *C. drummondii* individuals to a similar-sized forb (*Solidago canadensis*) in thin-soil locations with varying fire frequency (4-, 20-year) and grazer abundance (bison present or absent). Gas exchange rates were relatively constant for *C. drummondii*, while *S. canadensis* declined across the growing season. For *S. canadensis*, maximum photosynthesis ($A_{\max}$), daytime transpiration (E), and stomatal conductance (g_s) were higher on ungrazed than grazed treatments. Nighttime E rates were higher in *C. drummondii*, accounting for over 10 % of the daytime E rates. The water source used did not vary among contrasts, with the majority of water uptake occurring from 30 cm depth for both species. These results highlight a unique ecohydrology of *C. drummondii* (static water flux, and high rates of nighttime E) compared to a similar-sized, co-occurring forb. Whereas *C. drummondii* is infrequent in thin-soil locations, the climate conditions occurring during measurements were not a likely filter restricting persistence. Rather, drier conditions or interactions with other grassland disturbances are likely required to restrict *C. drummondii* encroachment in the thins-soil locations of tallgrass prairie.

Keywords Konza Prairie · Mesic grassland · Photosynthesis · Stable water isotopes · Transpiration · Woody encroachment

Introduction

The tallgrass prairie of the central United States was a landscape historically maintained by fire, which typically minimized woody vegetation in regions outside of riparian corridors (Abrams et al. 1986; Gibson and Hulbert 1987). Anthropogenic land-use changes in the western region of this ecosystem have resulted in an expansion of C_3 woody plant species,

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negatively affecting the historically dominant C_4 grasses (Abrams et al. 1986; Briggs et al. 2002). When tallgrass prairie is not burned more frequently than every 4 years, this ecosystem can transition to a shrubland, reducing management options for future return to a grassland state (Briggs et al. 2005; Ratajczak et al. 2014). The transition from grassland to shrubland can reduce plant biodiversity (Ratajczak et al. 2012) and ultimately impact site biogeochemistry and ecosystem carbon balance (McCarron et al. 2003; Knapp et al. 2008; Barger et al. 2011; Logan and Brunsell 2015).

The primary factors causing increased woody plant cover in tallgrass prairie include elevated atmospheric CO_2 concentrations, changes in grazing interactions, and fire suppression (Polley et al. 1997; Roques et al. 2001). Decreased fire frequency has caused exaggerated expansion of the woody encroacher, rough-leaf dogwood (*Cornus drummondii* C.A. Mey.), within the tallgrass prairies of Kansas (Briggs et al. 2002; Ratajczak et al. 2014). *Cornus drummondii* forms clonal islands with decreased graminoid growth in their understory resulting from low light availability (Lett and Knapp 2005; Ratajczak et al. 2011). Once these clonal islands are established, frequent fires no longer regulate woody expansion as fire does not carry because of reduced fine–fuel accumulation in the island's understory (Lett and Knapp 2005; Ratajczak et al. 2011). *C. drummondii* also develops deep roots in the center of the clonal island that transfer water via rhizomatous connections to developing stems in the grass matrix on the island periphery (Ratajczak et al. 2011). This transfer of resources provides access to a stable source of water for developing stems and reduces competition with shallow-rooted grasses for soil moisture in the top 30 cm of the soil (Ratajczak et al. 2011; Nippert et al. 2013). The greater reliance on a deep and stable water source and avoidance of competition with grasses for surface soil moisture permits rough-leaf dogwood to persist during moderate droughts and facilitates expansion in this C_4-grass dominated landscape (McCarron and Knapp 2001; Ratajczak et al. 2011; Nippert et al. 2013).

In the Flint Hills of eastern Kansas, USA, tallgrass prairie exists across a weathered landscape, with shallow, thin-soil in upland topographic positions and loess-deposits producing deeper soils in lowland topographic positions (Oviatt 1998). In upland locations with thin-soils, the advantage of reliance on a deep-water source is reduced, as all plants must compete for similar sources of soil moisture in a reduced soil volume. Shallow-rooted prairie plants typically exhibit variable water source uptake strategies (Nippert and Knapp 2007) and physiological drought tolerance (Tucker et al. 2011) because shallow soils dry faster, support a smaller total volume of soil water, and are inaccessible to groundwater (Nippert et al. 2011). While many grass and forb species are abundant and exhibit stable populations over time in upland soils (Turner et al. 1995; Collins and Calabrese 2012), woody species typically have reduced abundance and cover in these locations (Ratajczak et al. 2014), suggesting that woody plants are unable to persist in dry locations or are poorer competitors for water than shallow-rooted plants. Consequently, the shallow soils of the upland tallgrass prairie are a presumed regulator of woody encroachment (Ratajczak et al. 2014). However, little is known about how woody encroachers use water in xeric, upland soils, or if ecohydrological and gas exchange responses in upland locations are similar to those previously reported in lowland locations.

The objective of this research was to quantify the ecohydrology (diel flux patterns and source water use) of *C. drummondii* in upland (thin-soil) locations of tallgrass prairie. We compared daytime and nighttime transpirative fluxes of *C. drummondii* with Canada goldenrod (*Solidago canadensis* L.), a large C_3 forb that is common in thin-soil regions of tallgrass prairie. *S. canadensis* was chosen for comparison because it is of similar size and leaf area to rough-leaf dogwood (prior to *C. drummondii* clonal island formation). We predicted that *C. drummondii* would have more static water flux patterns, based on previous research across a range of size classes and in lowland locations (Nippert et al. 2013). By comparison, we predicted that *S. canadensis* would have more dynamic water flux patterns, with higher fluxes during periods with greater soil moisture availability and reduced flux during periods of soil moisture stress. Similar to predictions of daytime water flux, rates of nighttime transpiration were predicted to be higher and more static in *C. drummondii* than in *S. canadensis*. Given that the tallgrass prairie ecosystem is regulated by fire frequency x grazing interactions (Knapp et al. 1998), we hypothesized water flux rates might vary among species according to management legacies within this grassland.

Materials and methods

Study location

This research was performed at the Konza Prairie Biological Station (KPBS), a 3487-ha unplowed tallgrass prairie ecosystem located in northeast Kansas, USA (39.0931°N, 96.5586°W). KPBS consists of watershed-level experimental manipulations of fire frequency (1-, 2-, 4-, 20-year burn frequencies) and grazer abundance (grazed by bison or cattle, or ungrazed). The landscape topography of the site is variable, reflecting erosional patterns of the layered chert and limestone bedrock. The weathering mosaic has resulted in thin-soil upland locations (typically Florence soil series) and deep-soil lowland locations (typically Tully soil series).

From 1982 to 2014, the average annual rainfall on site was 829 ± 175 mm (±1 SD), of which 73 % of the total rainfall occurred during the vegetation growing season (April-September). Precipitation during 2014 was 706 mm, with 480 mm during the growing season. During 1982–2014, January was the coldest month of the year with average maximum and minimum air temperatures of 4.87 ± 3.24 °C and −7.14 ± 2.30 °C (±1 SD), respectively. July was the hottest month of the year, with average maximum and minimum air temperatures of 32.69 ± 2.02 °C and 19.78 ± 1.49 °C (±1 SD), respectively. July, 2014 had air temperatures similar to the long-term averages, with an average maximum and minimum temperature of 31.7 °C and 17.05 °C.

Experimental design

Data were collected from four different experimental watersheds at KPBS that include 4- and 20-year burn frequencies without bison present (watershed ID: 4B and 20B) and with bison present (N4D and N20B). Within each watershed, five replicate locations were selected in upland locations where *Solidago canadensis* (Canada goldenrod) and *Cornus drummondii* (rough-leaf dogwood) were present within 3 m proximity. We selected *C. drummondii* individuals of similar physiognomy as *S. canadensis* (~ 1 to 1.25 m) that had yet to develop the clonal 'dogwood island' structure common to this species in deep-soil locations on KPBS.

Environmental data

Environmental data were recorded as 30-min averages in the upland location of watershed 4B using a CR10X datalogger (Campbell Scientific Inc. Logan, UT). Soil moisture at 10 cm and 30 cm depths were recorded using Hydraprobe II sensors (Stevens Water Monitoring Systems, Portland, OR 97220), and air temperature (100 K thermistor, Betatherm, Hampton, VA) and relative humidity (HMP60-L, Vaisala Inc., Vantaa, Finland) were measured in an enclosed radiation shield (41003, RM Young, Traverse City, MI). Measured relative humidity and air temperature were used to calculate the vapor pressure deficit (VPD), reported here at the average minimum (3 a.m.) and maximum (3 p.m.) daily conditions.

Gas exchange measurements

Within each sampling location per watershed, one individual from each species was permanently marked for repeated leaf gas exchange measurements throughout the summer of 2014. Some *S. canadensis* phytomers were trampled by grazers or died throughout the course of the summer. In this situation, we then measured gas exchange on an adjacent phytomer for the remainder of the summer. Gas exchange measurements occurred on 6 dates (2014 day of year—164, 174, 182, 190, 200, 204), corresponding with the period of peak growth during the growing season. Day of year 164 in 2014 corresponded with June 13, 2014.

Leaf-level gas exchange (maximum photosynthetic rate—$A_{\max}$; stomatal conductance to vapor—g_s; leaf transpiration—E) was measured using a Li-6400 open-system gas analyzer (Li-Cor, Inc., Lincoln, NE). Gas exchange was measured on the largest and healthiest looking leaves of each individual/species between 10:00 and 16:00 h for 'daytime' measurements and between 22:00 and 03:00 for 'nighttime' measurements on the same leaf/individual within each sampling period. Sample order was randomized between sample periods to minimize any variability associated with measurement time of day. Ongoing work from this site has shown a lack of midday stomatal depression and consistent gas exchange rates during the 'daytime' and 'nighttime' periods used here (O'Keefe, unpublished data). Conditions within the cuvette were maintained at ambient levels ($[CO_2] = 400$ μmol CO_2 mol^{-1}, relative humidity = 40 − 60 %, and photosynthetically active radiation = 2000 μmol m^{-2} s^{-1} photon flux density). During nighttime measurements, lights within the cuvette were kept off. Leaves were allowed to stabilize for 2–5 min in the cuvette before measurements were recorded.

Stable isotope measurements

Within each watershed, three sampling locations were selected for stable isotopic measurements. Individuals from each species were selected based on close proximity (~3 m) and comparable size to the individuals measured for gas exchange. Samples were collected between 12:00 and 15:00 (midday) and 23:00–2:00 (midnight) on 07/14/2014 and 08/20/2014. For *S. canadensis*, non-photosynthetic stem tissue was collected at ground-level, whereas stem tissue from low branches was collected from *C. drummondii*. Soil samples were collected at 10- and 30-cm depth within each sampling location using a hand auger. These soil depths were selected based on previous source water analysis for *C. drummondii* individuals at KPBS (Ratajczak et al. 2011). Given the rocky nature of these upland soils, sample collection beyond 30 cm depth was not possible. Stem and soil samples were stored in Exetainer vials (Labco, Ltd) at 5 °C until analysis.

Water was cryogenically extracted from plant stem and soil samples under vacuum and then analyzed for the stable oxygen ($\delta^{18}O$) and hydrogen (δD) isotope ratios in the Stable Isotope Mass Spectrometry Laboratory at Kansas State University. Water samples were analyzed using a Picarro WS-CRDS isotopic water analyzer using ChemCorrect software to identify possible interference or sample contamination. The stable isotopic ratios of water samples ($\delta^{18}O$ and δD) are reported as deviations from international standards using δ- notation in parts per thousand (‰):

$$\delta = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000\right],$$

where R is the absolute ratio of the rare to common isotope, respectively. Variability of working standards within runs were <0.3 and 0.8 ‰ (for $\delta^{18}O$ and δD) and analysis of QA/QC standards were within 0.20 ‰ of the calibrated value. The Bayesian isotopic mixing model SIAR was used to quantify the proportion of deep and shallow water sources in the isotopic signature of the plant xylem water (Parnell et al. 2010).

Statistical analysis

Gas exchange data were analyzed using a linear mixed-effects model with species, fire frequency, bison presence, and sampling date as fixed effects and plant ID as a random effect. Assessment of gas exchange differences among species or treatments within a time period were assessed using Tukey's HSD. All data were analyzed with the 'lme4' package V1.1-7 (Bates et al. 2014) in the open-source statistical program R V3.1.0 (R Core Team 2012).

Results

Soil moisture at 10 and 30 cm declined over the course of the growing season with the highest recorded values between DOY 160–170 and the lowest values at DOY 220 (Fig. 1a). A 35 mm rain event on DOY 220 increased 10 cm soil moisture and a 32 mm rain event on DOY 243–244 increase soil moisture at both measured depths (Fig. 1a). The vapor pressure deficit (VPD) was variable over the course of the growing season (Fig. 1b). Maximum values for diurnal and nocturnal VPD occurred on DOY 235/236, respectively (Fig. 1b).

Gas exchange responses including $A_{\max}$, g_s (day and night), and E (day and night) varied significantly ($p < 0.05$) over the course of the growing season, with differences among species and among grazing treatments (Table 1; Fig. 2). For *C. drummondii*, rates of $A_{\max}$, g_s, and E were similar among grazing treatments and constant over the course of the growing season (Fig. 2). Daytime gas exchange rates declined across the growing season for *S. canadensis.* Rates were higher for *S. canadensis* than *C. drummondii* over the 2–3rd sampling dates, but were lower in the forb than shrub over the final 2 sampling dates (Fig. 2a–f). *C. drummondii* had higher rates of g_s and E at night compared to *S. canadensis* (Fig. 2i, j). For *C. drummondii*, these rates did not vary in the grazed treatment, but declined over time in the ungrazed treatment (Fig. 2i, j).

Leaf gas exchange responses varied significantly by burning*grazing*date interactions ($P < 0.05$)

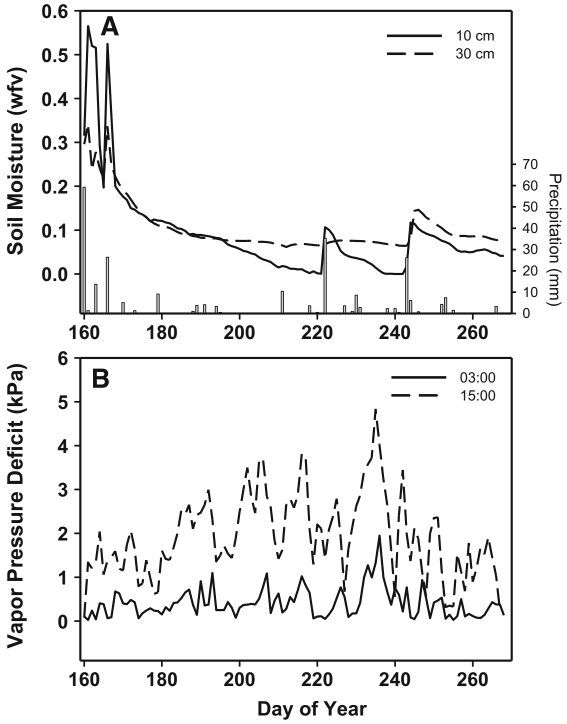

Fig. 1 Changes in environmental data from the upland location on watershed 4B between day of year 160–270, 2014. In **a**, soil moisture at 10 cm and 30 cm are presented as daily averages as water fraction by volume, whereas daily rainfall is reported as a cumulative daily value. In **b**, the vapor pressure deficit (VPD) is reported at the time period corresponding with the average daily minimum (3 a.m.) and maximum (3 p.m.) conditions

(Table 1; Fig. 3). In both the 4-year and 20-year burned watersheds, $A_{\max}$ was relatively constant in the grazed watershed but declined over time in the ungrazed watershed (Fig. 3a, b). For the 4-year burn frequency, g_s was the highest in the ungrazed watershed for the first sampling date (DOY 164), but lowest on the last sampling date (DOY 204) (Fig. 3c). E was highest on the first two sampling dates in the ungrazed watershed for the 4-year burn, but no differences in E were present among grazing contrasts for the remainder of the growing season (Fig. 3e). For the 20-year burn frequency, g_s (Fig. 3d) and E (Fig. 3f) had a decreasing trend over the growing season between the second to the sixth sampling points.

Nighttime E varied significantly between species and between grazing and burning treatments (Table 1). *C. drummondii* had the highest rates of nighttime %E (>10 % of daytime water flux), with no significant differences over time, grazing, or burning treatments (Table 1; Fig. 4). Rates were higher in the 4-year burn treatment than the 20-year burn treatment for *S. canadensis* (Fig. 4).

Differences in the source of water uptake between day- and night-time periods were investigated using the oxygen and hydrogen isotopic signature of water extracted from plant xylem and soil at 2 depths. Both species proportionally used the majority of water from 30 cm soil depth, and this source water reliance did not vary between dates of sample collection (Table 2).

Discussion

Topography influences site ecohydrology because upland soils are generally drier, coarser, shallower, and experience greater runoff than deep soils in lowland topographic positions (Wu and Archer 2005; Nippert et al. 2011). At the Konza Prairie, *C. drummondii* does not establish large clonal islands in shallow upland soils, despite having widespread cover, and abundance in lowland topographic locations (Ratajczak et al. 2014). Here, we proposed that *C. drummondii* in upland locations would have static leaf-level ecohydrology compared to more variable patterns in a common coexisting forb species. During the 2014 growing season, precipitation was below-average, but within 1 standard deviation of the long-term mean. Soil moisture declined over the vegetative sampling period (Fig. 1a), but *C. drummondii* exhibited relatively constant flux rates compared to *S. canadensis*. *C. drummondii* also had higher rates of nighttime transpiration, accounting for >10 % of daytime rates. Static physiological responses during the growing season are similar to previous research on *C. drummondii* conducted across many locations at Konza (Nippert et al. 2013), which did not illustrate water limitation as a filter regulating long-term persistence of *C. drummondii* in the thin-soils of upland tallgrass prairie.

The two species measured here had varying seasonal patterns of gas exchange in response to changes in soil moisture availability. Many tallgrass prairie plant species adjust seasonal gas exchange rates in drier topographic locations, or during periods of extreme drought (Hoover et al. 2014). Dynamic leaf-level physiological responses are common during conditions when drought and grassland disturbance co-occur (Knapp 1985). In the results shown here, *C.*

Table 1 Linear mixed-effects model of gas exchange responses with species, grazing, burn interval, and sample date as fixed effects, and plant as a random effect

	A_{max}	$g_{\text{s day}}$	E_{day}	$g_{\text{s night}}$	E_{night}	% E_{night}
Species						
F	5.864	0.243	0.016	170.288	188.339	88.228
P	0.0213*	0.626	0.901	<0.001*	<0.001*	<0.001*
Grazing						
F	0.584	0.688	5.091	5.676	5.849	2.204
P	0.450	0.413	0.031*	0.018*	0.017*	0.147
Burn						
F	0.486	0.166	0.811	1.624	4.299	4.381
P	0.499	0.687	0.375	0.204	0.040*	0.044*
Date						
F	33.659	64.908	74.717	6.000	2.529	1.940
P	<0.001*	<0.001*	<0.001*	<0.001*	0.031*	0.091
Species* Grazing						
F	0.028	0.093	0.005	0.476	0.730	0.017
P	0.868	0.762	0.942	0.491	0.394	0.898
Species*Burn						
F	0.346	0.132	0.220	0.253	0.004*	1.132
P	0.560	0.719	0.642	0.615	0.951	0.295
Burn* Grazing						
F	2.115	2.300	5.014	0.022	0.223	0.113
P	0.156	0.139	0.032*	0.883	0.637	0.739
Species*Date						
F	9.303	6.938	11.540	5.659	3.586	2.154
P	<0.001*	<0.001*	<0.001*	<0.001*	0.004*	0.062
Grazing *Date						
F	10.546	12.039	11.592	1.718	1.968	1.467
P	<0.001*	<0.001*	<0.001*	0.132	0.085	0.204
Burn*Date						
F	1.417	1.625	1.673	1.089	0.636	1.248
P	0.221	0.156	0.144	0.368	0.673	0.290
Species* Grazing *Burn						
F	0.683	4.128	2.548	2.287	1.319	0.712
P	0.415	0.051	0.120	0.132	0.252	0.405
Species* Grazing *Date						
F	5.090	2.719	4.531	1.411	1.781	1.144
P	<0.001*	0.022*	0.001*	0.222	0.119	0.340
Species*Burn*Date						
F	0.891	1.695	2.136	0.961	0.360	0.412
P	0.489	0.139	0.064	0.443	0.875	0.840
Grazing *Burn*Date						
F	2.674	5.835	5.867	0.762	1.446	1.237
P	0.024*	<0.001*	<0.001*	0.579	0.210	0.295
Species* Grazing *Burn *Date						
F	0.401	0.823	0.887	0.785	0.891	0.533
P	0.847	0.535	0.491	0.562	0.488	0.751

Shown are *F*- and *P*-values for CO_2 assimilation at ambient C_a, A_{max}, daytime stomatal conductance of water vapor, $g_{\text{s day}}$ (mol m^{-2} s^{-1}), daytime transpiration rate, E_{day} (mmol m^{-2} s^{-1}), nighttime stomatal conductance of water vapor, $g_{\text{s night}}$ (mol m^{-2}s^{-1}), nighttime transpiration rate, E_{night} (mmol m^{-2} s^{-1}), and percent E_{night} of E_{day}. Significance is indicated at the $\alpha = 0.05$ level with an asterisk (*)

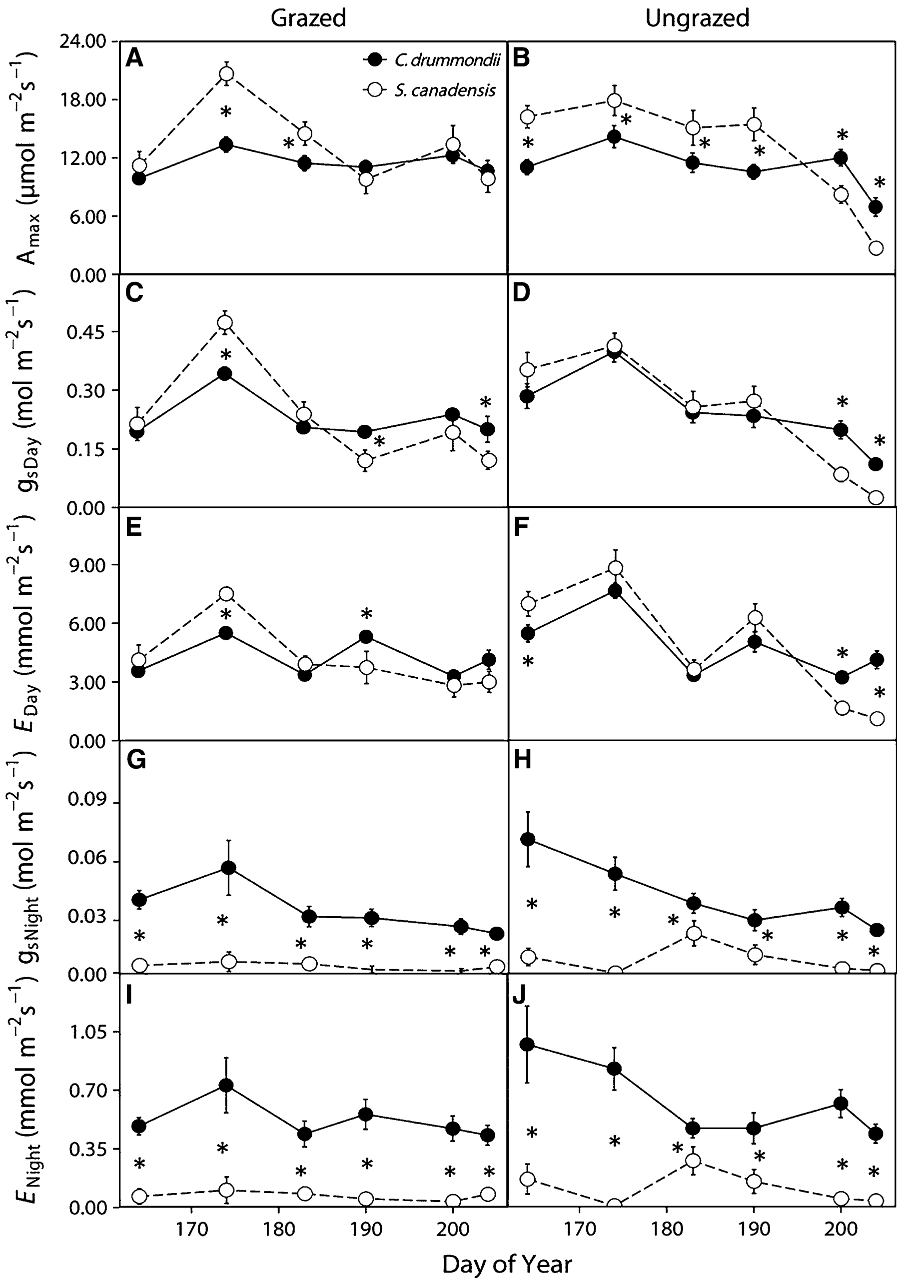

Fig. 2 Leaf gas exchange responses of *C. drummondii* and *S. canadensis* to grazing treatments (grazed and ungrazed) over time, including (**a**, **b**) CO_2 assimilation at ambient C_a, A_{max}, (**c**,**d**) daytime stomatal conductance of water vapor, $g_{s\ day}$, (**e**,**f**) daytime transpiration rate, E_{day}, (**g**, **h**) nighttime stomatal conductance of water vapor, $g_{s\ night}$, and (**i**,**j**) nighttime transpiration rate, E_{night}. Shown are mean ± 1 SEM. Asterisks indicate significant differences ($P < 0.05$) among species within a sampling date

drummondii had low variability in transpiration fluxes when assessed temporally or between different grazing treatments, in contrast to responses for *S. canadensis*. The lack of differences in *C. drummondii* gas exchange between burned and unburned sites varies from previous work conducted in mature shrub islands in lowland locations (McCarron and Knapp 2003). Differences in *C. drummondii* age, size, and in soil depth between upland and lowland locations likely account for differences measured here versus McCarron and Knapp (2003). We hypothesized that gas exchange responses would vary according to landscape treatments of grazing and burn frequency, given the fundamental role of these treatments in this ecosystem. Indeed, gas exchange rates varied among burning and grazing contrasts, with the lowest rates

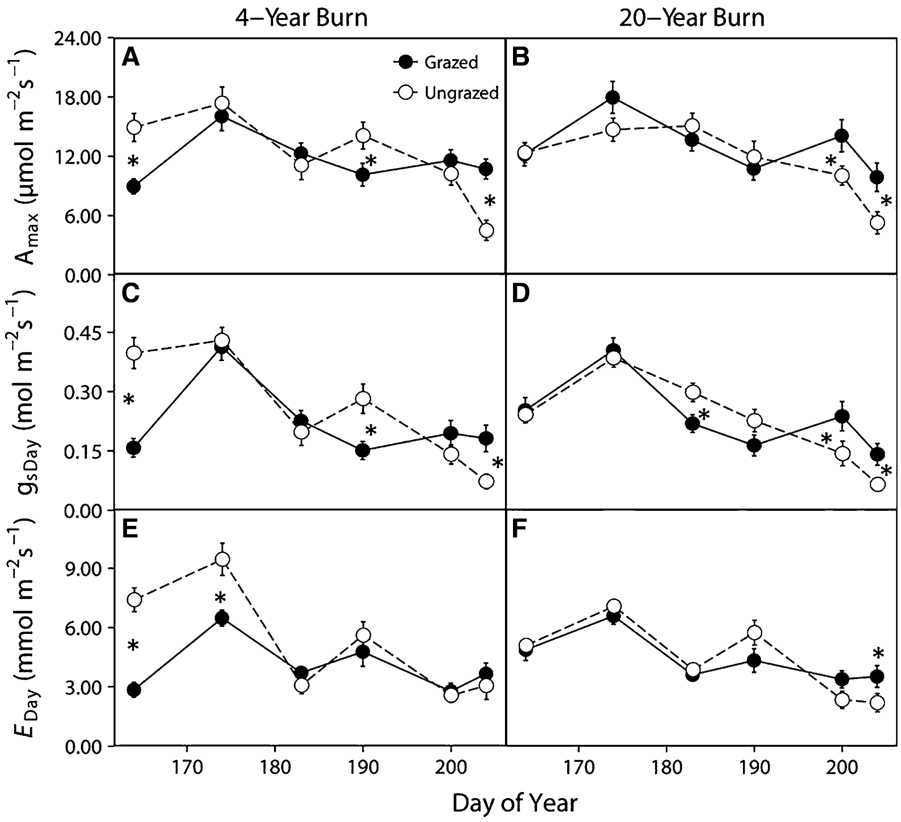

Fig. 3 Leaf gas exchange responses for ungrazed and grazed locations to burning treatments (4-year burn and 20-year burn) over time, including (**a**,**b**) CO_2 assimilation at ambient C_a, A_{max}, (**c**,**d**) daytime stomatal conductance of water vapor, $g_{s\ day}$, (**e**, **f**) daytime transpiration rate, E_{day}, (**g**,**h**) nighttime stomatal conductance of water vapor, $g_{s\ ni1ght}$, and (**i**, **j**) nighttime transpiration rate, E_{night}. Shown are mean ± 1 SEM. Asterisks indicate significant differences ($P < 0.05$) among grazing treatments within a sampling date

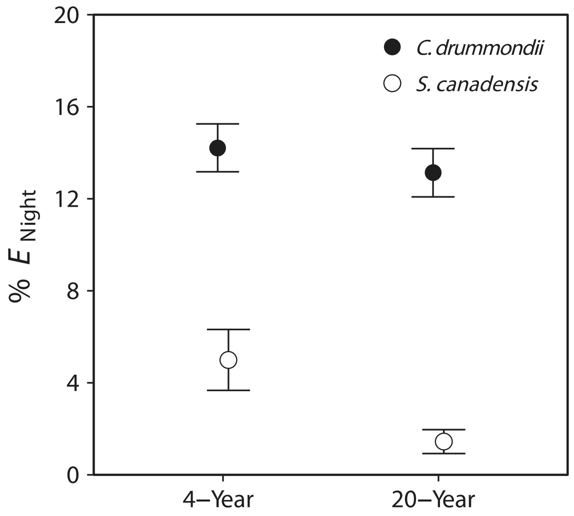

Fig. 4 Percent nighttime transpiration rate (% E_{night}) of daytime transpiration rate for *C. drummondii* and *S. canadensis* in 4-year and 20-year burned watersheds. Shown are mean ± 1 SEM

early in the growing season in the grazed, 4-year burned location (Fig. 3). By the last sampling date, rates of gas exchange were typically higher in grazed versus ungrazed locations (Fig. 3).

We also found that *C. drummondii* and *S. canadensis* were using roughly the same water source in the uplands and that neither was reliant on water from the shallowest soil layer, suggesting that both species have access to the same source of water. Despite these similarities in water source, *C. drummondii* had consistently higher rates of water flux than *S. canadensis*, indicating that *C. drummondii* uses water less conservatively or had access to a greater total volume of soil water than *S. canadensis*. A less conservative water-use strategy would potentially be a disadvantage during periods with prolonged drought or drier conditions than measured in 2014. Drought events in this ecosystem occur with regularity, and with varying intensity (Hoover et al. 2014). McCarron

Table 2 Proportion of shallow (10 cm) and deep (30 cm) water used by *C. drummondii* and *S. canadensis* during the day and at night

	Day		Night	
	Shallow	Deep	Shallow	Deep
Species				
C. drummondii	0.066 (0.000–0.141)	0.934 (0.859–1.002)	0.031 (0.000–0.084)	0.969 (0.916–1.004)
S. canadensis	0.022 (0.000–0.062)	0.978 (0.938–1.003)	0.035 (0.000–0.095)	0.965 (0.905–1.004)
Grazing				
Grazed	0.026 (0.000–0.074)	0.974 (0.926–1.003)	0.032 (0.000–0.091)	0.968 (0.909–1.004)
Ungrazed	0.060 (0.001–0.122)	0.940 (0.878–0.999)	0.039 (0.000–0.099)	0.961 (0.901–1.004)
Burn				
4-year	0.032 (0.000–0.088)	0.968 (0.912–1.004)	0.040 (0.000–0.108)	0.960 (0.892–1.005)
20-year	0.030 (0.000–0.079)	0.970 (0.921–1.003)	0.028 (0.000–0.077)	0.972 (0.923–1.003)

Presented are mean estimates with 95 % credibility intervals in parentheses for each species, grazing treatment, and burn treatment

and Knapp (2003) have shown significant seasonal photosynthetic declines correlated with reductions in predawn water potential in *C. drummondii* in lowland locations, illustrating the potential for susceptibility to water stress in this species.

The species measured here exhibited varying nighttime water use patterns. Little is known about nighttime water flux in grassland plants because it is typically assumed that stomata close at night to conserve water when photosynthesis ceases. However, recent studies have found that nighttime transpiration occurs in some plant species with the potential to reduce water-use efficiency, daytime transpiration rates, predawn and midday leaf water potential, and soil water availability (Caird et al. 2007; Daley and Phillips 2006; Snyder et al. 2003). Thus, nighttime transpiration may affect the ecohydrology and realized niche of a species, and could affect the ability of *C. drummondii* to persist in dry locations of the tallgrass prairie. We found that nighttime transpiration rates were consistently higher in *C. drummondii* than in *S. canadensis*. Additionally, *C. drummondii* nighttime water flux accounted for >10 % of its daytime water flux while the nighttime flux for *S. canadensis* was ~2 % of its daytime water flux. This is surprising because both species were located in similar soils and utilized the same water source. High nighttime transpiration in *C. drummondii* may therefore be a trait adapted to wetter locations like deep-soiled lowland prairies where the cost of water loss has marginal impact on the ecology and ecohydrology of the individual. In shallow upland soils, however, this trait may ultimately serve as a key disadvantage to *C. drummondii* during periods with more severe water limitation than seen in 2014.

In summary, our results show that *C. drummondii* exhibited static photosynthesis and water flux and high nighttime *E* in upland locations of tallgrass prairie in contrast to trends for a co-occurring forb species. Constant physiological functioning may favor *C. drummondii* over *S. canadensis* during an average climate year. More severe water limitation may be required to limit *C. drummondii* growth in the thin-soil of upland locations.

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