RESEARCH ARTICLE

Drivers of nocturnal water flux in a tallgrass prairie

Kimberly O'Keefe [ID] | Jesse B. Nippert

Division of Biology, Kansas State University, Manhattan, KS, USA

Correspondence
Kimberly O'Keefe
Email: okeefe4@wisc.edu

Present address
Kimberly O'Keefe, Department of Botany, University of Wisconsin, Madison, WI, USA

Abstract

1. Nocturnal transpiration can impact water balance from the local community to earth-atmosphere fluxes. However, the dynamics and drivers of nocturnal transpiration among coexisting plant functional groups in herbaceous ecosystems are unknown.

2. Here, we addressed the following questions: (1) How do nocturnal (E_{night}) and diurnal (E_{day}) transpiration vary among coexisting grasses, forbs, and shrubs in a tallgrass prairie? (2) What environmental variables drive E_{night} and do these differ from the drivers of E_{day}? (3) Is E_{night} associated with daytime physiological processes?

3. We measured diurnal and nocturnal leaf gas exchange on perennial grass, forb and woody species in a North American tallgrass prairie. Measurements were made periodically across two growing seasons (May–August 2014–2015) on three C_4 grasses (*Andropogon gerardii*, *Sorghastrum nutans* and *Panicum virgatum*), two C_3 forbs (*Vernonia baldwinii* and *Solidago canadensis*), one C_3 sub-shrub (*Amorpha canescens*) and two C_3 shrubs (*Cornus drummondii* and *Rhus glabra*).

4. By extending our study to multiple functional groups, we were able to make several key observations: (1) E_{night} was variable among co-occurring plant functional groups, with the highest rates occurring in C_4 grasses, (2) E_{night} and E_{day} exhibited different responses to vapour pressure deficit and other environmental drivers, and (3) rates of E_{night} were strongly related to predawn leaf water potential for grasses and woody species, and were likely modulated by small-scale changes in soil moisture availability.

5. Our results provide novel insight into an often-overlooked portion of ecosystem water balance. Considering the high rates of E_{night} observed in C_4 grasses, as well as the widespread global occurrence of C_4 grasses, nocturnal water loss might constitute a greater proportion of global evapotranspiration than previously estimated. Additionally, future predictions of nocturnal water loss may be complicated by stomatal behaviour that differs between the day and at night. Finally, these data suggest a water-use strategy by C_4 grasses wherein the high rates of E_{night} occurring during wet periods may confer a competitive advantage to maximize resource consumption during periods of greater availability.

KEYWORDS
evapotranspiration, gas exchange, grassland, nocturnal stomatal conductance

1 | INTRODUCTION

The conventional notion that plants close their stomata at night to minimize water loss during periods without carbon gain reinforces an optimized efficiency perspective of gas exchange dynamics (Buckley, Farquhar, & Mott, 1999; Cowan & Farquhar, 1977). However, research over the last decade has shown that nocturnal transpiration is neither rare nor a passive process reflecting incomplete stomatal closure, and can contribute significantly to total plant water use (Dawson et al., 2007). In fact, nocturnal water loss typically ranges between 5% and 15% of daytime transpiration rates (Caird, Richards, & Donovan, 2007), accounting for 69% of total transpiration in certain species (Forster, 2014). Substantial nighttime transpiration has been observed in many ecosystem types (Caird et al., 2007), including temperate forests (Barbour et al., 2005; Daley & Phillips, 2006; Zeppel, Tissue, Taylor, Macinnis-Ng, & Eamus, 2010), tropical montane cloud forests (Alvarado-Barrientos et al., 2015), deserts (Ogle et al., 2012; Snyder, Richards, & Donovan, 2003), tropical savannas (Bucci et al., 2004; Domec et al., 2006) and tropical rainforests (Wallace & McJannet, 2010). Considering the widespread occurrence of this phenomenon, nocturnal transpiration is likely a significant component of global-scale evapotranspiration (Resco de Dios et al., 2015; Zeppel, Lewis, Phillips, & Tissue, 2014).

Despite the widespread observation of this phenomenon, nocturnal transpiration studies have typically focused on woody plants, with only a few species measured within each ecosystem (Barbeta, Ogaya, & Peñuelas, 2012; Buckley, Turnbull, Pfautsch, & Adams, 2011; Daley & Phillips, 2006; Kavanagh, Pangle, & Schotzko, 2007; Zeppel et al., 2010) or with multiple species measured across ecosystems (Dawson et al., 2007). Nocturnal transpiration is rarely measured in herbaceous species, small shrubs, or subdominant species, particularly within the same community (but see Ogle et al., 2012; Snyder et al., 2003). However, if patterns and rates of nocturnal transpiration vary among co-occurring species, this additional water loss may differentially affect species within the community and alter ecosystem water balance beyond estimates of daytime evapotranspiration only.

Improved estimates of ecosystem and global water balance require detail on the mechanistic controls over nocturnal transpiration. Given that nocturnal transpiration is dynamic in species over time, what are the drivers of nocturnal water loss and do these drivers differ from those of daytime transpiration? High rates of nocturnal transpiration are often attributed to high nocturnal VPD or high soil moisture content (Alvarado-Barrientos et al., 2015; Dawson et al., 2007; Forster, 2014; Fuentes, Mahadevan, Bonada, Skewes, & Cox, 2013; Phillips, Lewis, Logan, & Tissue, 2010; Zeppel et al., 2010); however, some studies have reported no response of nocturnal transpiration to VPD (Barbour et al., 2005; Resco de Dios et al., 2015) or a negative relationship between nocturnal transpiration and VPD (Barbour & Buckley, 2007). Other studies suggest that interactions among environmental drivers, carry-over effects from daytime processes, or endogenous circadian rhythm may modulate nocturnal transpiration to a greater extent than individual environmental variables (Resco de Dios et al., 2013, 2015). As these examples illustrate, there is no general consensus about what mechanisms control nocturnal transpiration. Mesic grasslands provide an ideal environment to test multiple, potentially interacting drivers of nocturnal transpiration given the range of variation in ecophysiological responses to environmental factors that can exist at small spatial scales (Asbjornsen, Shepherd, Helmers, & Mora, 2008; Klodd, Nippert, Ratajczak, Waring, & Phoenix, 2016; Nippert & Knapp, 2007a; Ocheltree, Nippert, & Prasad, 2013; Tucker, Craine, & Nippert, 2011). The high species richness of mesic grasslands accommodates comparisons among a wide range of species and plant functional groups within the same ecosystem.

Here, we measured nocturnal transpiration in a tallgrass prairie, located within the Great Plains of central North America. Previous studies have documented the occurrence of nocturnal water loss for several species within this system (Muench, O'Keefe, & Nippert, 2016; O'Keefe & Nippert, 2017b) but to date we lack mechanistic insight as well as high frequency sampling for multi-species community assemblages. Using leaf-level measurements of diel gas exchange, we addressed three primary questions: (1) How do nocturnal and diurnal transpiration vary among coexisting grasses, forbs, and shrubs in a tallgrass prairie? (2) What environmental variables drive nocturnal transpiration and do these differ from the drivers of daytime transpiration? (3) Are nocturnal transpiration and stomatal conductance associated with daytime physiological processes? We hypothesized that (1) nocturnal transpiration will occur among coexisting plant functional types including grasses, forbs, and shrubs, and will be greatest in species that have high daytime transpiration rates; (2) nocturnal and diurnal transpiration will both exhibit positive relationships with VPD and soil moisture; (3) Higher rates of nocturnal transpiration and stomatal conductance will be associated with higher photosynthetic rates, as has been suggested by other studies (Fuentes et al., 2013; Resco de Dios et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Study location

This research was conducted in 2014 and 2015 at the Konza Prairie Biological Station (KPBS), a Long Term Ecological Research (LTER) site located in the Flint Hills region of northeastern Kansas, USA (39.1°N, 96.9°W). KPBS is a 3,487-ha native tallgrass prairie that is divided into experimental watersheds, each of which receive varying combinations of grazing (grazed by *Bison bison*, cattle or ungrazed) and prescribed fire (burned every 1, 2, 4 or 20 years) treatments. Long-term weathering has created a topographically heterogeneous landscape consisting of shallow, rocky uplands, steep slopes, and lowlands with deep loess soils. KPBS is dominated by a few perennial C_4 grass species along with numerous subdominant C_3 grass, forb, and woody species (Smith & Knapp, 2003).

The Flint Hills region of Kansas experiences a mid-continental climate, characterized by cool, wet winters and warm, dry summers. Long-term mean annual precipitation at KPBS is 829 mm (1982–2014),

with 79% occurring during the growing season (April–September). Precipitation was 706 mm in 2014 and 1002 mm in 2015 (68% and 75% of which occurred during each respective growing season). The warmest average month of the year is July (1982–2014), with mean maximum and minimum air temperatures of 32.69 and 19.78°C respectively. The coldest average month is January (1982–2014), with mean maximum and minimum air temperatures of 4.87 and −7.14°C. The mean maximum and minimum air temperatures for July 2014 were 31.7 and 17.06°C respectively. The mean maximum and minimum air temperatures for July 2015 were 32.02 and 20.67°C.

2.2 | Experimental design

This study was conducted in a lowland topographic location within an ungrazed watershed that is burned every 4 years (last burned in 2013). A 4-year fire interval is similar to the historic frequency of fire for the region (Frost, 1998) and results in a landscape characterized by greater forb and shrub diversity than annually burned prairie (Collins & Calabrese, 2012; Koerner & Collins, 2014). We sampled commonly occurring species at KPBS including three dominant C_4 grasses (*Andropogon gerardii* Vitman, big bluestem; *Panicum virgatum* L., switchgrass; *Sorghastrum nutans* (L.) Nash., Indiangrass), two C_3 forbs (*Solidago canadensis* L., Canada goldenrod; *Vernonia baldwinii* Torr., Baldwin's ironweed), one leguminous C_3 subshrub (*Amorpha canescens* Pursh., leadplant) and two C_3 shrubs (*Rhus glabra* L., smooth sumac; *Cornus drummondii* C.A. Mey., rough-leaf dogwood). Plants were sampled randomly within 50 m from a micrometeorological station. All measurements were made from May through September of each year during the study.

2.3 | Environmental conditions

A micrometeorological station located at a lowland position within the same experimental watershed (<50 m from all study plants) was used to measure precipitation, air temperature, relative humidity and soil moisture. Daily cumulative precipitation (mm) was measured with an Ott Pluvio2 rain gauge (Ott Hydromet, Kempten, Germany). Vapour pressure deficit (VPD) was calculated from air temperature (T_{air}) measurements made with a 100 K thermistor (Betatherm, Hampton, VA, USA) and relative humidity measurements made, using a HMP45ASP sensor (Vaisala, Helsinki, Finland). Volumetric soil moisture (v/v) was measured at 10 cm depth, using a Hydraprobe II sensor (Stevens Water Monitoring Systems, Portland, OR). Data were recorded as 60 min averages using a CR10 datalogger (Campbell Scientific Inc. Logan, UT) throughout each growing season of the study. We used average daily soil moisture, as well as VPD and T_{air} reported at the average time of day (11.00 hr) and night (23.00 hr) gas exchange measurements, for all analyses.

2.4 | Leaf physiology measurements

Leaf physiology measurements (mid-day gas exchange, nocturnal gas exchange, mid-day water potential and predawn water potential) were made six times per growing season, approximately once every 2–4 weeks. For each sampling date, all measurements were made on the youngest, fully developed leaf from 3 to 5 randomly selected individuals per species. Leaf gas exchange was measured with an Li-6400xt infra-red gas analyser (Li-Cor, Inc., Lincoln, NE, USA). Mid-day measurements were made on clear days between 10.00 and 13.00 hrs and included maximum CO_2 assimilation at ambient C_a (A_{max}), daytime stomatal conductance of water vapour (g_{sday}), and daytime transpiration rate (E_{day}). Daytime cuvette conditions were set to $[CO_2] = 400\ \mu mol\ CO_2\ mol^{-1}$, photosynthetically active radiation = 1500 μmol m^{-2} s^{-1} photon flux density, and flow rate = 500 μmol/s. Relative humidity was kept at ambient levels (typically 40%–60%).

Nocturnal measurements were made on the same day as daytime gas exchange measurements, approximately 1 hr following sunset, and typically lasted 2–3 hrs (approximately 22.00–01.00 hrs). Cuvette conditions were set to daytime conditions except the light source was turned off. Nocturnal measurements were made on the same leaves used for daytime gas exchanges measurements and included nocturnal stomatal conductance (g_{snight}) and nocturnal transpiration rate (E_{night}). In the few instances where leaves were damaged between daytime and nocturnal measurements, a morphologically and developmentally similar leaf on the same plant was chosen for the nocturnal measurement. For all gas exchange measurements, each leaf was allowed to stabilize within the cuvette for 2–5 min and then a single measurement was recorded. Gas exchange calculations were adjusted for leaf area within the cuvette during data processing, if necessary.

Predawn (Ψ_{pd}) and mid-day (Ψ_{md}) leaf water potential were measured the same day during which gas exchange measurements were performed. Leaves for Ψ_{pd} measurements were collected approximately 1 hr prior to sunrise and leaves for Ψ_{md} measurements were collected at 12.00 hrs. Each leaf was cut with a razor blade, sealed in dark, humidified plastic bag, and allowed to equilibrate for 1 hr prior to measurement with a Scholander pressure chamber (PMS Instrument Company, Albany, OR, USA).

2.5 | Statistics

All analyses were performed with the statistical program R V3.3.3 (R Core Team, 2017). We used mixed-effects models to assess differences in nocturnal (E_{night} and g_{snight}) and diurnal (E_{day}, g_{sday}, A_{max}, Ψ_{pd}, and Ψ_{md}) physiology across plant functional groups, (i.e. grasses, forbs and woody species), and through time. For each physiological response variable, plant functional group, sampling date and their interaction were fixed effects and species nested within plant functional group (Schielzeth & Nakagawa, 2013) was included as a random effect using the "*lmer*" function of the "LME4" package V1.1-14 (Bates, Maechler, Bolker, & Walker, 2015).

We used Information Theoretic (IT) model averaging (Burnham & Anderson, 2004) to (1) identify the environmental drivers of E_{night} and g_{snight}, (2) identify the environmental drivers of E_{day} and g_{sday} and

(3) to assess whether daytime physiology is associated with E_{night} and g_{snight}. This method compares multiple competing models using information criteria, ranks and weights each competing model, and then averages a top model set to produce a final model that only includes predictor variables represented in the top model set. IT model averaging was chosen over traditional null hypothesis testing in order to account for model uncertainty, avoid over-parameterization, provide more robust parameter estimates and to quantitatively evaluate multiple hypotheses rather than a single null model (Burnham & Anderson, 2004; Grueber, Nakagawa, Laws, & Jamieson, 2011). We ran six separate mixed-effects models to address each question individually. In the first two models (response variables E_{night} and g_{snight}), nocturnal VPD, nocturnal T_{air}, soil moisture, plant functional group and their pairwise interactions were fixed effects. In the next two models (response variables E_{day} and g_{sday}), diurnal VPD, diurnal T_{air}, soil moisture, plant functional group and their pairwise interactions were fixed effects. In the final two models (response variables E_{night} and g_{snight}), Ψ_{pd}, Ψ_{md}, A_{max}, plant functional group and their pairwise interactions were fixed effects. In all models, plant species nested within plant functional group and sampling date were random effects.

For each analysis, we first created a global model that included all fixed and random effects using the "*lmer*" function. We then defined the global model and used the "*standardize*" function in the "ARM" package V1.9-3 (Gelman & Su, 2016) to standardize the input variables. Next, we used the "*dredge*" function in the "MUMIN" package V1.40.0 (Bartoń, 2017) to create a full submodel set and used the "*get.models*" function in the "MUMIN" package to reduce the full set to a top model set with 4AICc as a cutoff, according to Grueber et al. (2011). Finally, we calculated a final average model and determined the relative importance for each parameter included in the average model, using the "*model.avg*" function in the "MUMIN" package. Relative importance, a unitless metric, sums Akaike weights for all top models in which the parameter appear and ranges from 1 (indicating that the parameter is included in all top models) to 0 (indicating that the parameter has no explanatory weight) (Burnham & Anderson, 2004).

3 | RESULTS

3.1 | Environmental conditions

Soil moisture measured at 10 cm depth declined over each growing season (Figure 1a,b) with highest values at DOY 166 in 2014 and DOY 156 in 2015. Minimum soil moisture occurred at DOY 212 in 2014 and DOY 249 in 2015. Soil moisture was generally higher throughout the mid- and late portions of the 2015 growing season compared to 2014, which was associated with greater annual precipitation and larger precipitation events in 2015 (Figure 1c,d). T_{air} was generally similar between 2014 and 2015 (Figure 1e,f), with maximum T_{air} measured during the day (11.00 hr) occurring on DOY 206 in 2014 and DOY 171 in 2015, and minimum T_{air} measured at night (23.00 hr) occurring on DOY 255 in 2014 and DOY 140 in 2015. VPD was variable over each growing season but

generally had greater magnitude in 2014 than 2015 (Figure 1g,h). Maximum VPD measured during the day (11.00 hr) occurred on DOY 236 in 2014 and DOY 161 in 2015, while minimum VPD measured at night (23.00 hr) occurred on DOY 160 in 2014 and DOY 183 in 2015.

3.2 | How do nocturnal and diurnal transpiration vary among coexisting grasses, forbs and shrubs in a tallgrass prairie?

Measurable rates of nocturnal gas exchange occurred in all functional groups (Figure 2) and varied significantly among functional groups and sampling dates (significant functional group × date interactions for E_{night} and g_{snight}, see Table S1 in Supporting Information). In 2014, E_{night} and g_{snight} were high early and late in the growing season, but declined between DOY 196 and 229 (Figure 2a,c). In 2015, E_{night} and g_{snight} were high on DOY 152 and DOY 211, and were lower between these dates as well as at the end of the growing season (Figure 2b,d). Grasses generally had the maximal E_{night} and g_{snight} values, and had higher overall rates in 2015 between DOY 152 and 211. However, forbs had larger E_{night} rates during the latter portion of 2014.

Diurnal gas exchange rates also varied by functional group and sampling date (significant functional group × date interactions for E_{day} and g_{sday}, Table S1). However, unlike nocturnal gas exchange, grasses typically showed the lowest E_{day} and g_{sday} values throughout 2014 (Figure 2e,g) and 2015 (Figure 2f,h). This conservative use of water corresponded with the highest A_{max} rates of any functional group (Figure S1a-b), as is typical for C_4 grasses. Conversely, forbs had the maximal diurnal gas exchange rates in early 2014 (Figure 2e,g) and throughout 2015 (Figure 2f,h), but lower A_{max} than the grasses (Figure S1a-b). Woody species generally had intermediate diurnal gas exchange rates (Figure 2e,g; Figure S1a-b).

3.3 | What environmental variables drive nocturnal transpiration and do these differ from the drivers of daytime transpiration?

Variability in E_{night} was best described by a weak relationship with nocturnal VPD, soil moisture, and nocturnal T_{air} (Table 1). E_{night} declined with increasing nocturnal VPD, and to a lesser extent, increasing nocturnal T_{air} (Figure 3a,b). Nocturnal VPD and T_{air} were also both drivers of g_{snight} (Table 1), although g_{snight} showed a somewhat stronger decline in response to increasing nocturnal VPD and T_{air} (Figure 3c,d).

The response of daytime gas exchange to environmental drivers differed from that of nocturnal gas exchange (Table 2). Variability in E_{day} was best described by diurnal VPD, T_{air}, and soil moisture, while variability in g_{sday} was best described by soil moisture and diurnal T_{air} (Table 2). Contrary to the negative relationship observed between nocturnal gas exchange and VPD, E_{day} increased with increasing diurnal VPD and g_{sday} did not respond to

variations in diurnal VPD (Figure 4). Instead, g_{sday} increased with increasing soil moisture and diurnal T_{air} (Figure S2). Furthermore, the response of E_{day} to environmental drivers often varied among plant functional groups (Table 2). For instance, E_{day} increased with increasing soil moisture, but this trend was observed only in forbs and woody species (Figure S3).

3.4 | Is nocturnal transpiration associated with daytime physiological processes?

Variability in E_{night} was partially explained by diurnal physiology measured the day prior to nocturnal gas exchange measurements (Table 3). E_{night} was higher at higher Ψ_{pd} and Ψ_{md} values, particularly
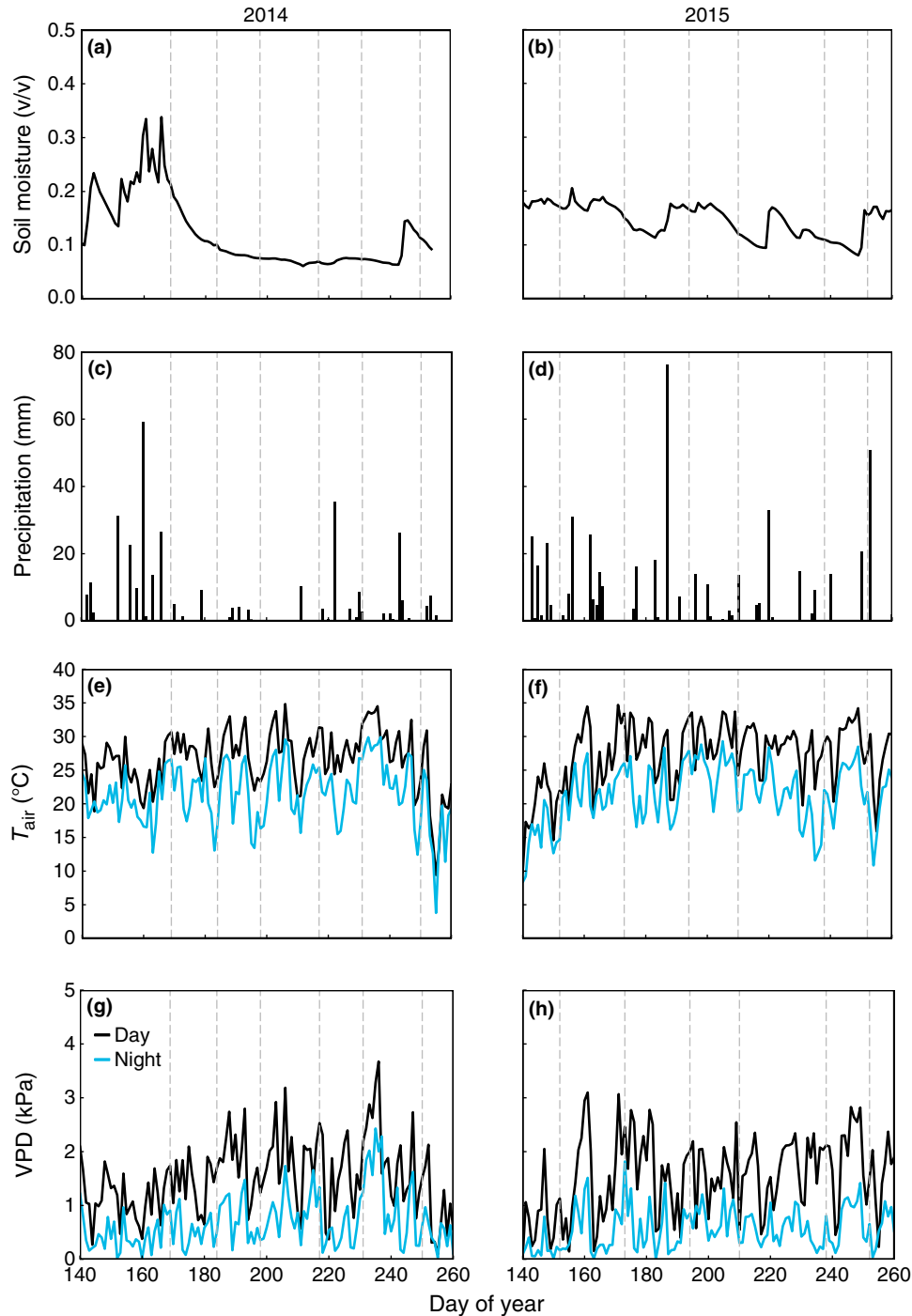

FIGURE 1 Environmental data measured between day of year 140–260 in 2014 and 2015. Shown are daily mean soil moisture at 10 cm (a, b), cumulative daily precipitation (c,d), air temperature (T_{air}) reported at average time of day (11.00 hr) and night (23.00 hr) gas exchange measurements (e, f), and vapour pressure deficit (VPD) reported at average time of day (11.00 hr) and night (23.00 hr) gas exchange measurements (g, h). Dashed vertical lines indicate sampling days on which gas exchange measurements occurred during each growing season
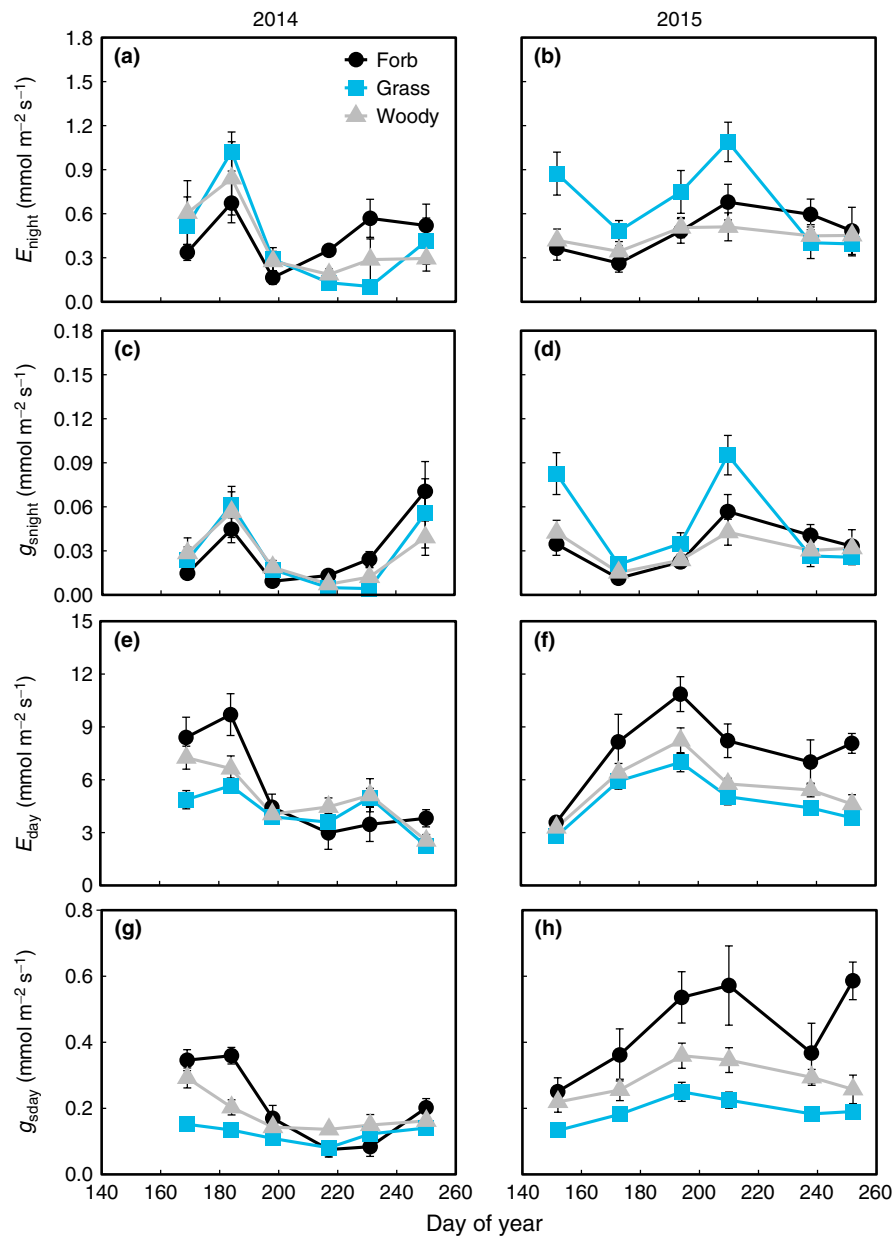
FIGURE 2 Nocturnal and diurnal physiology measured in 2014 and 2015. Shown are the $M \pm 1$ SEM nocturnal transpiration rate, E_{night} (a, b), nocturnal stomatal conductance of water vapour, g_{snight} (c, d), diurnal transpiration rate, E_{day} (e, f), and diurnal stomatal conductance of water vapour, g_{sday} (g, h) measured for each functional group

TABLE 1 Effects of nocturnal environmental conditions on E_{night} and g_{snight}. Shown are summary results after model averaging, including the average model estimates, *SE*, adjusted *SE* (Adj *SE*), *Z* value, *p* value, 95% confidence interval (95% CI), relative importance (Importance), and number of models in which the factor occurs (*N* models)

| Parameter	Estimate	SE	Adj SE	Z value	p value	95% CI	Importance	N models
E_{night}								
Intercept	0.479	0.068	0.069	6.959	<.001	0.343, 0.613		
VPD	−0.194	0.106	0.106	1.831	.067	−0.402, 0.014	0.25	1
Soil moisture	0.130	0.112	0.113	1.152	.250	−0.091, 0.351	0.11	1
T_{air}	−0.124	0.115	0.116	1.071	.284	−0.351, 0.103	0.10	1
g_{snight}								
Intercept	0.033	0.006	0.006	5.605	<.001	0.021, 0.045		
VPD	−0.027	0.008	0.009	3.182	.001	−0.044, −0.010	0.22	1
T_{air}	−0.026	0.009	0.009	2.959	.003	−0.043, −0.009	0.15	1
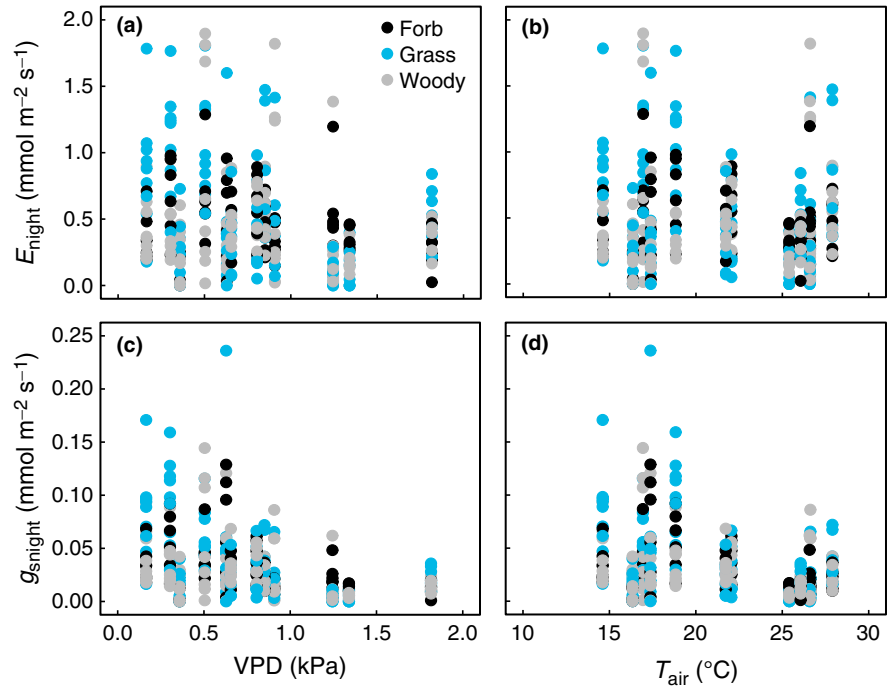
FIGURE 3 Relationships between nocturnal transpiration (E_{night}) and nocturnal vapour pressure deficit (VPD) (a), E_{night} and nocturnal air temperature (T_{air}) (b), nocturnal stomatal conductance of water vapour (g_{snight}) and nocturnal VPD (c), and g_{snight} and nocturnal T_{air} (d). Nocturnal VPD and T_{air} are reported from average time of night (23.00 hr) gas exchange measurements. Corresponding statistics are shown in Table 1

TABLE 2 Effects of diurnal environmental conditions on E_{day} and g_{sday}. Shown are summary results after model averaging, including the average model estimates, SE, adjusted SE (Adj SE), Z value, p value, 95% confidence interval (95% CI), relative importance (Importance), and number of models in which the factor occurs (N models)

Parameter	Estimate	SE	Adj SE	Z value	P value	95% CI	Importance	N models
E_{day}								
Intercept	6.749	0.965	0.969	6.963	<.001	4.849, 8.648		
Grass	−1.900	0.714	0.717	2.649	.008	−3.306, −0.494	1	10
Woody	−1.136	0.713	0.717	1.585	.113	−2.540, 0.269	1	10
Soil moisture (SM)	3.111	1.910	1.918	1.622	.105	−0.648, 6.891	1	10
T_{air}	1.110	1.974	1.982	0.560	.575	−2.774, 4.994	1	10
VPD	0.845	2.133	2.142	0.394	.693	−3.352, 5.042	1	10
Grass × SM	−2.048	0.569	0.572	3.581	<.001	−3.168, −0.927	1	10
Woody × SM	−1.362	0.553	0.555	2.454	.014	−2.449, −0.274	1	10
SM × T_{air}	2.374	2.790	2.801	0.847	.397	−3.118, 7.865	0.86	8
SM × VPD	1.775	3.189	3.202	0.554	.579	−4.501, 8.052	0.81	7
T_{air} × VPD	−2.440	2.633	2.644	0.923	.356	−7.623, 2.743	0.86	8
Grass × VPD	−0.913	0.715	0.718	1.272	.203	−2.320, 0.494	0.31	4
Woody × VPD	−0.769	0.715	0.718	1.071	.284	−2.175, 0.638	0.31	4
Grass × T_{air}	0.261	0.953	0.956	0.273	.785	−1.612, 2.133	0.15	2
Woody × T_{air}	0.330	0.924	0.927	0.356	.721	−1.487, 2.147	0.15	2
g_{sday}								
Intercept	0.226	0.035	0.035	6.448	<.001	0.158, 0.295		
SM	0.099	0.041	0.041	2.406	.016	0.018, 0.180	0.26	1
T_{air}	0.090	0.045	0.045	2.003	.045	0.002, 0.178	0.15	1

in grasses (Figure 5a,d). For instance, E_{night} rates measured in grasses were >0.5 mmol m^{-2} s^{-1} at Ψ_{pd} > −0.5 MPa, but dropped substantially when Ψ_{pd} < −0.5 MPa (Figure 5a). A similar, but weaker

relationship was exhibited between E_{night} and leaf water potential for woody plants (Figure 5c,f), and no relationship was observed for forbs (Table 3; Figure 5b,e). Additionally, E_{night} exhibited a
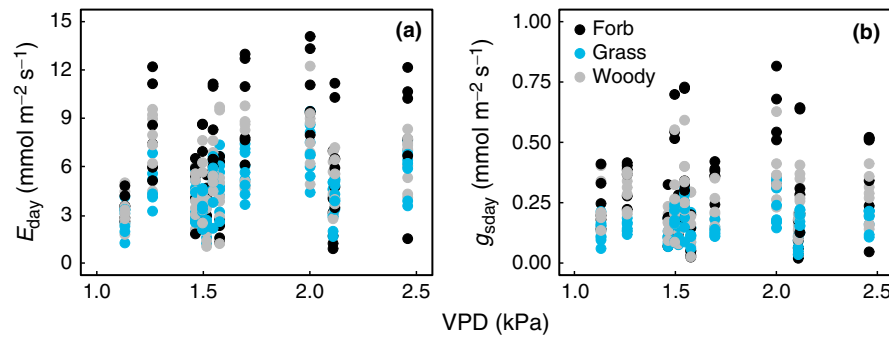
FIGURE 4 Relationships of diurnal transpiration (E_{day}) (a) and diurnal stomatal conductance of water vapor (g_{sday}) (b) with diurnal vapour pressure deficit (VPD). Diurnal VPD is reported from average time of day (11.00 hr) gas exchange measurements. Corresponding statistics are shown in Table 2

positive relationship with A_{max}, but only when Ψ_{md} was higher than −1.25 MPa (Table 3; Figure S4). Daytime physiology did not impact g_{snight} (Table 3).

4 | DISCUSSION

4.1 | How do nocturnal and diurnal transpiration vary among coexisting grasses, forbs, and shrubs in a tallgrass prairie?

Despite the increasing recognition of the frequency and impact of nocturnal water loss on ecosystem water budgets, we lack a comprehensive understanding of how this process varies among coexisting species and plant functional groups other than trees (but see Ogle et al., 2012). Here, we measured substantial rates of nocturnal water loss in dominant C_4 grasses, as well as in subdominant C_3 forbs and shrubs. Mean E_{night} rates ranged from 0.104 to 1.089 mmol m^{-2} s^{-1} in grasses, 0.164–0.678 mmol m^{-2} s^{-1} in forbs, and 0.186–0.841 mmol m^{-2} s^{-1} in shrubs. These values varied over

time, with greater rates of nocturnal water loss generally occurring earlier and later during the growing seasons (Figure 2). While ecosystem consequences of nocturnal water loss are limited without scaling these leaf-level measurements to the landscape, the rates of E_{night} observed here suggest that nocturnal water loss by herbaceous and subdominant plant groups may contribute more to grassland hydrological budgets than previously considered. Furthermore, the importance of E_{night} in this ecosystem is likely underestimated by this study because we measured nocturnal gas exchange at the beginning of the night when g_{snight} is often lowest (Resco de Dios et al., 2013).

Of the three functional groups, grasses generally had the highest rates of E_{night}, particularly during periods of high water availability (Figures 1 and 2). This pattern is unsurprising given that grasses exhibit a functional reliance on water from shallow soil layers over time (Nippert & Knapp, 2007a,b; O'Keefe & Nippert, 2017a), with low daytime transpiration rates when these layers are dry (Knapp, 1985). Similarly, Lombardozzi, Zeppel, Fisher, and Tawfik (2017) calculated high g_{snight} values for C_4 grasses, using a global land-surface model.

TABLE 3 Effects of diurnal physiology on E_{night} and g_{snight}. Shown are summary results after model averaging, including the average model estimates, *SE*, adjusted *SE* (Adj *SE*), *Z* value, *p* value, 95% confidence interval (95% CI), relative importance (Importance) and number of models in which the factor occurs (*N* models)

Parameter	Estimate	*SE*	Adj *SE*	*Z* value	*p* value	95% CI	Importance	*N* models
E_{night}								
Intercept	0.480	0.080	0.080	5.978	<.001	0.323, 0.637		
A_{max}	0.132	0.057	0.057	2.304	.021	0.020, 0.245	0.48	4
Ψ_{md}	−0.027	0.147	0.147	0.181	.856	−0.315, 0.261	0.26	4
$\Psi_{md} \times A_{max}$	0.215	0.080	0.081	2.668	.008	0.057, 0.374	0.08	1
Grass	−0.001	0.145	0.145	0.005	.996	−0.286, 0.284	0.19	3
Woody	−0.041	0.137	0.138	0.294	.769	−0.311, 0.230	0.19	3
Grass × Ψ_{md}	0.453	0.109	0.110	4.119	<.001	0.237, 0.669	0.12	2
Woody × Ψ_{md}	0.156	0.110	0.110	1.411	.158	−0.061, 0.372	0.12	2
Ψ_{pd}	−0.239	0.092	0.093	2.574	.010	−0.420, −1.057	0.07	1
Grass × Ψ_{pd}	0.472	0.100	0.101	4.678	<.001	0.274, 0.670	0.07	1
Woody × Ψ_{pd}	0.319	0.104	0.105	3.039	.002	0.113, 0.525	0.07	1
	Estimate		**SD**		**df**		**t value**	**p value**
g_{snight} [a]								
Intercept	0.033		0.006		14.45		5.231	<.001

[a]Intercept model results are presented for g_{snight}, as no predictor variables were included in the final average model.
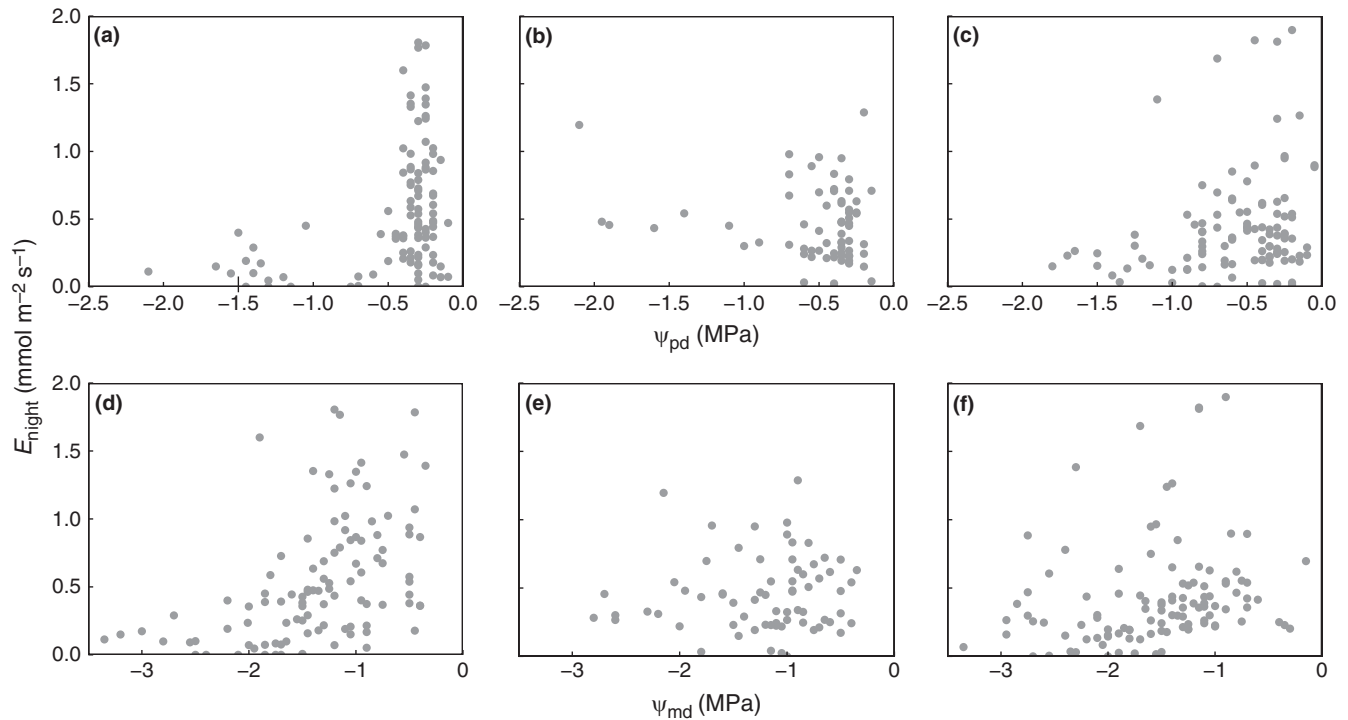
FIGURE 5 Relationships between nocturnal transpiration (E_{night}) and predawn leaf water potential (Ψ_{pd}) for grasses (a), forbs (b) and woody species (c), as well as relationships between E_{night} and mid-day leaf water potential (Ψ_{md}) for grasses (d), forbs (e), and woody species (f). Corresponding statistics are shown in Table 3

Forbs and shrubs, which exhibit plasticity in source water use based on changes in soil water availability (Nippert & Knapp, 2007a,b), generally had more stable rates of E_{night} through time, particularly in 2015. C_4 grasses exhibited the lowest transpiration rates during the day, which is unsurprising given their ability to maintain high photosynthetic rates with lower g_{sday} (Figure 2). Consequently, E_{night} expressed as a percentage of E_{day} was greatest for the C_4 grasses, with maximum values of 35.5% in grasses, 15.5% in forbs and 23.6% in shrubs. Although this result is contrary to previous evidence showing that plants with high g_{sday} also have high g_{snight} (Barbour et al., 2005; Snyder et al., 2003), it suggests that photosynthetic pathway may be an important factor to consider when determining the contribution of E_{night} to daily water budgets.

4.2 | What environmental variables drive nocturnal transpiration and do these differ from the drivers of daytime transpiration?

A growing body of evidence suggests that E_{night} is at least partially controlled by nocturnal environmental factors (Caird et al., 2007; Zeppel, Logan, Lewis, Phillips, & Tissue, 2013; Zeppel et al., 2014); however, there is no general consensus regarding the importance of each factor, how abiotic factors potentially interact to affect E_{night}, or how environmental controls of E_{night} may vary from those of E_{day}. Nocturnal VPD and soil water content are the most frequently reported abiotic drivers of nocturnal water loss. Many studies have observed a positive relationship of E_{night} with VPD (Alvarado-Barrientos

et al., 2015; Dawson et al., 2007; Forster, 2014; Phillips et al., 2010; Zeppel et al., 2010) and soil moisture (Barbeta et al., 2012; Fuentes et al., 2013; Howard & Donovan, 2007; Moore, Cleverly, & Owens, 2008), which are similar to patterns observed during the day (Zeppel et al., 2011). However, other studies have reported negligible relationships of E_{night} with VPD (Barbour et al., 2005; Resco de Dios et al., 2015), or stronger relationships of E_{night} with other environmental variables such as wind speed (Karpul & West, 2016; Phillips et al., 2010) or atmospheric CO_2 concentration (Zeppel et al., 2011). Further complicating our understanding of the mechanisms controlling E_{night} may be interactions among environmental factors (Zeppel et al., 2014), leaf age (Phillips et al., 2010), responses to nutrient availability (Eller, Jensen, & Reisdorff, 2017; Kupper et al., 2012; Rohula, Kupper, Räim, Sellin, & Sõber, 2014; Scholz et al., 2007), differential diurnal and nocturnal stomatal behavior (Ogle et al., 2012), species-specific effects of hydraulic architecture on water loss (Sack & Holbrook, 2006), positive relationships of g_{snight} with VPD (Howard & Donovan, 2007), or effects of endogenous circadian rhythm (Caldeira, Jeanguenin, Chaumont, & Tardieu, 2014; Resco de Dios, Loik, Smith, Aspinwall, & Tissue, 2016; Resco de Dios et al., 2013, 2015).

We evaluated the relationships of nocturnal and diurnal transpiration with VPD, T_{air}, soil moisture and their interactions. Contrary to previous studies, we found that E_{night} and g_{snight} decreased with increasing nocturnal VPD for all functional groups (Figure 3). Furthermore, these relationships differed from those observed during the day, where E_{day} and g_{sday} did not vary with fluctuating

diurnal VPD (Figure 4). For the species and location measured here, g_{snight} and g_{sday} appear to be regulated by different mechanisms because stomatal sensitivity to changes in VPD was greater at night than during the day. Weak stomatal responses to diurnal VPD indicate that optimizing carbon gain rather than minimizing water loss may be an important physiological strategy in this ecosystem. Alternatively, interactions of VPD with a host of other, unmeasured environmental variables (e.g. wind speed, irradiance) may drive E_{day}. Greater stomatal responses to nocturnal VPD suggest that minimizing water loss becomes more important when carbon gain is absent. Because nights with higher VPD often occur on very warm days, greater stomatal regulation at night may result in overall water savings for these species. This will become especially important as nocturnal air temperatures increase more rapidly than daytime temperatures in future climates (Davy, Esau, Chernokulsky, Outten, & Zilitinkevich, 2017). In support of this interpretation, Ogle et al. (2012) reported differential stomatal behaviour during the day and at night in several desert species and suggested that diurnal and nocturnal stomatal behaviour could be under varying selection pressures (Christman et al., 2008).

4.3 | Is nocturnal transpiration associated with daytime physiological processes?

Another factor that may complicate our understanding of the mechanistic controls over nocturnal water loss is the potential influence of daytime physiological processes. Although not yet rigorously investigated, previous studies have suggested that photosynthetic rates may influence subsequent E_{night} if carbohydrate supply regulates g_{snight} (Gao et al., 2016; Lasceve, Leymarie, & Vavasseur, 1997; Resco de Dios et al., 2015). Here, we assessed whether nocturnal water loss was statistically correlated with the previous day's photosynthetic rates and with leaf water potential. We did not find any significant relationships between g_{snight} and daytime physiology, but we did observe that E_{night} was related to both leaf water potential and photosynthetic rates. The relationship between E_{night} and leaf water potential varied by plant functional type. For the grasses, and to a lesser extent the woody species, E_{night} exhibited an exponential relationship with Ψ_{pd} and Ψ_{md} (Figure 5). For the grasses, E_{night} was very low when Ψ_{pd} was < −0.5 MPa, and high E_{night} was only possible when Ψ_{pd} > 0.5 MPa (Figure 5a). These results suggest that plant water status was a critical determinant of nocturnal water loss, as has been observed in other studies (Fuentes et al., 2013; Ogle et al., 2012), but this response was most prevalent for the grasses compared to the other two functional types. Interestingly, E_{night} was only weakly related to soil moisture content (Table 1). This discrepancy may have occurred because we measured soil moisture at one central location, not directly in the rhizosphere of each plant, which would not identify heterogeneity in soil water availability at small spatial scales compared to leaf Ψ_{pd}.

We also found a weak positive relationship between E_{night} and A_{max}, but only at higher Ψ_{md} values (Figure S4). While this result may

suggest that photosynthetic rates and carbohydrate availability influence E_{night} under certain hydrological conditions, the fact that g_{snight} did not vary with A_{max} indicates that carbohydrate regulation of g_{snight} is not driving these higher E_{night} rates. Rather, E_{night} may be correlated with A_{max} simply because those plants that had high E_{night} rates also exhibited high A_{max} rates (i.e. grasses). These results suggest that "carry-over" effects might not be driving nocturnal water loss for these species; however, they do illustrate the importance of fine-scale variation of soil water availability on driving E_{night}. Finally, we should note that the relationships between nocturnal transpiration and daytime physiological processes, as well as between nocturnal transpiration and nocturnal environmental conditions, are based on measurements made early at night; whether these conclusions could be extended throughout an entire night is yet to be determined.

4.4 | Ecological implications

Our observations of greater stomatal regulation of E_{night} at high nocturnal VPD, combined with greater rates of E_{night} at high water potentials, show that these grassland plants increase E_{night} when water is available in surface soil layers, but more tightly regulate water use at night when water is less available. These results suggest that, rather than nocturnal transpiration existing as a detriment to plant functioning (Bucci et al., 2004; Christman et al., 2008; Coupel-Ledru et al., 2016; Dawson et al., 2007; Donovan, Linton, & Richards, 2001; Kavanagh et al., 2007), stomatal regulation of nocturnal water loss may provide adaptive value to certain species during periods of high water availability. Specifically, we suggest that nocturnal transpiration may promote rapid water loss from surface soils as a competitive strategy within a community. Species that exhibit characteristics of fast growth during periods of high resource availability, as well as traits that permit tolerance of dry soil conditions, will benefit from a strategy that maximizes resource consumption (Tilman, 1982). For example, high soil water uptake and flux when readily available and not replaced may negatively impact other species through resource depletion and more frequent dry soil conditions. Neighbouring species lose out twice; once by not fully exploiting high soil moisture availability, and second because low moisture availability imparts greater physiological stress on drought-sensitive species. C_4 grasses in tallgrass prairie exhibit functional traits of drought tolerance (Nippert & Knapp, 2007a; Tucker et al., 2011), and also had the highest rates of nocturnal transpiration under wet soil conditions in this study. In this scenario, C_4 grasses maintain a physiological advantage under conditions of both high and low surface soil water availability compared to neighbouring species with lower nocturnal water flux and greater sensitivity to dry soil conditions.

Overall, these data show that E_{night} is not constant across a group of coexisting plant functional groups and does not always respond to environmental drivers in a manner similar to E_{day}. Although most land surface models are parameterized with few values for g_{sday} and assume no g_{snight} (Kowalczyk et al., 2006; Sitch et al., 2003), there is growing recognition that land surface models

should parameterize g_{sday} for a wider range of plant functional types and biomes (Lin et al., 2015) and should include estimates of g_{snight} (Lombardozzi et al., 2017; Zeppel et al., 2014). Our observation of differential diurnal and nocturnal stomatal behaviour supports the idea that g_{sday} and g_{snight} should be parameterized separately. Additionally, considering the rates of E_{night} observed here, we encourage future model parameterizations to also include g_{snight} and E_{night} for a greater range of plant functional groups in simulations of nocturnal water flux. Finally, we demonstrate that E_{night} rates were generally greater in C_4 grasses than in any other functional group, particularly during wet periods. Whether regulation of E_{night} based on changes in water availability serves as an ecological strategy for these grasses remains to be tested; however, considering the widespread global occurrence of C_4 grasses, E_{night} may contribute more greatly to global evapotranspiration than previously considered.

AUTHORS' CONTRIBUTIONS

K.O. and J.B.N. conceived the ideas and methodology; K.O. collected the data, analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All data presented in this manuscript are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.5401972 (O'Keefe & Nippert, 2018).

ORCID

Kimberly O'Keefe (ID) http://orcid.org/0000-0001-7799-0514

REFERENCES

Alvarado-Barrientos, M. S., Holwerda, F., Geissert, D. R., Munoz-Villers, L. E., Gotsh, S. G., Asbjornsen, H., & Dawson, T. E. (2015). Nighttime transpiration in a seasonally dry tropical montane cloud forest environment. *Trees*, 29, 259–274. https://doi.org/10.1007/s00468-014-1111-1

Asbjornsen, H., Shepherd, G., Helmers, M., & Mora, G. (2008). Seasonal patterns in depth of water uptake under contrasting annual and perennial systems in the corn belt region of the Midwestern US. *Plant and Soil*, 308, 69–92. https://doi.org/10.1007/s11104-008-9607-3

Barbeta, A., Ogaya, R., & Peñuelas, J. (2012). Comparative study of diurnal and nocturnal sap flow of *Quercus ilex* and *Phillyrea latifolia* in a Mediterranean holm oak forest in Prades (Catalonia, NE Spain). *Trees*, 26, 1651–1659. https://doi.org/10.1007/s00468-012-0741-4

Barbour, M. M., & Buckley, T. N. (2007). The stomatal response to evaporative demand persists at night in *Ricinus communis* plants with high nocturnal conductance. *Plant, Cell, & Environment*, 30, 711–721. https://doi.org/10.1111/j.1365-3040.2007.01658.x

Barbour, M. M., Cernusak, L. A., Whitehead, D., Griffen, K. L., Turnbull, M. H., Tissue, D. T., & Farquhar, G. D. (2005). Nocturnal stomatal conductance and implications for modeling $\delta^{18}O$ of leaf-respired CO_2 in temperate tree species. *Functional Plant Biology*, 32, 1107–1121. https://doi.org/10.1071/FP05118

Bartoń, K. (2017). MuMIn: multi-model inference. R package, version 1.40.0. Retrieved from https://CRAN.R-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.

Bucci, S. J., Scholz, F. G., Goldstein, G., Meinzer, F. C., Hinojosa, J. A., Hoffmann, W. A., & Franco, A. C. (2004). Processes preventing nocturnal equilibration between leaf and soil water potential in tropical savanna woody species. *Tree Physiology*, 24, 1119–1127. https://doi.org/10.1093/treephys/24.10.1119

Buckley, T. N., Farquhar, G. D., & Mott, K. A. (1999). Carbon-water balance and patchy stomatal conductance. *Oecologia*, 118, 132–143. https://doi.org/10.1007/s004420050711

Buckley, T. N., Turnbull, T. L., Pfautsch, S., & Adams, M. A. (2011). Nocturnal water loss in mature subalpine *Eucalyptus delegatensis* tall open forests and adjacent *E. pauciflora* woodlands. *Ecology and Evolution*, 1, 435–450. https://doi.org/10.1002/ece3.44

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33, 261–304. https://doi.org/10.1177/0049124104268644

Caird, M. A., Richards, J. H., & Donovan, L. A. (2007). Nighttime stomatal conductance and transpiration in C_3 and C_4 plants. *Plant Physiology*, 143, 4–10.

Caldeira, C. F., Jeanguenin, L., Chaumont, F., & Tardieu, F. (2014). Circadian rhythms of hydraulic conductance and growth are enhanced by drought and improve plant performance. *Nature Communications*, 5, 5365. https://doi.org/10.1038/ncomms6365

Christman, M. A., Richards, J. H., McKay, J. K., Stahl, E. A., Juenger, T. E., & Donovan, L. A. (2008). Genetic variation in *Arabidopsis thaliana* for night-time leaf conductance. *Plant, Cell & Environment*, 31, 1170–1178. https://doi.org/10.1111/j.1365-3040.2008.01833.x

Collins, S. L., & Calabrese, L. B. (2012). Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *Journal of Vegetation Science*, 23, 563–575. https://doi.org/10.1111/j.1654-1103.2011.01369.x

Coupel-Ledru, A., Lebon, E., Chrisophe, A., Gallo, A., Gago, P., Pantin, F., ... Simonneau, T. (2016). Reduced nighttime transpiration is a relevant breeding target for high water-use efficiency in grapevine. *Proceedings of the National Academy of the Sciences*, 1132, 8963–8968. https://doi.org/10.1073/pnas.1600826113

Cowan, I. R., & Farquhar, G. D. (1977). Stomatal function in relation to leaf metabolism and environment. *Symposia of the Society for Experimental Biology*, 31, 471–505.

Daley, M. J., & Phillips, N. G. (2006). Interspecific variation in nighttime transpiration and stomatal conductance in a mixed New England deciduous forest. *Tree Physiology*, 26, 411–419. https://doi.org/10.1093/treephys/26.4.411

Davy, R., Esau, I., Chernokulsky, A., Outten, S., & Zilitinkevich, S. (2017). Diurnal asymmetry to the observed global warming. *International Journal of Climatology*, 37, 79–93. https://doi.org/10.1002/joc.4688

Dawson, T. E., Burgess, S. S. O., Tu, K. P., Oliveira, R. S., Santiago, L. S., Fisher, J. B., ... Ambrose, A. R. (2007). Nighttime transpiration in

woody plants from contrasting ecosystems. *Tree Physiology*, 27, 561–575. https://doi.org/10.1093/treephys/27.4.561

Domec, J. C., Scholz, F. G., Bucci, S. J., Meinzer, F. C., Goldstein, G., & Villalobos-Vega, R. (2006). Diurnal and seasonal variation in root xylem embolism in neotropical savanna woody species: Impact on stomatal control of plant water status. *Plant Cell & Environment*, 29, 26–35. https://doi.org/10.1111/j.1365-3040.2005.01397.x

Donovan, L. A., Linton, M. J., & Richards, J. H. (2001). Predawn plant water potential does not necessarily equilibrate with soil water potential under well-watered conditions. *Oecologia*, 129, 328–335. https://doi.org/10.1007/s004420100738

Eller, F., Jensen, K., & Reisdorff, C. (2017). Nighttime stomatal conductance differs with nutrient availability in two temperate floodplain tree species. *Tree Physiology*, 37, 428–440.

Forster, M. A. (2014). How significant is nocturnal sap flow? *Tree Physiology*, 34, 757–765. https://doi.org/10.1093/treephys/tpu051

Frost, C.C. (1998). Pre-settlement fire frequency regimes of the United States: A first approximation. In: T. L. Pruden & L. A. Brennan (Eds.), *Fire in ecosystem management: shifting the paradigm from suppression to prescription*. Proceedings of the 20"tall timbers fire ecology conference (pp. 70–81). Tallahassee, FL: Tall Timbers Research Station.

Fuentes, S., Mahadevan, M., Bonada, M., Skewes, M. A., & Cox, J. W. (2013). Night-time sap flow is parabolically linked to midday water potential for field-grown almond trees. *Irrigation Science*, 31, 1265–1275. https://doi.org/10.1007/s00271-013-0403-3

Gao, J., Zhou, J., Sun, Z., Niu, J., Zhou, C., Gu, D., … Zhao, P. (2016). Suppression of nighttime sap flux with lower stem photosynthesis in *Eucalyptus* trees. *International Journal of Biometeorology*, 60, 545–556. https://doi.org/10.1007/s00484-015-1050-6

Gelman, A., & Su, Y.S. (2016). arm: data analysis using regression and multilevel/hierarchical models. R package, version 1.9-3. Retrieved from http://CRAN.R-project.org/package=arm

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology*, 24, 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Howard, A. R., & Donovan, L. A. (2007). *Helianthus* nighttime conductance and transpiration respond to soil water but not nutrient availability. *Plant Physiology*, 143, 145–155.

Karpul, R. H., & West, A. G. (2016). Wind drives nocturnal, but not diurnal, transpiration in *Leucospermum conocarpodendron* trees: Implications for stilling on the Cape Peninsula. *Tree Physiology*, 36, 1–13.

Kavanagh, K. L., Pangle, R., & Schotzko, A. D. (2007). Nocturnal transpiration causing disequilibrium between soil and stem predawn water potential in mixed conifer forests of Idaho. *Tree Physiology*, 27, 621–629. https://doi.org/10.1093/treephys/27.4.621

Klodd, A. E., Nippert, J. B., Ratajczak, Z., Waring, H., & Phoenix, G. K. (2016). Tight coupling of leaf area index to canopy nitrogen and phosphorus across heterogeneous tallgrass prairie communities. *Oecologia*, 182, 889–898. https://doi.org/10.1007/s00442-016-3713-3

Knapp, A. K. (1985). Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology*, 66, 1309–1320. https://doi.org/10.2307/1939184

Koerner, S. E., & Collins, S. L. (2014). Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. *Ecology*, 95, 98–109. https://doi.org/10.1890/13-0526.1

Kowalczyk, E. A., Wang, Y. P, Law, R. M., Davies, H. L., McGregor, J. L, & Abramowitz, G. (2006). *The CSIRO Atmosphere Biosphere Land Exchange (CABLE) model for use in climate models and as an offline model* (pp. 1–37) Victoria, Australia: CSIRO Marine and Atmospheric Research

Kupper, P., Rohula, G., Saksing, L., Sellin, A., Lõhmus, K., Ostonen, I., … Sõber, A. (2012). Does soil nutrient availability influence night-time water flux of aspen saplings? *Environmental and Experimental Botany*, 82, 37–42. https://doi.org/10.1016/j.envexpbot.2012.03.013

Lasceve, G., Leymarie, J., & Vavasseur, A. (1997). Alterations in light-induced stomatal opening in a starch deficient mutant of *Arabidopsis thaliana* L. deficient in chloroplast phosphoglucomutase activity. *Plant, Cell, & Environment*, 20, 350–358. https://doi.org/10.1046/j.1365-3040.1997.d01-71.x

Lin, Y., Medlyn, B. E., Duursma, R. A., Prentice, I. C., Wang, H., Baig, S., … Wingate, L. (2015). Optimal stomatal behavior around the world. *Nature Climate Change*, 5, 459–464. https://doi.org/10.1038/nclimate2550

Lombardozzi, D. L., Zeppel, M. J. B., Fisher, R. A., & Tawfik, A. (2017). Representing nighttime and minimum conductance in CLM4.5: Global hydrology and carbon sensitivity analysis using observational constraints. *Geoscientific Model Development*, 10, 321–331. https://doi.org/10.5194/gmd-10-321-2017

Moore, G. W., Cleverly, J. R., & Owens, M. K. (2008). Nocturnal transpiration in riparian Tamarix thickets authenticated by sap flux, eddy covariance and leaf gas exchange measurements. *Tree Physiology*, 28, 521–528. https://doi.org/10.1093/treephys/28.4.521

Muench, A. T., O'Keefe, K., & Nippert, J. B. (2016). Comparative ecohydrology between *Cornus drummondii* and *Solidago canadensis* in upland tallgrass prairie. *Plant Ecology*, 217, 267–276. https://doi.org/10.1007/s11258-016-0567-z

Nippert, J. B., & Knapp, A. K. (2007a). Linking water uptake with rooting patterns in grassland species. *Oecologia*, 153, 261–272. https://doi.org/10.1007/s00442-007-0745-8

Nippert, J. B., & Knapp, A. K. (2007b). Soil water partitioning contributes to species coexistence in tallgrass prairie. *Oikos*, 116, 1017–1029. https://doi.org/10.1111/j.0030-1299.2007.15630.x

Ocheltree, T. W., Nippert, J. B., & Prasad, P. V. V. (2013). Stomatal responses to changes in vapor pressure deficit reflect tissue-specific differences in hydraulic conductance. *Plant Cell & Environment*, 37, 132–139.

Ogle, K., Lucas, R. W., Bentley, L. P., Cable, J. M., Barron-Gafford, G. A., Griffith, A., … Tissue, D. T. (2012). Differential daytime and nighttime stomatal behaviour in plants from North American deserts. *New Phytologist*, 194, 464–476. https://doi.org/10.1111/j.1469-8137.2012.04068.x

O'Keefe, K., & Nippert, J. B. (2017a). Grazing by bison is a stronger driver of plant ecohydrology in tallgrass prairie than fire history. *Plant and Soil*, 411, 423–436. https://doi.org/10.1007/s11104-016-3048-1

O'Keefe, K., & Nippert, J. B. (2017b). An assessment of diurnal water uptake in a mesic prairie: Evidence for hydraulic lift? *Oecologia*, 183, 963–975. https://doi.org/10.1007/s00442-017-3827-2

O'Keefe, K., & Nippert, J. B. (2018). Data from: Drivers of nocturnal water flux in a tallgrass prairie. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.5401972

Phillips, N. G., Lewis, J. D., Logan, B. A., & Tissue, D. T. (2010). Inter- and intra-specific variation in nocturnal water transport in *Eucalyptus*. *Tree Physiology*, 30, 586–596. https://doi.org/10.1093/treephys/tpq009

R Core Team. (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from http://www.R-project.org/

Resco de Dios, V., Diaz-Sierra, R., Goulden, M. L., Barton, C. V. M., Boer, M. M., Gessler, A., … Tissue, D. T. (2013). Woody clockworks: Circadian regulation of night-time water use in *Eucalyptus globulus*. *New Phytologist*, 200, 743–752. https://doi.org/10.1111/nph.12382

Resco de Dios, V., Loik, M. E., Smith, R., Aspinwall, M. J., & Tissue, D. T. (2016). Genetic variation in circadian regulation of nocturnal stomatal conductance enhances carbon assimilation and growth. *Plant, Cell, & Environment*, 39, 3–11. https://doi.org/10.1111/pce.12598

Resco de Dios, V., Roy, J., Ferrio, J. P., Alday, J. G., Landais, D., Milcu, A., & Gessler, A. (2015). Processes driving nocturnal transpiration and implications for estimating land evapotranspiration. *Scientific Reports*, *5*, 10975. https://doi.org/10.1038/srep10975

Rohula, G., Kupper, P., Räim, O., Sellin, A., & Sõber, A. (2014). Patterns of night-time water use are interrelated with leaf nitrogen concentration in shoots of 16 deciduous woody species. *Environmental and Experimental Botany*, *99*, 180–188. https://doi.org/10.1016/j.envexpbot.2013.11.017

Sack, L., & Holbrook, N. M. (2006). Leaf hydraulics. *Annual Review of Plant Biology*, *57*, 361–381. https://doi.org/10.1146/annurev.arplant.56.032604.144141

Schielzeth, H., & Nakagawa, S. (2013). Nested by design: Model fitting and interpretation in a mixed model era. *Methods in Ecology and Evolution*, *4*, 14–24. https://doi.org/10.1111/j.2041-210x.2012.00251.x

Scholz, F. G., Bucci, S. J., Goldstein, G., Meinzer, F. C., Franco, A. C., & Miralles-Wilhelm, F. (2007). Removal of nutrient limitations by long-term fertilization decreases nocturnal water loss in savanna trees. *Tree Physiology*, *27*, 551–559. https://doi.org/10.1093/treephys/27.4.551

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., … Venevsky, S. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, *9*, 161–185. https://doi.org/10.1046/j.1365-2486.2003.00569.x

Smith, M. D., & Knapp, A. K. (2003). Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters*, *6*, 509–517. https://doi.org/10.1046/j.1461-0248.2003.00454.x

Snyder, K. A., Richards, J. H., & Donovan, L. A. (2003). Night-time conductance in C_3 and C_4 species: Do plants lose water at night? *Journal of Experimental Botany*, *54*, 861–865. https://doi.org/10.1093/jxb/erg082

Tilman, D. (1982). *Resource competition and community structure*. Princeton, NJ: Princeton University Press.

Tucker, S. S., Craine, J. M., & Nippert, J. B. (2011). Physiological drought tolerance and the structuring of tallgrass prairie assemblages. *Ecosphere*, *2*, 1–19.

Wallace, J., & McJannet, D. (2010). Processes controlling transpiration in the rainforests of north Queensland, Australia. *Journal of Hydrology*, *384*, 107–117. https://doi.org/10.1016/j.jhydrol.2010.01.015

Zeppel, M. J. B., Lewis, J. D., Medlyn, B., Barton, C. V. M., Duursma, R. A., Eamus, D., … Tissue, D. T. (2011). Interactive effects of elevated CO2 and drought on nocturnal water fluxes in *Eucalyptus saligna*. *Tree Physiology*, *31*, 932–944. https://doi.org/10.1093/treephys/tpr024

Zeppel, M. J. B., Lewis, J. D., Phillips, N. G., & Tissue, D. T. (2014). Consequences of nocturnal water loss: A synthesis of regulating factors and implications for capacitance, embolism and use in models. *Tree Physiology*, *34*, 1047–1055. https://doi.org/10.1093/treephys/tpu089

Zeppel, M., Logan, B., Lewis, J. D., Phillips, N., & Tissue, D. (2013). Why lose water at night? Disentangling the mystery of nocturnal sap flow, transpiration and stomatal conductance – When, where, who. *Acta Horticulturae*, *991*, 307–312. https://doi.org/10.17660/ActaHortic.2013.991.38

Zeppel, M., Tissue, D., Taylor, D., Macinnis-Ng, C., & Eamus, D. (2010). Rates of nocturnal transpiration in two evergreen temperate woodland species with differing water-use strategies. *Tree Physiology*, *30*, 988–1000. https://doi.org/10.1093/treephys/tpq053

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: O'Keefe K, Nippert JB. Drivers of nocturnal water flux in a tallgrass prairie. *Funct Ecol*. 2018;00:1–13. https://doi.org/10.1111/1365-2435.13072