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REGULAR ARTICLE

Grazing by bison is a stronger driver of plant ecohydrology in tallgrass prairie than fire history

Kimberly O'Keefe · Jesse B. Nippert

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Abstract
Background and Aims Fire and grazing are important disturbances in grasslands, yet we know little about how they impact a variety of plant physiological processes such as plant ecohydrology. Here, we assessed the impact of fire history and grazing by *Bison bison* on the source of water uptake and niche overlap in common grassland species at the Konza Prairie Biological Station, a temperate mesic grassland located in northeastern Kansas, USA.
Methods We used the stable isotopic signature of soil and xylem water to evaluate water uptake in *Andropogon gerardii*, *Vernonia baldwinii*, *Amorpha canescens*, and *Rhus glabra* within varying grazing (grazed, ungrazed), fire (0,1,2 or 3 years since last burn), topography (upland, lowland), and month (July, August) contrasts over 3 years (2013–2015).
Results The presence of grazers, not fire history, altered water uptake patterns in these common grassland species. Particularly, grazing increased the proportion of shallow water utilized by *A. gerardii* and *R. glabra*, reducing niche overlap with other co-occurring species. However, these responses varied intra-annually and were often modulated by topography.
Conclusions These results suggest that grazing can alter aspects of grassland ecohydrology at small scales, which may extend to impact community and ecosystem processes at larger spatial scales.

Keywords Fire · Herbivory · Stable isotopes · Source water · Niche overlap · Mesic grassland

Introduction

Fire and grazing are important drivers of ecosystem structure and function in grasslands and savannas worldwide (Bond and Keeley 2005; Knapp et al. 1999). In mesic grasslands, grazing and fire can have strong but contrasting effects on vegetation dynamics such as primary productivity, plant diversity, and vegetation heterogeneity. Depending on the evolutionary history of grazing (Cingolani et al. 2005; Milchunas et al. 1988), large herbivores can increase species diversity and structural heterogeneity (Belsky 1992; Collins et al. 1998; Eby et al. 2014; Hartnett et al. 1996; Knapp et al. 1999) because they preferentially graze on dominant C_4 grasses over subdominant C_3 grasses, forb, and shrubs (Fahnestock and Knapp 1993; Veen et al. 2008). Conversely, fire reduces diversity and increases productivity by creating high light, low nitrogen environments that favor the growth of dominant C_4 grasses (Briggs and Knapp 1995; Collins 1992; Collins and Calabrese 2012; Collins and Smith 2006; Seastedt et al. 1991; Veen et al.

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K. O'Keefe (✉) · J. B. Nippert
Division of Biology, Kansas State University, Manhattan, KS 66506, USA
e-mail: kokeefe@ksu.edu

2008). However when fire and grazing occur together, these drivers interact to create highly productive, diverse, and heterogeneous ecosystems (Anderson et al. 2006; Archibald et al. 2005; Collins et al. 1998; Collins and Calabrese 2012; Collins and Smith 2006; Hartnett et al. 1996; Noy-Meir 1995; Veen et al. 2008; Vinton et al. 1993). Consequently, these disturbances have been extensively studied and are often used as management tools to maintain grassland biodiversity (Fuhlendorf and Engle 2004; Hamilton 2007) and ecosystem structure (Briggs et al. 2002, 2005; Uys et al. 2004).

Although vegetation responses to fire and grazing have been well studied at the community and ecosystem levels, comparatively little is known about the physiological mechanisms that underpin these patterns. Most research detailing physiological responses to fire and grazing have been limited to studies of leaf-level gas exchange and water potential. These studies have shown that grazing generally increases photosynthetic rates following defoliation, allowing for rapid regrowth (Detling et al. 1979; Harrison et al. 2010; Painter and Detling 1981; Peng et al. 2007; Wallace 1990). Defoliation also reduces leaf area and thus, the amount of water transpired per ground area, which can increase soil moisture and leaf water potential of both the grazed plants (Archer and Detling 1986; Harrison et al. 2010; Svejcar and Christiansen 1987) and neighboring ungrazed plants (Fahnestock and Knapp 1993, 1994). Conversely, fire increases photosynthesis soon after burning but reduces leaf water potential later in the growing season due to enhanced transpiration during hot, dry periods (Knapp 1985), although responses are often species specific and can vary across ecosystems (Hodgkinson 1992; Knapp 1985; Potts et al. 2012; Turner et al. 1995).

While many studies show sensitive leaf-level responses to grassland disturbances, it is unclear how fire and grazing affect other aspects of plant functioning such as whole-plant ecohydrology. Grassland ecohydrology is complex, even without considering the effects of fire and grazing, because ecohydrological processes are often influenced by environmental heterogeneity. For example, shallow and deeply rooted grassland species commonly exhibit vertical niche partitioning of water from contrasting soil depths (Ward et al. 2013; Weaver 1968; Weaver and Albertson 1943). However, the extent of niche partitioning can vary through space and time, as C_4 grasses typically have a fixed reliance on water from the shallowest soil layers, while C_3 forbs and shrubs exhibit more opportunistic plasticity to utilize water from multiple soil layers depending upon availability (Asbjornsen et al. 2008; Kulmatiski and Beard 2013; Nippert and Knapp 2007a, b; Priyadarshini et al. 2015). The observation that plant water uptake shifts in response to changing resources suggests that water use is likely sensitive to environmental changes associated with grassland disturbances as well.

Multiple factors associated with fire and grazing, including changes in root growth and soil moisture, could alter water use dynamics in grasslands. Grazing often reduces shallow root biomass as plants allocate carbon aboveground for regrowth (Johnson and Matchett 2001; Klumpp et al. 2009; Nippert et al. 2012), which may limit shallow water uptake in grasses. Grazing can also increase soil moisture by reducing transpiration (Archer and Detling 1986; Harrison et al. 2010; Svejcar and Christiansen 1987) or reduce soil moisture by compacting soil and limiting infiltration (Greenwood and McKenzie 2001; Hamza and Anderson 2005; Naeth et al. 1991). Similarly, fire can reduce soil moisture by removing detrital layers and exposing soil to higher temperatures and evaporation rates (Hulbert 1969; McMurphy and Anderson 1965). Drier soil resulting from either disturbance may shift plant dependence on deeper water, as has been observed in certain grassland species during seasonal drought (Asbjornsen et al. 2008; Nippert and Knapp 2007a, b). Water uptake should therefore be responsive to fire and grazing, which could have compounding impacts on other ecological processes such as niche partitioning, interspecific competition, and community composition. Thus, assessing how water uptake varies across a range of disturbance regimes will improve our understanding of how ecological interactions respond to common grassland management practices.

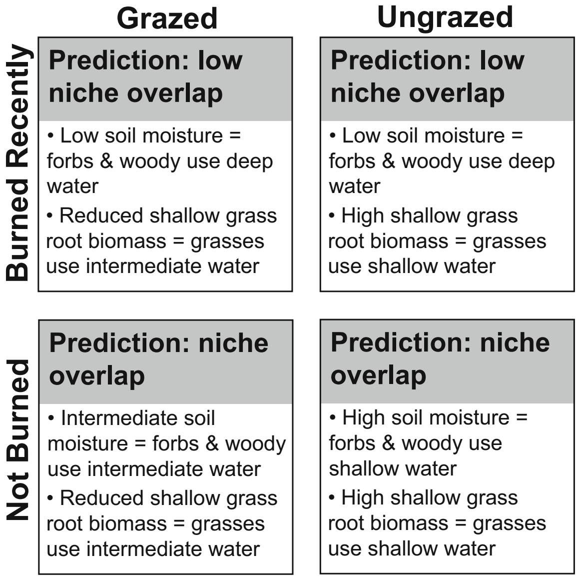
Here, we evaluated the role of common grassland disturbances on vertical water partitioning within a tallgrass prairie community. Specifically, we asked: 1) Does grazing by *Bison bison* (bison) alter the depth of water uptake in common grass, forb, and woody species? Grazing can reduce shallow grass root biomass (Johnson and Matchett 2001; Nippert et al. 2012), so we predicted that the presence of bison would lower the depth of water utilized by a dominant grass (*Andropogon gerardii* Vitman, big bluestem; Fig. 1). Because grazing can also reduce soil moisture (Archer and Detling 1986; Greenwood and McKenzie 2001;

Hulbert 1969), and because forbs and shrubs can shift dependence on water source according to availability (Asbjornsen et al. 2008; Nippert and Knapp 2007a, b), we predicted that bison would also lower the depth of water utilized by forb and woody species (Fig. 1). 2) Does time since last prescribed fire modify the depth of water uptake in these species? Fire can also reduce soil moisture, so we predicted that forbs and woody species would use deeper water in recently burned areas compared to areas that were burned less recently (Fig. 1). 3) Do shifts in water uptake alter the degree of niche overlap among species? We predicted that shifts in water associated with varying combinations of grazing and fire treatments would alter niche overlap among species (Fig. 1). 4) Are these responses modulated by topography or by time of year? Finally, we predicted that responses to low soil moisture associated with fire and grazing would be exacerbated in xeric uplands and later in the growing season, when soil water is more limiting.

Methods

Site description

Research was conducted at the Konza Prairie Biological Station (KPBS), a 3487-ha native tallgrass prairie supported by the NSF Long Term Ecological Research Network. KPBS is located within the Flint Hills of northeastern Kansas, USA (39.1°N, 96.9°W), where long-term weathering has created a topographically complex landscape consisting of flat upland ridges, deep-soiled lowlands, and steep slopes that span a relief of 40–70 m within watershed basins (Oviatt 1998). Layers of limestone and Permian shale alternate across the terrain (Jantz et al. 1975) and soil depth varies by topography, with shallow (<0.5 m), rocky soil in the uplands and deep (>2.0 m) silty-clay loams in the lowlands. Lowland soils are generally wetter than uplands and deep lowlands soils have water available throughout the growing season (Suppl. Fig. 1). KPBS is divided into watersheds that receive varying combinations of fire frequency (burned every 1, 2, 4, or 20 years) and grazing (grazed by cattle, bison, or ungrazed) treatments. The landscape is dominated by a few perennial C_4 grass species and also contains numerous subdominant C_3 grass, forb, and woody species (Smith and Knapp 2003).



	Grazed	Ungrazed
Burned Recently	**Prediction: low niche overlap** • Low soil moisture = forbs & woody use deep water • Reduced shallow grass root biomass = grasses use intermediate water	**Prediction: low niche overlap** • Low soil moisture = forbs & woody use deep water • High shallow grass root biomass = grasses use shallow water
Not Burned	**Prediction: niche overlap** • Intermediate soil moisture = forbs & woody use intermediate water • Reduced shallow grass root biomass = grasses use intermediate water	**Prediction: niche overlap** • High soil moisture = forbs & woody use shallow water • High shallow grass root biomass = grasses use shallow water

Fig. 1 Hypothesized changes in source water use and niche partitioning for grass, forb, and woody species with changes in grazing and fire

The Flint Hills region experiences a mid-continental climate, with cool, dry winters and warm, wet summers. Mean annual precipitation for the region (1982–2014) is 829 mm, of which 73 % occurs during the growing season (April – September). Precipitation was 783 mm in 2013 (77 % of which occurred during the growing season), 706 mm in 2014 (68 % of which occurred during the growing season), and 1002 mm in 2015 (75 % of which occurred during the growing season). The average coldest month of the year (1982–2014) is January, with mean minimum and maximum air temperatures of −7.14 °C and 4.87 °C, respectively. The average warmest month (1982–2014) is July, with mean minimum and maximum air temperatures of 19.78 and 32.69 °C, respectively. Mean minimum air temperatures during July 2013, 2014, and 2015 were 18.46, 17.06, and 20.67 °C respectively. Maximum air temperatures during July 2013, 2014, and 2015 were 30.99, 31.7, and 32.02 °C, respectively.

Sampling description

We sampled four species representative of different plant functional types, including one C_4 grass (*A. gerardii*), one C_3 forb (*Vernonia baldwinii* Torr., Baldwin's ironweed), one leguminous C_3 sub-shrub (*Amorpha canescens* Pursh., leadplant), and one C_3 shrub (*Rhus glabra* L., smooth sumac). These species are deep-rooted (Weaver 1968; Weaver and Albertson

1943) and are common across KPBS. Additionally, *A. gerardii* is the only of these species that is grazed by bison, as bison prefer the highly nutritious, palatable new growth of C_4 grasses (Coppedge and Shaw 1998; Fuhlendorf and Engle 2001; Plumb and Dodd 1993). Although white-tailed deer (*Odocoileus virginianus*) are also present at the site, they also prefer to browse on herbaceous growth rather than woody species (van der Hoek et al. 2002). Sampling occurred in two grazed (N4B and N4D) and two ungrazed (4B and 4F) watersheds at KPBS. All watersheds were burned once every 4 years, but not in the same calendar year (Table 1). Samples were collected from three spatially separate 50 × 50 m permanent plots (>100 m apart) in both topographic positions within each watershed, and one sample per species was collected from a random location within each plot, resulting in $n = 3$ for each species. *R. glabra* was not present in N4D lowlands. Due to the destructive nature of collecting plant tissue for isotopic analyses, separate but similarly sized individuals were randomly sampled within each sampling location during each collection period.

Samples were collected two times per growing season, during early July (mid growing season) and during late August (late growing season) for three consecutive years (2013–2015). During each sampling period, all samples were collected when no precipitation had occurred for at least 5 days to prevent contamination of soil water with the isotopic signature of rainwater.

Isotope samples

To assess the source of water uptake in each species, approximately 20–30 g of non-photosynthetic crown tissue was collected from each species. Plant tissue was collected from one stem per species at each sampling location excluding *A. gerardii*, which required 5–10 tillers to produce enough water for analyses. Samples were immediately stored in exetainer vials (Labco, UK) on ice until transferred to a 1–2 °C refrigerator. One 25 cm deep soil core per replicate sampling location was also collected with a hand corer. Soil cores were split into 5 cm sections (0–5 cm, 5–10 cm, 10–15 cm, 15–20 cm, and 20–25 cm depths), placed in double-layered plastic bags, and stored on ice until transferred to a −5 °C freezer. The frozen soil was later transferred to exetainer vials for water extraction. All isotope samples were collected on two consecutive days within each sampling period due to time constraints, on climatically similar days during which no precipitation occurred. Water was extracted from plant and soil tissue using the cryogenic vacuum distillation method (Ehleringer and Osmond 1989; Nippert and Knapp 2007a). The stable hydrogen (δD) and oxygen ($\delta^{18}O$) ratios of water samples were then analyzed using a Picarro WS-CRDS isotopic water analyzer and possible interference or contamination were checked using ChemCorrect software. The δD and $\delta^{18}O$ ratios are reported as deviations from an international standard in parts per thousand (‰) using δ-notation:

$$\delta = \left[\left(\frac{R_{sample}}{R_{standard}} - 1\right) * 1000\right] \tag{1}$$

where R is the absolute ratio of the rare and common isotope for the sample and standard.

Table 1 Fire histories for the grazed and ungrazed watersheds burned in different calendar years

	2013	2014	2015
Ungrazed			
4B	0	1	2
4F	2	3	0
Grazed			
N4B	2	3	0
N4D	0	1	2

Numbers indicate years since last burn within each sampling year. 0 = burned that year, 1 = 1 year since previous burn, 2 = 2 years since previous burn, and 3 = 3 years since previous burn

Leaf water potential

Midday leaf water potential (Ψ_{md}) was measured on one individual per species in every sampling location and during every sampling period. Measurements were made on different days with similar weather conditions to those when isotope samples were collected. The youngest, fully developed leaf was collected from similarly sized individuals, stored in a darkened, humidified plastic bag, and allowed to equilibrate for an hour. Leaf water potential was then measured with a Scholander pressure chamber (PMS Instrument Company, Albany, OR).

Soil moisture

The relative water content (RWC) of the top 10 cm soil was measured with a Hydra Probe II Soil Sensor (Stevens Water Monitoring Systems, Portland, OR, USA) in units of water fraction by volume (wfv). Five subsample measurements were made randomly within each sampling location during days on which isotope samples were collected. These subsamples were then averaged to calculate a mean shallow soil moisture value for each sampling location.

Statistics

All analyses were conducted using the statistical program R V3.1.0 (R Core Team 2012). We used Information Theoretic (IT) model averaging (Burnham and Anderson 2004) to assess the influence of grazing, time since last fire, month, and topographic position on xylem $\delta^{18}O$, midday leaf water potential, and soil RWC. For all response variables, model averaging was performed for each species individually. First, we created a linear mixed effects global model including all factors using the '*lmer*' function of the 'lme4' package V1.1-7 (Bates et al. 2014). In each global model, grazing treatment, time since fire, month, and topography were fixed effects, and sampling year and sampling location within watershed were random effects. After the global model was defined we standardized the input variables with the '*standardize*' function in the 'arm' package (Gelman et al. 2009). We then created a full submodel set with the '*dredge*' function in the 'MuMIn' package (Bartoń 2009) and obtained the top model set using 4AICc as a cutoff with the '*get.models*' function in the 'MuMIn' package, according to Grueber et al. (2011). The top model set was then averaged using the zero method with the '*model.avg*' function in the 'MuMIn' package. Relative importance was determined for each parameter included in the final average model. Relative importance is a unitless metric that sums Akaike weights for all top models in which the parameter appears and ranges from 0 (indicating that the parameter has no explanatory weight) to 1 (indicating that the parameter is included in all top models) (Burnham and Anderson 2004).

Stable Isotope Analysis in R (SIAR), a Bayesian mixing model, was used to estimate the proportion of surface and deep water sources in plant tissue (Parnell et al. 2010). We ran two sets of analyses; the first set ran individual models for each grazing × month × topography combination and the second set ran individual models for each fire × month × topography combination. Each analysis ran for 500,000 iterations, of which the first 50,000 iterations were discarded. Surface water sources were obtained from the 5–10 cm deep section of the soil cores collected at each location and the corresponding sample for each watershed × topography × month contrast was used for each analysis (Suppl. Table 1). A deep soil core (1–2 m deep) was collected from five random lowland locations across KPBS with a 540MT Geoprobe Systems hydraulic-push corer (Salina, KS, USA) and was used as the deep source in all analyses.

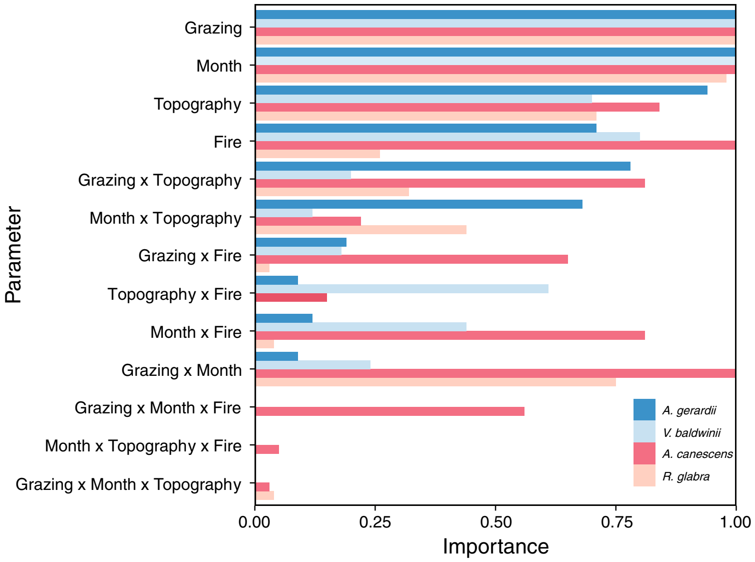


Fig. 2 Relative importance of all parameters included in the average $\delta^{18}O$ models for all species

To evaluate whether shifts in source water alter niche overlap with other species, we calculated the proportional similarity index (PS) (Colwell and Futuyma 1971) of source water between all possible species pairs using the following equation:

$$\mathrm{PS} = 1 - 0.05 \sum_{i=1}^{n} \left| p_{1i} - p_{2i} \right|$$

where p is the proportional contribution of source i for species 1 and 2, and $n = 2$ sources (surface and deep). Proportional similarity values range from 0 (no niche overlap) to 1 (complete niche overlap).

Results

Isotope analyses

Variability in xylem water δ^{18}O was best described by the individual effects of grazing and month for *A. gerardii*, *V. baldwinii*, and *R. glabra* (importance ≥ 0.98 for both predictors in each species; Fig. 2; Suppl. Tables 2,3,5). Xylem δ^{18}O was lower (more depleted) in ungrazed areas compared to grazed areas for *A. gerardii*, *V. baldwinii*, and *R. glabra* (Suppl. Table 6). Xylem δ^{18}O was also lower in July for *A. gerardii* and *V. baldwinii*, and lower in August for *R. glabra* (Suppl. Tables 6). Conversely, *A. canescens* δ^{18}O was lower in ungrazed areas, but only in August (grazing × month importance = 1.0; Fig. 2; Suppl. Tables 4,6). Topography and fire were generally less important in describing xylem water δ^{18}O for all species (Fig. 2; Suppl. Tables 2–5). However, xylem δ^{18}O was lower in lowland locations for all species except *R. glabra* (Suppl. Table 6), and lower during years 1 and 3 post-fire (Suppl. Table 7).

We estimated the proportion of surface and deep water used by each species within each month, grazing, and topography contrast and found that the effects of month, grazing treatment, and topography on source water were variable across species. *A. gerardii* generally used more surface water (5–10 cm deep) than the other species and used more surface water in August (63–90 %) than in July (53–72 %) (Fig. 3). Grazing generally increased the proportion of surface water used by *A. gerardii*, although this shift primarily occurred in lowland locations. *A. gerardii* used 12 % more shallow water in grazed areas compared to ungrazed areas during July (Fig. 3c–d) and 16 % more in grazed areas during August (Fig. 3g–h). No shift in water source occurred in upland locations during July, and *A. gerardii* used 11 % less shallow water in upland grazed areas than in upland ungrazed areas during August.

Although the effects of grazing and month on *V. baldwinii* and *A. canescens* δ^{18}O had high importance values (Fig. 2), the modeled estimates of surface and deep water sources used by these species were generally consistent across treatments (Table 2). These species used ≥ 90 % deep water across all treatment contrasts, and any detectable variation typically occurred in the shape of the posterior density distributions (Suppl. Fig. 2–3), rather than in mean source values. *R. glabra* also primarily used deep water, although the proportion of surface and deep water occurring in *R. glabra* xylem water varied by months and grazing treatments (Fig. 4). *R. glabra* used proportionally more surface water in July (4–19 %) than in August (2–4 %). Like *A. gerardii*, *R. glabra* also used more surface water in grazed watersheds, both in upland (8 % increase) and lowland locations (9 % increase) during July.

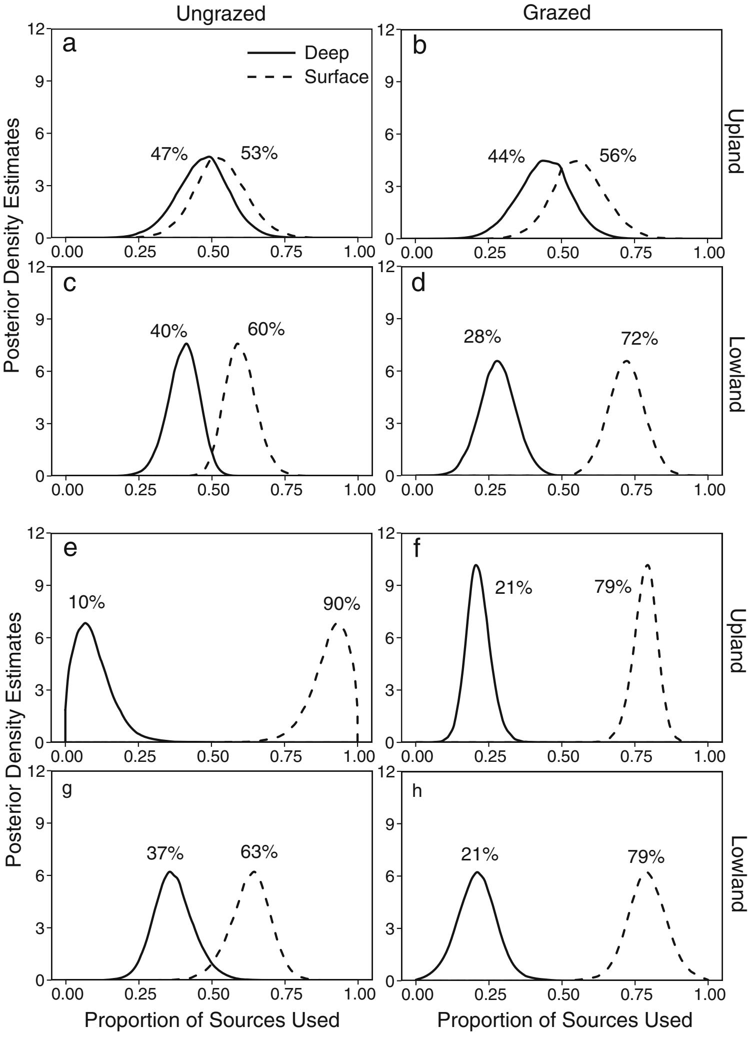
We also estimated the proportion of shallow and deep water used by each species within each month, topography, and fire contrast, and found that source water varied little by time since previous fire. *V. baldwinii*, *A. canescens*, and *R. glabra* used proportionally more shallow water during 1 and 3 years since the previous fire, but these trends were variable across months and topographic positions (Suppl. Table 8).

Finally, we used the modeled estimates of source water contribution to evaluate niche overlap between each species pair (Table 3). *A. gerardii* had lower niche overlap with all other species in lowland grazed areas (0.279–0.323 in July and 0.210–0.303 in August) compared to lowland ungrazed areas (0.402–0.462 in July and 0.370–0.423 in August). *R. glabra* also had lower niche overlap with other species in lowland grazed areas (0.270–0.854) than in ungrazed areas (0.402–0.954), but only in July. *V. baldwinii* and *A. canescens* consistently had high niche overlap with each other (0.950–0.999).

Leaf water potential

Midday leaf water potential was best explained by different variables for each species (Suppl. Tables 9–12). Generally, leaf water potential values were higher in July than in August, particularly for *A. gerardii* (importance = 1.0; Suppl. Table 9; Fig. 5a) and *A. canescens* (importance = 1.0; Suppl. Table 11; Fig. 5c). Leaf water

Fig. 3 Posterior density estimates for the proportion of surface and deep water sources used by *A. gerardii* in ungrazed (**a,c,e,g**) and grazed (**b,d,f,h**) watersheds, upland (**a,b,e,f**) and lowland (**c,d,g,h**) topographic positions, and during July (**a–d**) and August (**e–h**)



potential values were also greater in ungrazed areas compared to grazed areas during July (Fig. 5a, b, d) for *V. baldwinii* (importance = 1.0; Suppl. Table 10) and *R. glabra* (importance = 1.0; Suppl. Table 12). Finally, *A. gerardii* had lower leaf water potential values in upland (−1.738 MPa ± 0.085 SE) than in lowland (1.442 MPa ± 0.065 SE) areas, as well as in watersheds that were burned the previous year (−2.123 MPa ± 0.177 SE) than in years 0, 2, or 3 post-fire (−1.476 MPa ± 0.088 SE, −1.358 MPa ± 0.508 SE, and −1.746 MPa ± 0.091 SE, respectively).

Soil moisture

Variability in soil moisture was best described by month × topography, grazing × topography, and month × fire interactions in the average model for soil RWC (importance = 1.0 for each interaction; Suppl. Table 13). Soil RWC was lower in upland locations than lowland locations, and ungrazed upland locations had lower soil RWC than grazed upland locations during July (Fig. 6). Finally, soil RWC was lower during years 1 and 3 since the previous burn, but only during August (Suppl. Table 14).

Discussion

We used the stable isotopic signatures of soil and xylem water to assess the impacts of bison grazing and fire history on water uptake and hydrological niche overlap in common grassland species of North America. Our

Table 2 SIAR estimates of the proportion of shallow and deep water used by *V. baldwinii* and *A. canescens* within each month, topography, and grazing contrast

		July		August	
		Surface	Deep	Surface	Deep
V. baldwinii					
Grazed	Upland	0.038 (0.000, 0.116)	0.962 (0.884, 1.006)	0.045 (0.000, 0.134)	0.955 (0.866, 1.006)
	Lowland	0.045 (0.000, 0.136)	0.955 (0.864, 1.007)	0.043 (0.000, 0.125)	0.957 (0.875, 1.006)
Ungrazed	Upland	0.047 (0.000, 0.140)	0.953 (0.860, 1.007)	0.050 (0.000, 0.149)	0.950 (0.851, 1.007)
	Lowland	0.048 (0.000, 0.143)	0.952 (0.857, 1.007)	0.043 (0.000, 0.127)	0.957 (0.873, 1.006)
A. canescens					
Grazed	Upland	0.050 (0.000, 0.150)	0.950 (0.850, 1.007)	0.038 (0.000, 0.110)	0.962 (0.890, 1.005)
	Lowland	0.044 (0.000, 0.134)	0.956 (0.866, 1.006)	0.093 (0.000, 0.249)	0.907 (0.751, 1.011)
Ungrazed	Upland	0.050 (0.000, 0.147)	0.950 (0.853, 1.007)	0.042 (0.000, 0.120)	0.958 (0.880, 1.006)
	Lowland	0.059 (0.000, 0.183)	0.940 (0.817, 1.009)	0.053 (0.000, 0.163)	0.947 (0.837, 1.008)

Shown are mean estimates for shallow and deep sources, with the 95 % credible interval in parentheses

results are consistent with previous observations of source water partitioning in grasslands, where dominant C_4 grasses generally rely on water from shallow depths while some C_3 forbs and shrubs exhibit plasticity in water use depending on availability. However, we also found that grazing, not fire, impacted water uptake in certain species (*A. gerardii* and *R. glabra*), and that changes in the depth of water uptake were associated with shifts in niche overlap among co-occurring species. Grazing responses also varied intra-annually and were altered by topography. Our results suggest that grazing can impact grassland ecohydrology at small scales, although responses are species-specific and are modulated by other spatial and temporal factors.

We expected that grazing-induced reductions in shallow root biomass (Kitchen et al. 2009; Nippert et al. 2012) and soil moisture (Greenwood and McKenzie 2001; Hamza and Anderson 2005; Naeth et al. 1991) would cause grasses to rely on deeper water in grazed areas than in ungrazed areas, increasing niche overlap with co-occurring species (Fig. 1). Contrary to our hypothesis, we found that grazing actually increased the proportion of shallow water used by both *A. gerardii* and *R. glabra*, and this resulted in reduced niche overlap (Figs. 3 and 4; Table 3). Soil moisture availability did not likely drive this trend, since soil RWC did not differ between grazing treatments (Fig. 6). It is also unlikely that changes in shallow root biomass altered depth of water uptake because our data show increased reliance on water from shallow depths. These results suggest that *A. gerardii* can effectively use shallow water in grazed locations, despite reduction in root biomass, and is likely able to maintain constant water use due to physiological drought tolerance (Knapp 1984; Nippert et al. 2009; Tucker et al. 2011).

Rather than the amount of soil moisture or root biomass, we suggest that the shift in proportional water uptake is related to varying plant communities in grazed and ungrazed watersheds. Bison preferentially graze on C_4 grasses such as *A. gerardii*, which reduces dominant grass cover and increases the cover of forb and woody species. For example, the presence of bison at the Konza Prairie have been shown to reduce the percent cover of *A. gerardii* (Hartnett et al. 1996; Vinton et al. 1993) and increase the percent cover of *V. baldwinii* (Vinton et al. 1993), *A. canescens* (Hartnett et al. 1996), and common shrubs and trees (Briggs et al. 2002). As a result, locations that are grazed also have greater plant diversity, richness, and evenness (Hartnett et al. 1996). Previous work has shown that local diversity can impact resource acquisition and niche space within communities (Grossiord et al. 2014; Kunert et al. 2012; Verheyen et al. 2008). Niche partitioning of resources results from either: 1) interspecific differences in traits that allow plants to inherently exploit different resources, or 2) interspecific interactions that cause plastic shifts in resource use as species avoid competition (Valverde-Barrantes et al. 2013; von Felten et al. 2009). When plasticity arises from interspecific interactions, niche breadth and overlap are often reduced in an effort to

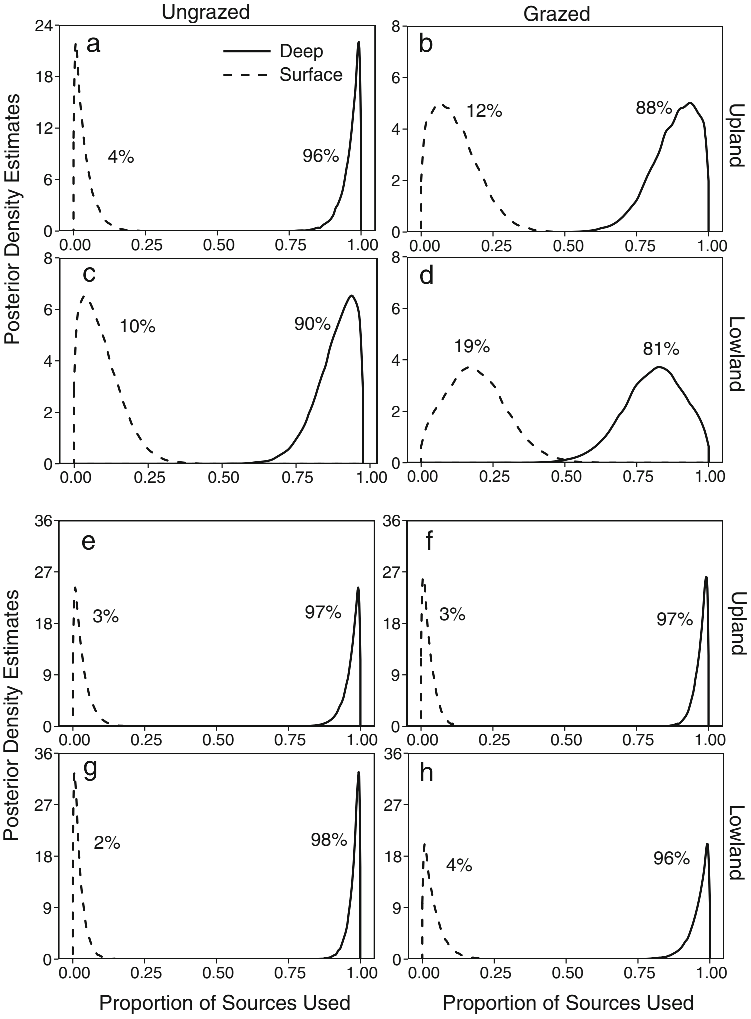


Fig. 4 Posterior density estimates for the proportion of surface and deep water sources used by *R. glabra* in ungrazed (**a,c,e,g**) and grazed (**b,d,f,h**) watersheds, upland (**a,b,e,f**) and lowland (**c,d,g,h**) topographic positions, and during July (**a–d**) and August (**e–h**)

reduce competition (Silvertown et al. 1999). In this case, depth of water uptake may shift as plants alter niche space to avoid competition in diverse communities (Hoekstra et al. 2014; Grossiord et al. 2014; Meißner et al. 2012).

Our results suggest that the high plant diversity resulting from the presence of grazers (Belsky 1992; Collins et al. 1998; Eby et al. 2014; Hartnett et al. 1996; Knapp et al. 1999) may create more numerous and smaller hydrological niches in this system. Reduced niche space per species may influence *A. gerardii* towards increased reliance on surface water to avoid niche overlap with species that use water at deeper depths (Fig. 3; Table 3), particularly because this grass species can tolerate drier soils than the other abundant species at this site (Knapp 1984; Nippert et al. 2009; Tucker et al. 2011). Previously, Hoekstra et al. (2014) found that grasses shift reliance to shallow water when grown in mixtures with deep-rooted species. We also found that *R. glabra* used proportionally less deep water in grazed areas, which reduced niche overlap with other deep-rooted species, while *V. baldwinii* and *A. canescens* continued to rely primarily on deep water (Fig. 4; Tables 2 and 3). These results indicate that plasticity and tolerance of niche overlap are species-specific. Shifts in niche overlap due to grazing also suggest that competition for water may be lower in high diversity, grazed locations, although further investigation comparing community diversity with competition for water is required.

Grazers also impacted leaf-level physiology, as midday leaf water potential was lower in grazed areas than in ungrazed areas for *A. gerardii*, *V. baldwinii*, and *R. glabra* during July (Fig. 5). This result may have occurred despite the higher soil RWC measured in

Table 3 Proportional similarity of source water use between different species pairs

	July				August			
	Ungrazed		Grazed		Ungrazed		Grazed	
Comparison	Upland	Lowland	Upland	Lowland	Upland	Lowland	Upland	Lowland
AG – VB	0.520	0.462	0.491	0.323	0.138	0.423	0.252	0.303
AG – RG	0.470	0.402	0.441	0.279	0.096	0.370	0.214	0.210
AG – AC	0.517	0.450	0.479	0.324	0.146	0.413	0.259	0.253
VB – AC	0.997	0.989	0.998	0.999	0.992	0.990	0.993	0.95
VB – RG	0.989	0.954	0.918	0.854	0.981	0.980	0.981	0.996
AC – RG	0.986	0.966	0.930	0.853	0.989	0.970	0.988	0.946

Shown are comparisons between combinations of all *A. gerardii* (AG), *V. baldwinii* (VB), *A. canescens* (AC), and *R. glabra* (RG) pairs

grazed watersheds during July (Fig. 6) because grazed areas are often characterized by more bare ground than ungrazed areas. Depending on the amount of solar radiation, the albedo of soil and plant cover, and the roughness of the terrain, bare ground can increase sensible heat and may consequently increase leaf temperatures and reduce leaf water potential (Nippert et al. 2013). This result is contrary to the commonly observed increases in leaf water potential with grazing (Harrison et al. 2010; Svejcar and Christiansen 1987), and may explain why others have also reported conflicting results (Archer and Detling 1986). Thus, grazing can impact additional aspects of plant ecohydrology independent of changes in soil moisture or source water use.

Although grazing can alter depth of water uptake and niche overlap in some species, fire history was generally not an important predictor of source water, particularly for *A. gerardii* and *R. glabra* (Fig. 2; Suppl. Tables 2–5). The SIAR mixing models showed that surface water contributed proportionally more to *V. baldwinii*, *A. canescens*, and *R. glabra* xylem water in years 1 and 3 since last burn (Suppl. Table 8). However, "time since burn" had low importance values for all species except *A. canescens*, suggesting that, when the variability associated with "year" was accounted for as a random effect, this trend was simply an artifact of the calendar year in which the "time since burn" treatment occurred (i.e., years 1 and 3 since last burn both occurred in 2014, while years 0 and 2 occurred in both 2013 and 2015; Fig. 2; Table 1; Suppl. Tables 2–5). If plant diversity of the local community is indeed the primary driver of differences in water uptake between

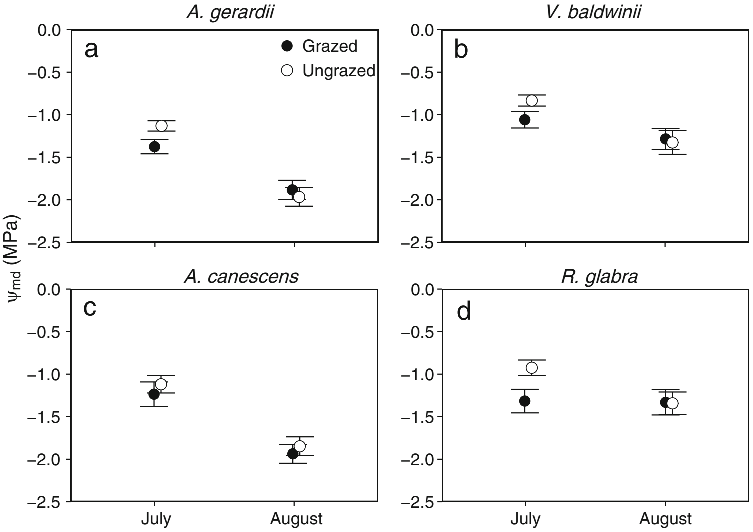


Fig. 5 Midday leaf water potential (Ψ_{md}) measured on *A. gerardii* (**a**), *V. baldwinii* (**b**), *A. canescens* (**c**), and *R. glabra* (**d**) in ungrazed and grazed locations. Shown are mean ± 1SE

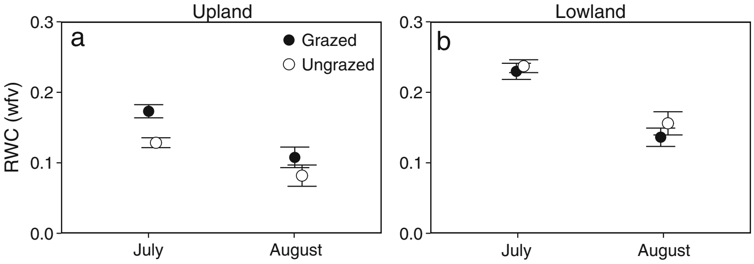


Fig. 6 Soil relative water content (RWC), measured in units of water fraction by volume (wfv) within the top 10 cm of the soil in all grazing treatments, months, and topographic locations. Shown are mean ± 1SE

grazed and ungrazed locations, we would not expect fire history to impact source water because all watersheds studied here are burned every 4 years and therefore have similar plant diversity within grazing treatments despite being burned in different calendar years.

Finally, we investigated seasonal patterns and topographic differences in water uptake. Seasonal differences occurred in *R. glabra*, as source water varied among grazing treatments only in July (Fig. 4). As is typical in other studies of C_3 woody species, (Asbjornsen et al. 2008; Kulmatiski and Beard 2013; Nippert and Knapp 2007a, b; Priyadarshini et al. 2015), *R. glabra* shifted reliance to deep water during drier periods, regardless of grazing treatment (Figs. 4 and 6). Thus, soil water availability is still an important mediator of vertical niche partitioning for water, even when differences in partitioning are associated with varying plant communities. We also observed topographic differences in water uptake, particularly in *A. gerardii*. Whereas lowland *A. gerardii* consistently increased its reliance on surface water in grazed areas, upland *A. gerardii* did not use different water sources among grazing treatments during July and used proportionally less shallow water in grazed areas during August (Fig. 3).

To conclude, the results from this study provide novel insights into the role of disturbance-driven heterogeneity in water uptake patterns and niche overlap in a diverse grassland community. Grazers modified functional niches in this tallgrass prairie plant community by altering the depth of water uptake and degree of niche overlap. These results highlight that *A. gerardii*, a dominant C_4 grass in the region, is more plastic in its water use than previously described, and it suggests that niche partitioning may be very sensitive to changes in plant diversity within this heterogeneous ecosystem. These responses to grazing varied within growing seasons and are dependent on topography, suggesting that spatiotemporal variation in resource heterogeneity is an important driver of plant functioning in mesic grasslands. These results clearly show that grassland disturbance can have strong impacts on plant functioning at small scales, with important consequences for local ecohydrology.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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