Oecologia (2017) 183:963–975
DOI 10.1007/s00442-017-3827-2

PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

An assessment of diurnal water uptake in a mesic prairie: evidence for hydraulic lift?

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Received: 26 February 2016 / Accepted: 22 January 2017 / Published online: 2 February 2017

Abstract Hydraulic lift, the passive movement of water through plant roots from wet to dry soil, is an important ecohydrological process in a wide range of water-limited ecosystems. This phenomenon may also alter plant functioning, growth, and survival in mesic grasslands, where soil moisture is spatially and temporally variable. Here, we monitored diurnal changes in the isotopic signature of soil and plant xylem water to assess (1) whether hydraulic lift occurs in woody and herbaceous tallgrass prairie species (*Rhus glabra*, *Amorpha canescens*, *Vernonia baldwinii*, and *Andropogon gerardii*), (2) if nocturnal transpiration or grazing by large ungulates limits hydraulic lift, and (3) if a dominant grass, *A. gerardii*, utilizes water lifted by other tallgrass prairie species. Broadly, the results shown here suggest that hydraulic lift does not appear to be widespread or common in this system, but isolated instances suggest that this process does occur within tallgrass prairie. The isolated instance of hydraulic lift did not vary by grazing treatment, nor did they result in facilitation for neighboring grasses. We suggest that the topographic complexity of this tallgrass prairie and the high rates of nocturnal transpiration observed in this study likely limit the frequency and occurrence of hydraulic lift. These results suggest that hydraulic lift can be a patchy process, particularly in heterogeneous landscapes.

Keywords Hydraulic lift · Tallgrass prairie · Stable isotopes · Nocturnal transpiration · Water potential

Introduction

Tallgrass prairies are dynamic ecosystems that experience tremendous spatial variability in water availability through time (Knapp et al. 1993; Nippert et al. 2011). Precipitation occurs stochastically in these systems, resulting in long dry periods during which plants must either tolerate water stress (Tucker et al. 2011) or access deep water sources (Nippert and Knapp 2007a, b; Asbjornsen et al. 2008) to persist through drought. In this periodically dry landscape, prairie plants may also exhibit hydraulic lift, defined as the passive movement of water across soil water potential gradients through plant roots (Breazeale and Crider 1934; Richards and Caldwell 1987; Caldwell et al. 1998). Hydraulic lift typically occurs at night when plant stomata close and the water potential gradient between shallow and deep soil is more pronounced than the gradient between deep soil and plant leaves. This gradient redistributes deep water to shallow soil, reducing water limitation in the rhizosphere for both the plant lifting the water and for neighboring plants that grow within the zone of lifted water (Dawson 1993; Moreira et al. 2003).

Hydraulic lift is most commonly observed in arid and semi-arid ecosystems (reviewed in Neumann and Cardon 2012; Prieto et al. 2012a; Sardans and Penuelas 2014). Few examples of hydraulic lift exist in grasslands or herbaceous plants and these instances have only been observed in semi-arid regions (Espeleta et al. 2004; McCulley et al. 2004),

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Communicated by Susanne Schwinning.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-017-3827-2) contains supplementary material, which is available to authorized users.

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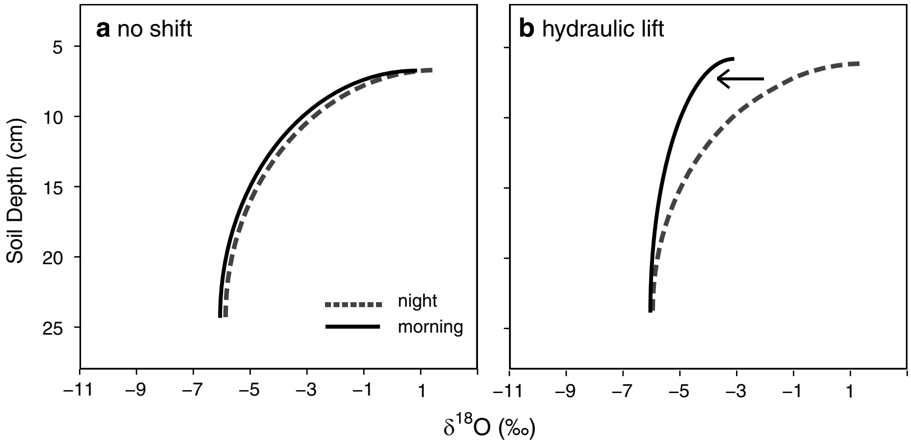

Fig. 1 Predicted diurnal changes in soil water δ^{18}O (‰) within soil cores adjacent to plants. Shown are predictions for no diurnal change (**a**), and a negative shift indicating hydraulic lift (**b**)

deserts (Schulze et al. 1998; Yoder and Nowak 1999), and greenhouses (Armas et al. 2012). However, hydraulic lift may play an important role in tallgrass prairies because the long dry periods that occur during the growing season cause significant drying within the shallow soil layers (0–30 cm; Abrams and Knapp 1986; Williams and Rice 2007; Zeglin et al. 2013), and should therefore produce the soil water potential gradient necessary to drive hydraulic lift. Most tallgrass prairie plants are also deep-rooted (typically ≥2 m deep; Weaver 1919) and utilize at least some deep soil water during the growing season (up to 47% deep water in grasses, 56% deep water in forbs, and 76% deep water in shrubs; Nippert and Knapp 2007a). Thus, these species should have the capability to redistribute water via hydraulic lift, if environmental conditions are favorable.

However, certain characteristics of the prairie may also limit water redistribution. In grasslands that are grazed, large ungulates such as *Bison bison* (American bison) reduce shallow root biomass (Johnson and Matchett 2001; Nippert et al. 2012), which may reduce water efflux from the shallow roots of grazed grasses. Grazers also reduce leaf area, and thus, transpiration, which can increase soil moisture (Archer and Detling 1986; Svejcar and Christiansen 1987; Harrison et al. 2010) and eliminate the driving gradient necessary for hydraulic lift for both grazed and nearby ungrazed plants. Alternatively, nocturnal transpiration may create a competing sink for water movement and limit hydraulic lift, as has commonly been observed in other systems (Donovan et al. 2001, 2003; Kavanagh et al. 2007; Scholz et al. 2008; Howard et al. 2009). Considering the effects of grazing on soil moisture and root biomass, as well as the dependence of hydraulic lift on soil water potential gradients and shallow root biomass, it seems likely that hydraulic lift may be spatially and temporally variable within a tallgrass prairie exposed to different grazing regimes. However, it is unknown if hydraulic lift occurs in tallgrass prairie ecosystems or how this process may change within grazed and ungrazed tallgrass prairie.

Here, we assessed whether hydraulic lift occurs in a native tallgrass prairie located in northeastern Kansas, USA. Previous studies have identified hydraulic lift with methods that are typically time consuming, destructive, or require expensive equipment (e.g., time-domain reflectrometry probes, soil psychrometers, sap flow sensors, enriched stable isotope tracers, or radioactive dye; reviewed in Prieto et al. 2012a). In this study, however, we used the natural variation in the isotopic signature of soil water to identify hydraulic lift, which is a relatively cheap and non-destructive approach. The stable isotopic signature of soil water varies predictably by depth due to evaporation-driven fractionation, with enriched water found near the soil surface and depleted water found in deep soil (Ehleringer and Dawson 1992). If hydraulic lift occurs, shallow soil water should develop a depleted δ^{18}O signature overnight as deep water is redistributed (Fig. 1). Furthermore, this shift in δ^{18}O should be reflected in plant stem water because tallgrass prairie plants typically utilize some water overnight (O'Keefe and Nippert, unpublished data) and because the isotopic signature of water within the stem reflects the water source used (White et al. 1985).

By analyzing diurnal changes in the isotopic signature of plant and soil water, we addressed the following questions: (1) Does hydraulic lift occur in common woody, forb, and grass species in a tallgrass prairie? We hypothesized that these deep-rooted (≥2 m deep) species will all exhibit hydraulic lift, (2) If hydraulic lift does not occur, is it limited by bison grazing or nocturnal transpiration? We hypothesized that any absence of hydraulic lift will be associated with bison grazing and/or nocturnal transpiration, (3) If hydraulic lift does occur in forbs or shrubs, but not a dominant grass, *Andropogon gerardii* Vitman, can the grass utilize water lifted by neighboring deep-rooted forbs and shrubs? We hypothesized that if hydraulic lift occurs in shrubs or forbs but not *A. gerardii*, *A. gerardii* will instead utilize water lifted to shallow soil by neighboring shrubs or forbs, as has been observed in other systems (Caldwell 1990; Dawson 1993; Moreira et al. 2003).

Methods

Site description

Field work was conducted 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 3487 ha tallgrass prairie that is dominated by a few perennial C_4 grass species along with numerous sub-dominant C_3 grass, forb, and woody species (Smith and Knapp 2003). The site is divided into watershed-level plots that are burned at varying frequencies (every 1, 2, 4 or 20 years) and are either grazed or ungrazed by cattle and the ungulate *Bison bison*. KPBS is also topographically heterogeneous, with layers of Permian shale and limestone alternating across a non-uniform terrain of flat upland ridges, steep slopes, and lowland valleys (Jantz et al. 1975; Oviatt 1998). Soil depth varies by topographic position; upland ridges are characterized by shallow, rocky soils (<0.5 m) derived from the chert-bearing limestone, while lowlands are characterized by deep (>2 m) silty-clay loams (Tully soil series) derived from alluvial–colluvial deposits (Oviatt 1998; Ransom et al. 1998). Clay content in lowland soils ranges from 35 to 40% at the surface and 45 to 60% in the lower subsoil (Ransom et al. 1998). Although lowland soils are generally deep, many areas are shallower and contain numerous rock fragments (up to 15% rock fragment by soil volume; Ransom et al. 1998). Lowland soils are also moderately well drained, and deep soil water is recharged during the winter when rain or snowmelt infiltrates to a greater depth in the soil and moves laterally between layers of shale and limestone (Ransom et al. 1998; Nippert and Knapp 2007a). Due to these topoedaphic differences, the deep lowland soils are typically more mesic and have higher primary productivity than shallow upland soils (Knapp et al. 1993; Nippert et al. 2011).

Long-term mean annual precipitation at KPBS is 829 mm (1982–2014), with 73% occurring during the growing season (April–September). Precipitation was 783 mm in 2013 and 706 mm in 2014 (77 and 68% of which occurred during each respective growing season; Figure A1). July is the warmest average month of the year (1982–2014), with mean maximum and minimum air temperatures of 32.69 and 19.78 °C, respectively. January is the coldest average month in (1982–2014), with mean maximum and minimum air temperatures of 4.87 and −7.14 °C. Maximum air temperatures during July 2013 and 2014 were 30.99 and 31.7 °C, respectively. Minimum air temperatures during July 2013 and 2014 were 18.46 and 17.06 °C, respectively.

Sampling description

We sampled from two watersheds that are burned in 4-year intervals, as these locations are most representative of historic burn frequencies for tallgrass prairie in northeastern Kansas (Frost 1998), and they also contain more forb and woody plant diversity than annually or biannually burned plots (Collins and Calabrese 2012; Koerner and Collins 2014). To assess the impact of large herbivore grazing on hydraulic lift, we sampled in one watershed grazed by bison and one ungrazed watershed. While watershed treatments were not replicated due to their large size and low availability at KPBS, we sampled from three spatially separated lowland sites (>100 m apart) within each watershed to achieve spatial independence among samples.

We sampled four different species that have widespread distribution and abundance at KPBS: one clonal C_3 shrub (*Rhus glabra* L., smooth sumac), one leguminous C_3 subshrub (*Amorpha canescens* Pursh., leadplant), one C_3 forb (*Vernonia baldwinii* Torr., Baldwin's ironweed), and one C_4 grass (*A. gerardii*, big bluestem). These species have the potential to exhibit hydraulic lift because they are all deeply rooted, having maximum rooting depths of 2.3 m (*R. glabra*), 2.3 m (*A. canescens*), 3.3 m (*V. baldwinii*), and 1.8 m (*A. gerardii*) (Weaver 1919). Additionally, *R. glabra*, *A. cancescens*, and *V. baldwinii* utilize deep water as a primary water source in this system (Nippert and Knapp 2007a, b; O'Keefe and Nippert, unpublished data). Although grazing typically increases the abundance of forbs and shrubs relative to ungrazed sites, all four species were present at each study site included here.

We conducted four sampling campaigns throughout 2013 (DOY 187 and 241) and 2014 (DOY 188 and 233). In each year, we sampled once in early July (mid growing season) and once in late August (late growing season). These sampling times were chosen because the majority of growing season precipitation occurs earlier in the year (April–June) at this site and thus, strong water potential gradients do not typically exist throughout the soil until later in the growing season (Abrams and Knapp 1986; Williams and Rice 2007; Zeglin et al. 2013). Additionally, each sampling campaign occurred at least 5–7 days after a rainfall event to allow a water potential gradient to establish between shallow and deep soil (Figure A1).

During each campaign, we collected plant samples for isotopic analysis at 18:00 h (night) and again at 05:00 h the following morning (morning). We sampled individuals that were located at least 1 m apart from other deep-rooted plants to reduce the possibility of detecting hydraulic lift from neighbors. Due to the destructive nature of isotope sampling (see below), we could not sample the same individual more than once and thus had to sample similarly sized individuals for each time point. One individual per species was sampled at each site within a watershed for all time points ($n = 3$ plants per species in each watershed at each sampling time point; total $n = 24$ per time point). To assess whether *A. gerardii* utilizes lifted water by shrubs or forbs, we sampled one "isolated" *A. gerardii* and one "neighboring" *A. gerardii* adjacent to each "target plant" (*R. glabra*, *V. baldwinii*, and *A. canescens*) at each sampling site during each time point ($n = 3$ isolated/adjacent *A. gerardii* plants in each watershed and time point; total $n = 24$). Isolated *A. gerardii* functioned as a control and were located at least 1 m from other deep-rooted forbs or shrubs, and the neighboring *A. gerardii* were located within a 0.25 m radius from the main stem of the target plant.

Water isotope samples

Plant tissue and soil cores were collected for isotope analyses during each night and morning sampling time points. For forb and shrub xylem water isotope samples, we collected 20–30 g of non-photosynthetic stem tissue, located immediately above ground level (0–2 cm high) prior to photosynthetic growth. For *A. gerardii* xylem water isotope samples, we collected crown tissue, which is located immediately below ground level but above any rhizomes or root tissue. We collected one stem for all species except *A. gerardii*, which required 5–10 crowns to provide enough water for the extraction and analysis processes. Plant tissues were immediately sealed in exetainer vials (Labco, Ltd., UK) and stored on ice until transferred to a 1–2 °C refrigerator. We collected soil cores within 0.10 m from the main stem sampled for plant tissue using a 25 cm hand corer. The core was split up into 5 cm deep segments (0–5 cm, 5–10 cm, 10–15 cm, 15–20 cm, and 20–25 cm depths), stored in double-layered plastic bags, and placed on ice until transferred to a −5 °C freezer. The soil was then removed from the freezer and immediately placed in exetainer vials for water extraction. Deep soil cores (1–2 m deep) were also collected for use as a "deep" endpoint in an isotopic mixing model (see *Statistics*). Cores were collected at five random lowland locations using a 540MT Geoprobe Systems hydraulic-push corer (Salina, KS, USA). The soil from the very bottom of these cores was collected and saved in exetainer vials for later water extraction and analysis.

We extracted xylem and soil water using the cryogenic vacuum distillation method (Ehleringer and Osmond 1989; Nippert and Knapp 2007a) and analyzed the stable hydrogen (δD) and oxygen (δ^{18}O) signatures of these water samples using a Picarro WS-CRDS isotopic water analyzer.

Leaf water potential measurements

To assess whether hydraulic lift is associated with differences in leaf pressure potential, we measured predawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potential on the same plants collected for isotope analyses. Ψ_{md} was measured on each night individual at 12:00 h the day of night measurements. Ψ_{pd} was measured on each morning individual immediately before each plant was harvested for morning isotope samples. For all measurements, the youngest, most fully developed leaf was cut and placed in a dark, humidified plastic bag for approximately 1 hour. After the equilibration period, leaf water potential was measured using a Scholander pressure chamber (PMS Instrument Company, Albany, OR). We made Ψ_{pd} and Ψ_{md} measurements on all four study species at each sampling site ($n = 3$ plants) as well as *A. gerardii* adjacent to *R. glabra*, *V. baldwinii*, and *A. canescens* ($n = 3$ plants).

Nighttime transpiration measurements

To assess whether nocturnal water loss is associated with a potential absence of hydraulic lift, as has been observed in other species (Howard et al. 2009), we measured nocturnal transpiration using an Li-6400xt open gas exchange system (Li-Cor, Inc., Lincoln, NE). Measurements were made during 2014, between 22:00–01:00 h, the night before isotope samples were collected. The youngest, fully developed leaf of each plant was allowed to stabilize in the Li-6400xt cuvette for 2-3 min and then measurements were logged every 10 s for 3 min. The last minute of data was averaged as a representative measurement for each plant. Measurements were made on all four study species at each sampling site ($n = 3$ plants), as well as one *A. gerardii* adjacent to each target plant ($n = 3$ plants).

Soil water content measurements

In addition to stable isotope measurements, we measured soil water content adjacent to each night and morning plant to evaluate whether hydraulic lift could be detected using soil moisture measurements alone. Soil water content was measured using two methods. First, we measured the relative water content (RWC) in the top 10 cm soil within a 10 cm radius from the main stem of each plant at the time it was sampled for isotope analyses. RWC was measured in situ with a Hydra Probe II Soil Sensor (Stevens Water Monitoring Systems, Portland, OR, USA) as a proportion in units of water fraction by volume (wfv). Second, we measured the gravimetric soil moisture content (GWC, θ_g) of each soil core depth using subsamples of the soil collected for isotopic analysis. The wet weight of the soil was determined with a microbalance (±0.1 mg; Ohaus Pioneer, Ohaus Corporation, Parsippany, NJ, USA). The soil was dried at 60 °C for 48 h, reweighed to measure the soil dry weight, and gravimetric water content was calculated following Black (1965).

Statistics

The Bayesian isotopic mixing model Stable Isotope Analysis in R (SIAR) was used to quantify the proportion of deep and shallow water sources to the isotopic signature of plant xylem water (Parnell et al. 2010). We used separate SIAR analyses for each sampling campaign (July 2013, August 2013, July 2014, and August 2014) and ran each model for 500,000 iterations, of which we discarded the first 50,000 iterations. We used shallow (0–5 cm deep) and deep soil water (1–2 m deep) as the two source endpoints in all analyses. For the shallow sources, we averaged the isotopic signatures of 0–5 cm soil collected at night for each year × month combination and used that average value ($n = 24$) for the corresponding SIAR model analysis. For the deep soil water source, we used the mean isotopic signature of soil water extracted from the bottom of 1–2 m deep soil cores ($n = 5$) for all SIAR analyses. Each analysis produced a posterior distribution predicting the proportion of shallow and deep source water contribution for each species at every sampling location and time point. We then used the mean value of each distribution to calculate the difference in deep water used by each species between night and morning time points for every grazing treatment × month × year combination. See Parnell et al. (2010) for a full description of the model.

We compared leaf water potential data among treatment combinations using a linear mixed-effects model in a completely randomized design (CRD) with year (2013 and 2014), month (July and August), grazing treatment (grazed and ungrazed), and species (*R. glabra*, *A. canescens*, *V. baldwinii*, and isolated *A. gerardii*) as fixed effects. Sampling site within watershed was included as a random effect to account for variability associated with grouped data (Pinheiro and Bates 2000). Nighttime transpiration data were analyzed using a linear mixed-effects model in a CRD with month, grazing treatment, and species as fixed effects and site within watershed as a random effect. We also conducted separate analyses comparing leaf water potential and nocturnal transpiration among differently positioned *A. gerardii* using year, month, grazing treatment, and *A. gerardii* location (isolated *A. gerardii*, *A. gerardii* near *R. glabra*, *A. gerardii* near *A. canescens*, and *A. gerardii* near *V. baldwinii*) as fixed effects and site within watershed as a random effect.

Soil water isotope data were analyzed using a linear mixed-effects model in a CRD with year, month, grazing treatment, sampling time (night, morning), species, and soil depth as fixed effects and site within watershed as a random effect. Soil RWC data were analyzed using a linear mixed-effects model in a CRD with year, month, grazing treatment, sampling time (night, morning), and species as fixed effects and site within watershed as a random effect. Finally, soil GWC data were analyzed using a linear mixed-effects model in a CRD with month, grazing treatment, sampling time, and soil depth as fixed effects and site within watershed as a random effect. Homogeneity of variances was assessed by examining residuals versus fitted plots, all data were checked for normality by examining normal qq-plots (Faraway 2005), and post hoc multiple comparisons were calculated using Tukey's Honest Significant Difference test (Tukey 1949). All analyses were conducted using the '*lmer*' function of the 'lme4' package V1.1-7 (Bates et al. 2014) in the statistical program R V3.1.0 (R Core Team 2012).

Results

Soil moisture data

We found a significant year × month × grazing × species interaction ($p = 0.02$) among RWC values, and significant month × grazing ($p = 0.03$) and species × grazing ($p = 0.01$) interactions among GWC values (Table A1). RWC was greater in July than August and lower in ungrazed locations than in grazed locations, while GWC was greater in July and greater in ungrazed locations (Tables A2–A3). We did not detect evidence of hydraulic lift with either method, as there were no significant differences in soil moisture between night and morning sampling times ($p > 0.05$; Table A1).

Soil isotope data

We found a significant year × month × grazing × sampling time × species interaction ($p = 0.01$) for soil core δ^{18}O signatures, indicating considerable variation in the isotopic signatures of soil cores (Table A4; Figs. 2, 3). Due to the complexity of interpreting a significant five-way interaction, we chose to report significant lower-order interactions as well, which include significant year × month × depth ($p < 0.01$), year × grazing × species ($p = 0.03$), grazing × depth ($p < 0.01$), grazing × sampling time ($p = 0.04$), and month × grazing ($p < 0.001$) interactions. Of the soil cores that exhibited shifts to deeper water signatures, only six instances were statistically different (Figs. 2e, h, l, n, 3h, l). However, non-significant shifts to deeper δ^{18}O signatures were also observed in additional soil cores representative of all species, in all grazing treatments, months, and years (Figs. 2–3). Positive overnight

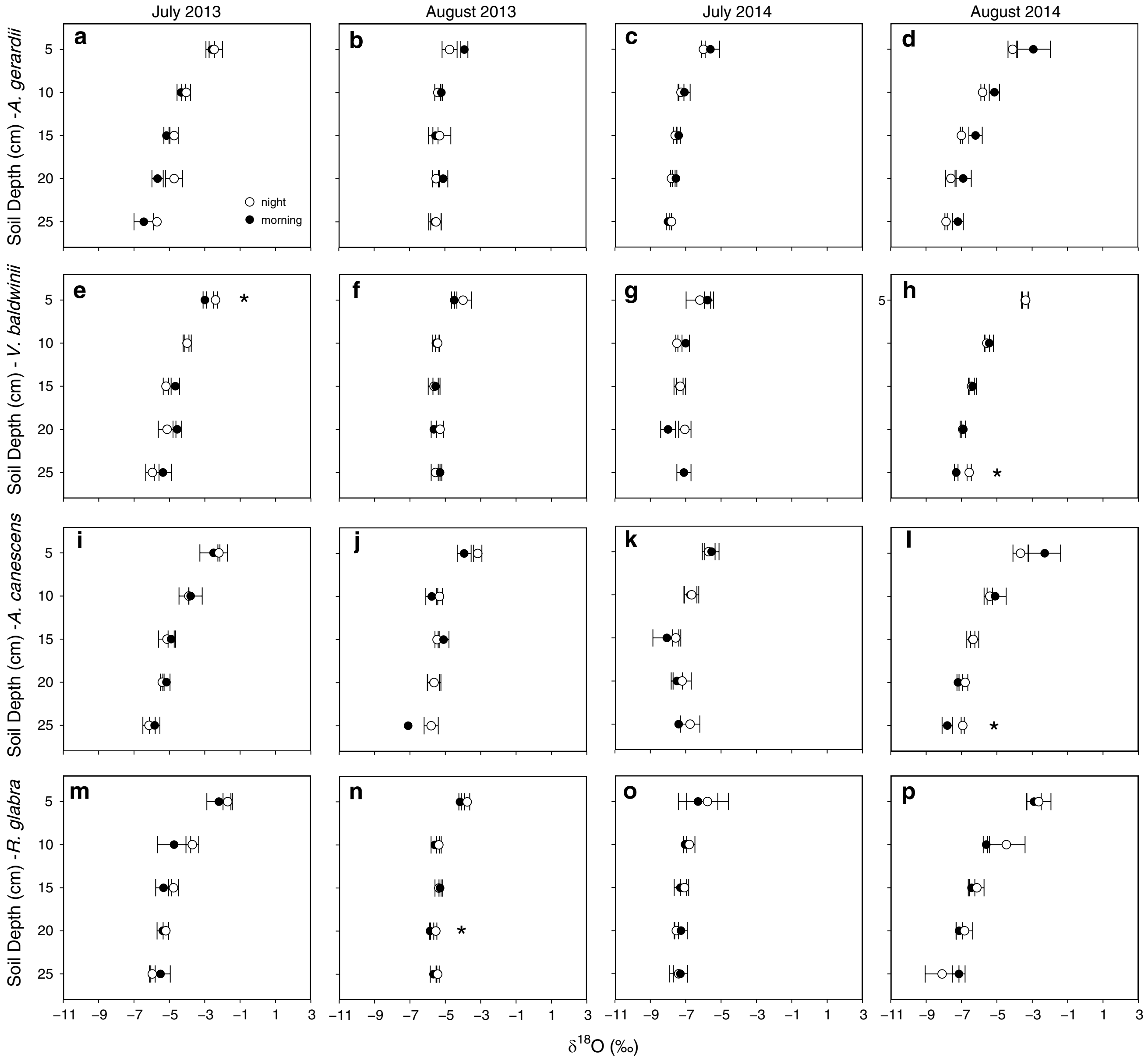

Fig. 2 Soil water δ^{18}O (‰) measured at various depths within soil cores adjacent to each plant in ungrazed locations. Shown are soil cores collected at night and morning time points adjacent to *A. gerardii* (**a**–**d**), *V. baldwinii* (**e**–**h**), *canescens* (**i**–**l**), and *R. glabra* (**m**–**p**) during July 2013 (**a**, **e**, **i**, **m**), August 2013 (**b**, **f**, **j**, **n**), July 2014 (**c**, **g**, **k**, **o**), and August 2014 (**d**, **h**, **l**, **p**). Shown are mean ± 1 SEM

shifts in the isotopic signature of soil water were generally not observed.

Relative deep soil water use

SIAR analyses showed that the proportion of deep water in plant xylem tissue varied between night and morning samples, and that these changes were variable across species and sampling periods (Fig. 4). Most species typically used less deep water during the morning time point compared to night, suggesting that hydraulic lift did not occur (illustrated by negative values in Fig. 4). Several exceptions were observed when species used deeper water during morning than night (illustrated by positive values in Fig. 4). These instances included grazed *V. baldwinii* and ungrazed *A. canescens* collected during July 2013, as well as ungrazed *R. glabra* collected during all time periods except 2013. We found no evidence of hydraulic lift or use of water lifted by target plants in neighboring *A. gerardii* (Table A5).

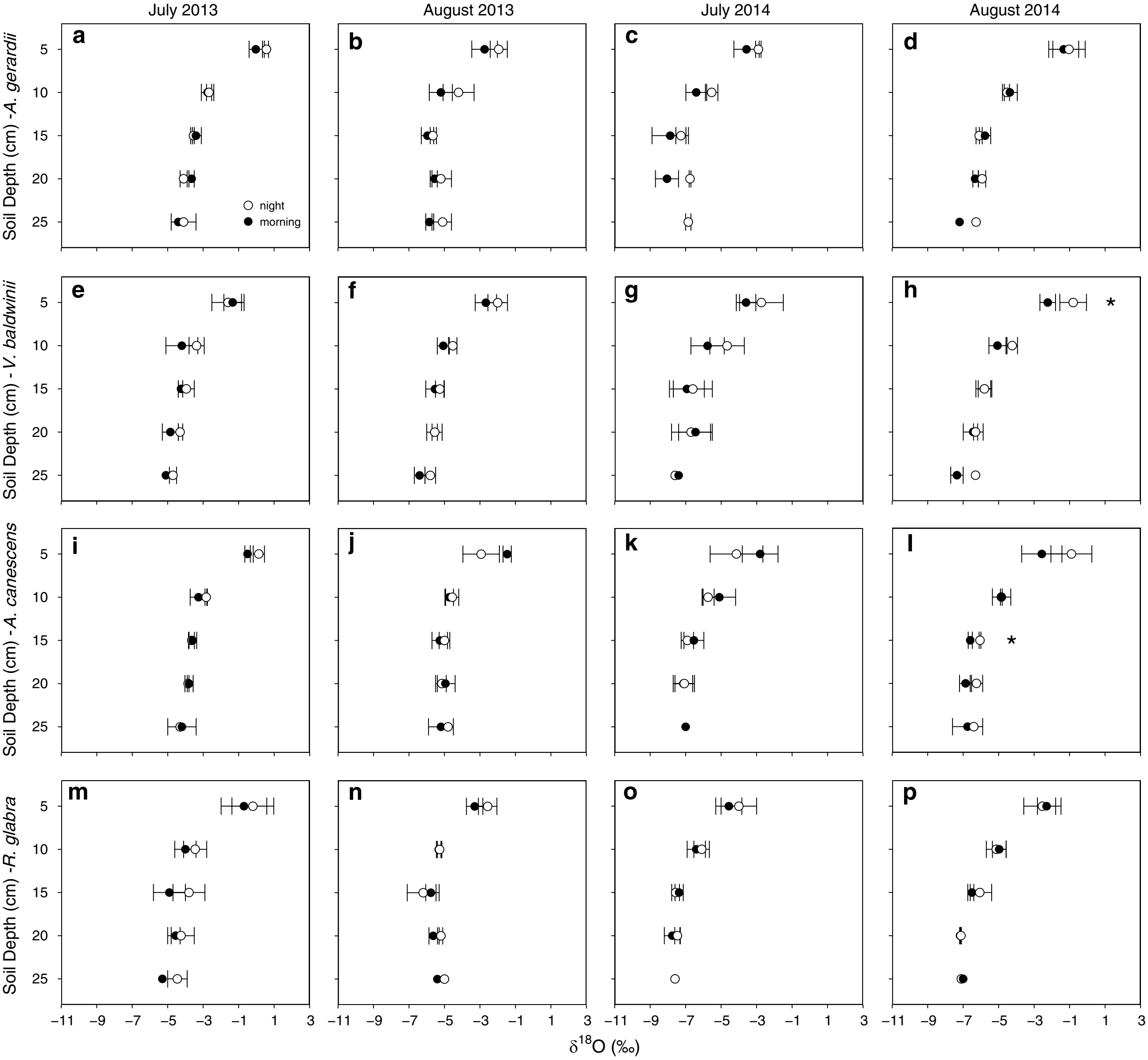

Fig. 3 Soil water δ^{18}O (‰) measured at various depths within soil cores adjacent to each plant in grazed locations. Shown are soil cores collected at night and morning time points adjacent to *A. gerardii* (**a**–**d**), *V. baldwinii* (**e**–**h**), *canescens* (**i**–**l**), and *R. glabra* (**m**–**p**) during July 2013 (**a**, **e**, **i**, **m**), August 2013 (**b**, **f**, **j**, **n**), July 2014 (**c**, **g**, **k**, **o**), and August 2014 (**d**, **h**, **l**, **p**). Shown are mean ± 1 SEM

Nighttime transpiration data

Nocturnal transpiration (E_{night}) was observed in all species and locations, in both July and August 2014 (Table 1). Mean E_{night} rates ranged from 0.21 mmol H_2O m^2s^{-1} to 0.84 mmol H_2O m^2s^{-1} (Table 1, Table A6). However, there were no significant differences in E_{night} among months, grazing treatments, or species ($p > 0.05$; Table A7). There were also no differences in E_{night} between isolated *A. gerardii* and *A. gerardii* near target plants ($p > 0.05$; Table A7).

Leaf water potential measurements

Predawn leaf water potential (Ψ_{pd}) showed a significant year × month × species × grazing interaction ($p = 0.02$; Table A8). Ψ_{pd} was lower in August than in July and lower in 2014 than 2013 (Table A9). Ψ_{pd} was also lower in grazed areas than in ungrazed areas in August 2013 and July 2014, for all species with the exception of *A. gerardii* (Table A9). Similarly, we found a significant year × month × species interaction ($p < 0.01$; Table A8) for midday leaf water potential (Ψ_{md}). Ψ_{md} was lower in August than in July and

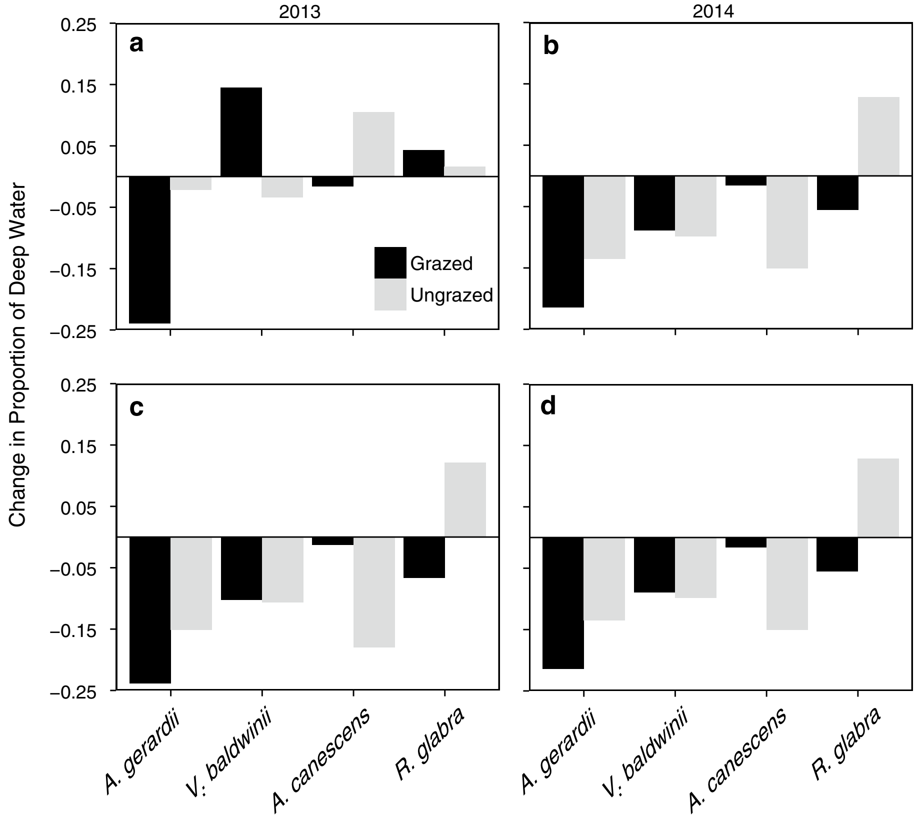

Fig. 4 Change in the proportion of deep water in plant xylem from night to morning time points, measured during July (**a**, **b**) and August (**c**, **d**) in 2013 and 2014. Positive values indicate an increase in deep water contribution to xylem water from night to morning, while negative values indicate a decrease in deep water contribution to xylem water from night to morning. Samples were collected for *A. gerardii*, *V. baldwinii*, *A. canescens*, and *R. glabra* in ungrazed and grazed locations. Values were calculated from the posterior distributions of the SIAR analyses

Table 1 Nocturnal transpiration (mmol H_2O m^2s^{-1}) during July and August 2014

	July 2014		August 2014	
	Ungrazed	Grazed	Ungrazed	Grazed
A. gerardii	0.5803 ± 0.2181	0.6282 ± 0.2520	0.5658 ± 0.3256	0.4495 ± 0.0869
V. baldwinii	0.3806 ± 0.1104	0.5577 ± 0.1840	0.4798 ± 0.0579	0.4683 ± 0.0984
A. canescens	0.4352 ± 0.1938	0.4837 ± 0.0506	0.3574 ± 0.0644	0.4797 ± 0.1251
R. glabra	0.2562 ± 0.0476	0.3141 ± 0.01272	0.2113 ± 0.0543	0.3310 ± 0.0999

Measurements were made on *A. gerardii*, *V. baldwinii*, *A. canescens*, and *R. glabra* in ungrazed and grazed locations. Shown are mean ± 1 SEM

also lower in 2014 than 2013 (Table A10). Ψ_{md} was similar among species, with the exception of the low values observed for *A. gerardii* and *A. canescens* in August 2013 (Table A10). There was no significant effect of grazing treatment on Ψ_{md} ($p > 0.05$; Table A8).

We found no differences in Ψ_{pd} or Ψ_{md} between isolated *A. gerardii* and *A. gerardii* near target plants ($p > 0.05$; Table A8). There were significant year ($p < 0.01$) and month ($p < 0.01$) effects when comparing Ψ_{pd} among *A. gerardii* samples (Table A8), as Ψ_{pd} was lower in 2014 than in 2013 and lower in August than in July (Table A11). Similarly, there were significant year ($p < 0.01$) and month × grazing ($p = 0.02$) effects observed for Ψ_{md} compared across *A. gerardii* samples (Table A8). Ψ_{md} was lower in 2014 than 2013 and lower in August than in July, although this was more prevalent in ungrazed areas than in grazed areas (Table A12).

Discussion

Hydraulic lift is an important ecohydrological process in many water-limited ecosystems, though the occurrence and relevance of this phenomenon in mesic grasslands is unknown. Here, we tested the hypotheses that (1) hydraulic lift does occur in deep-rooted grass, forb, and woody species in a tallgrass prairie, (2) any reductions in hydraulic lift will be associated with bison grazing or nocturnal transpiration, and (3) a dominant grass, *A. gerardii*, will utilize water lifted by neighboring forbs and shrubs if it does not lift water itself. We observed overnight shifts in the isotopic signature of soil water adjacent to deep-rooted plants, suggesting that our method was sufficient to detect hydraulic lift. In contrast to our predictions, we found that hydraulic lift was uncommon, did not differ between grazing treatments, and did not facilitate water use by neighboring grasses. We did measure substantial rates of nocturnal transpiration among all species, suggesting that nocturnal water loss may limit hydraulic lift in this system. Overall, our work demonstrates that hydraulic lift can occur, but is generally not widespread or common across this tallgrass prairie landscape.

Does hydraulic lift occur in common woody, forb, and grass species in a tallgrass prairie?

Using the stable isotopic signature of soil and plant water, we tested the hypothesis that all four deep-rooted species utilize hydraulic lift in a tallgrass prairie. We found evidence of short-term shifts in the stable isotopic signature of soil and plant water, indicating that hydraulic lift does occur in this system. These changes occurred rapidly between dawn and dusk and could not be explained by other slower processes such as capillary action. However, instances of hydraulic lift were rare and occurred in all treatment combinations. For example, hydraulic lift occurred in ungrazed *R. glabra* throughout all sampling months with the exception of July 2013, whereas July 2013 was the only month that hydraulic lift occurred in grazed *V. baldwinii* (Fig. 4). Additionally, diurnal shifts in δ^{18}O did not always occur simultaneously in both soil and plant tissue. Of the plants that experienced overnight δ^{18}O shifts, only two instances showed corresponding shifts in soil δ^{18}O (Figs. 2, 3, 4), and there were several instances of overnight shifts in soil δ^{18}O without associated shifts in plant δ^{18}O (Figs. 2, 3, 4). Furthermore, hydraulic lift did not correspond with shifts in leaf water potential, contrary to reports from previous studies (Kurz-Besson et al. 2006; Cardon et al. 2013).

The inconsistent isotopic shifts we observed between plant and soil water may have occurred for several reasons. In cases when δ^{18}O shifts were observed only in plant tissue, the deeply rooted plants may have lifted water to a soil depth below that of the 25 cm soil cores. A similar phenomenon has been previously reported by Bleby et al. (2010), illustrating that water can be redistributed to intermediate root depths by deep lateral roots. Alternatively, the shift in xylem δ^{18}O could represent a shift in the relative contribution of different soil layers to direct water uptake associated with nocturnal transpiration, rather than hydraulic lift. In the instances when δ^{18}O shifts were observed only in soil water, plants may have lifted water to shallow soil, but not yet incorporated that water into plant tissue.

Although we did observe isolated instances of hydraulic lift, the fact that hydraulic lift was not widespread across the landscape is interesting, considering that this system is characterized by deep lowland soils (Knapp et al. 1993), plants with deep-rooted dimorphic roots (Weaver 1919; Weaver and Albertson 1943), and seasonal drought that reduces shallow soil moisture (Nippert et al. 2011). The fact that hydraulic lift occurs but is generally uncommon under conditions that should promote this process raises several questions. Specifically, why is hydraulic lift uncommon when conditions are favorable? What other environmental or biotic factors limit hydraulic lift? Does spatial and temporal heterogeneity within an ecosystem impact the occurrence of hydraulic lift? We propose several alternative explanations for the rarity of hydraulic lift observed here. First, the heterogeneous structure of the tallgrass prairie may prevent hydraulic lift from occurring uniformly across the landscape. Although lowlands are generally characterized by deep silt–clay loams, patches of shallower soil and rocks are common throughout these locations (Ransom et al. 1998). Thus, it is possible that hydraulic lift only occurs when soil conditions are appropriate (e.g., the soil is sufficiently deep and free of rocks). If this is true, our results suggest that hydraulic lift is a patchy process and that topoedaphic features should be considered when observing and modeling hydraulic lift in heterogeneous environments. Second, hydraulic lift may not have been detected in *R. glabra* if the individuals we monitored transferred lifted water through its clonal network before being released into shallow soil, as has been observed by Ye et al. (2016). Finally, the low replication of this study ($n = 3$), as well as the limited spatial and temporal sampling design, may have limited our ability to detect hydraulic lift, particularly if soil water potential gradients were not strong. Had we sampled with greater intensity, or directly measured soil water potential gradients, we may have detected stronger evidence for this variable process.

Is hydraulic lift limited by grazing or nocturnal transpiration?

Considering that a variety of factors can influence the pattern and magnitude of hydraulic lift (Caldwell et al. 1998; Burgess et al. 2000; Egerton-Warburton et al. 2007; Scholz et al. 2008; Nadezhdina et al. 2009; Bleby et al. 2010; Prieto et al. 2012b; Wang et al. 2011; Neumann and Cardon 2012; Priyadarshini et al. 2015), we hypothesized that grazing and nocturnal transpiration would limit hydraulic lift in this system. Grazing by bison can have significant impacts on plant diversity, vegetation structure, soil physical properties, and nutrient cycling (Knapp et al. 1999). Grazing has also been shown to reduce shallow root biomass, as carbon allocation is shifted aboveground during regrowth following defoliation (Johnson and Matchett 2001; Klumpp et al. 2009; Nippert et al. 2012). Reduced shallow root biomass due to grazing may therefore reduce hydraulic lift because fewer shallow roots should reduce root–soil contact and limit water efflux from roots. Grazing also increases shallow soil moisture due to reduced transpirational water loss (Archer and Detling 1986; Svejcar and Christiansen 1987; Harrison et al. 2010), which could reduce the soil water potential gradient necessary to drive hydraulic lift. However, we did not find that grazing impacts hydraulic lift in this system, as the few instances of hydraulic lift occurred in both grazed and ungrazed locations. Despite this weak relationship, we should still consider land management practices such as grazing in future hydraulic lift studies, particularly in ecosystems where hydraulic lift may be more prevalent.

Previous studies have shown that incomplete stomatal closure and transpiration at night reduces hydraulic lift by creating a competing sink for water movement through plant canopies (Donovan et al. 2001, 2003; Kavanagh et al. 2007; Scholz et al. 2008; Howard et al. 2009). Reductions in hydraulic lift by nocturnal transpiration can be substantial, in some cases limiting the amount of water released by roots into soil by 73% (Howard et al. 2009). We found few instances of hydraulic lift but observed consistent rates of nocturnal transpiration in all species (Table 1). These results suggest that nocturnal transpiration likely limits hydraulic lift to some extent, although both processes can occur over long time periods depending on how the environment drives competing sinks between the plant and soil (Scholz et al. 2002; Donovan et al. 2003; Howard et al. 2009). Nocturnal transpiration may also explain why high predawn leaf water potential values were not always observed when hydraulic lift occurred, since nocturnal transpiration can prevent nocturnal equilibrium between soil and xylem water potential (Donovan et al. 2001, 2003).

If a dominant grass, *A. gerardii*, does not exhibit hydraulic lift, does it benefit using water lifted by neighboring deep-rooted forbs and shrubs?

Finally, we tested the hypothesis that, if *A. gerardii* does not exhibit hydraulic lift, it will utilize water by neighboring forbs and shrubs. Our results show that *A. gerardii* did not exhibit hydraulic lift, nor did it utilize water lifted by neighboring target plants. The lack of hydraulic lift utilized by *A. gerardii* is somewhat surprising considering that this species is deep-rooted and utilizes a small proportion of deep water (Weaver 1919; Nippert and Knapp 2007a, b), and because hydraulic lift has been observed in some grasses (Schulze et al. 1998; Yoder and Nowak 1999; Espeleta et al. 2004; Leffler et al. 2005; Armas et al. 2012). The lack of facilitation observed in cases where neighboring forbs or shrubs redistributed water is also surprising considering that facilitation of hydraulically lifted water by neighboring grasses or understory shrubs is so often reported in the literature (Caldwell 1990; Dawson 1993; Moreira et al. 2003; Warren et al. 2007; Hawkins et al. 2009).

Facilitation associated with hydraulic lift may not occur in this system for several reasons. First, competition for lifted water may have occurred between the lifting plants and neighboring grasses, outweighing any facilitative impact of hydraulic lift. A similar phenomenon has been observed in semi-arid African savannas, where *Acacia* trees utilized a substantial amount of lifted water in shallow soil layers, reducing soil moisture as well as the biomass of neighboring grasses (Ludwig et al. 2003, 2004). However, *A. gerardii* has high rates of diel transpiration (Table 1; O'Keefe and Nippert, unpublished data) and has a fibrous root system (Weaver 1954) that primarily utilizes shallow soil water (Nippert and Knapp 2007a, b; Asbjornsen et al. 2008), suggesting that this grass should be an effective competitor for lifted water in shallow soil layers. Another explanation could be that hydraulic lift moved deep soil water to intermediate depths below which *A. gerardii* can access, as previously discussed.

Conclusion

In summary, hydraulic lift occurred infrequently in a native tallgrass prairie, making it unlikely that this process is an important component of local ecohydrology under current climate conditions. However, climate models predict that precipitation patterns will become increasingly variable in the North American Great Plains over the next century which, when coupled with elevated air temperatures, will result in drier conditions throughout the region (Christensen 2007). Simulations show that future climate conditions will decrease soil moisture and carbon assimilation in grasslands, with concomitant increases in growing season carbon and water flux variability (Petrie et al. 2012). Additional models have shown that hydraulic lift can maintain shallow soil moisture and transpiration during drought, which could maintain these canopy-scale water and carbon fluxes (Domec et al. 2010). Thus, hydraulic lift may buffer the negative consequences of future climate change under conditions drier than those experienced during this study.

In the few instances, where we did observe hydraulic lift, we found no evidence that this process is influenced by grazing, nor does it result in facilitation for neighboring grasses. The rarity of hydraulic lift found here is somewhat surprising, considering the ecology and climate of North American tallgrass prairies. However, identifying the conditions when hydraulic lift is infrequent in water-limited ecosystems provides insight as important as identifying the mechanisms and drivers of this phenomenon when it occurs. In this grassland, high rates of nocturnal transpiration, topographic complexity, and patchy resource availability likely reduce the occurrence of hydraulic lift. Ultimately, our study provides further evidence that hydraulic lift is an extremely patchy process regulated by many factors, and that multiple physiological and environmental factors should be considered in studies of hydraulic lift in heterogeneous landscapes.

Acknowledgements We would like to thank Robert Briwa, Julie Commerford, Andy Muench, Rachel Keen, Ben Ketter, Patrick O'Neal, Lindsey Swartz, Jeff Taylor, and Josh Taylor for their help with sample collection and data processing. We also thank John Blair, Nate Brunsell, and Tony Joern for helpful comments on the manuscript. Funding was provided for K. O'Keefe by the Kansas State University NSF GK-12 program (Grant#NSF DGE-0841414), and a Prairie Biotic Research Small Grant. Funding for both K. O'Keefe and J. Nippert was provided by the Konza Prairie LTER program (NSF DEB-1440484).

Author contribution statement JBN and KO conceived and designed the study. KO performed the study and analyzed the data. KO and JBN wrote the manuscript.

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