

# Impacts of seasonality and surface heterogeneity on water-use efficiency in mesic grasslands

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## ABSTRACT

Woody encroachment is occurring in grasslands worldwide, with largely unknown effects on local carbon and water fluxes and the energy balance. Water-use efficiency ( $\lambda$ ) is a measure of carbon assimilation per evapotranspiration. Here,  $\lambda$  was compared among three different grassland ecosystems in eastern KS, USA, by using the eddy covariance technique. Variation in  $\lambda$  was examined at multiple timescales and across different burning regimes. Site-specific variations in  $\lambda$  were more readily observed at seasonal and inter-annual timescales rather than daily and monthly averages. Annually burned grassland with homogeneous C<sub>4</sub> grass cover had less negative values of  $\lambda$  [lower water-use efficiency (WUE)] than infrequently burned grassland that is presently undergoing woody encroachment and a transition to a shrub-dominated ecosystem. The most likely explanation for differences in  $\lambda$  are differences in rooting depth and source-water acquisition between encroaching woody plants and the native grass community. Reliance on a deeper water source by the woody community may buffer the negative consequences of forecasted climate variability and drought, resulting in greater landscape WUE and reduced susceptibility to water stress when compared with the coexisting grass species. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS water-use efficiency; eddy covariance; woody encroachment; scale; land use; land cover

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## INTRODUCTION

Predicting the impacts of anthropogenic climate change on local ecosystem processes is one of the most pressing scientific issues of the 21st century (Walther *et al.*, 2002). The temperate grasslands in North America are extremely susceptible to the consequences of climate change (Burke *et al.*, 1991; Soussana and Lüscher, 2007), including changes in precipitation variability (Knapp *et al.*, 2002), increased air temperatures (Brunsell *et al.*, 2010), and elevated [CO<sub>2</sub>] (Morgan *et al.*, 2004; Gill *et al.*, 2002; Polley *et al.*, 2008). One of the many possible impacts of climate change on temperate grassland ecosystems is the potential for changing carbon source/sink dynamics (Hall *et al.*, 1995; Thornley and Cannell, 1997; Scurlock and Hall, 1998). Predicted increases in temporal variability of precipitation increase plant water stress and alter carbon cycling processes in grasslands (Knapp *et al.*, 2002; Fay *et al.*, 2008). Because grasslands constitute a large fraction of the terrestrial land surface (Emmerich, 2007; Novick *et al.*, 2004), the effects of climate change on grasslands' processes have consequences for global carbon and water cycling (Cramer *et al.*, 2001; Knapp *et al.*, 2008).

Grasslands are generally considered to be water-limited, as increases in soil water availability result in increased aboveground productivity (Noy-Meir, 1973; Sala *et al.*, 1988; Knapp *et al.*, 2001). To effectively scale local carbon and water fluxes from the plant level to the atmosphere requires greater understanding of stomatal responses regulating gas exchange of the leaf (Buckley, 2005; Manzoni *et al.*, 2011). The economy of gas exchange via the stomata is termed water-use efficiency ( $\lambda$ ), defined as the cost of carbon uptake in units of water lost (Buckley *et al.*, 2002). Interpretation of changes in  $\lambda$  reflect environmental conditions and depend upon the spatial scale of examination. At the leaf-level, water-stress impacts  $\lambda$  via reductions in transpiration and/or carbon assimilation by stomatal regulation of gas exchange (Buckley, 2005) or by biochemical limitations of photosynthetic capacity (Lawlor and Tezara, 2009). Changes in  $\lambda$  at the ecosystem scale reflect leaf-level processes, as well as evaporation of soil or surface water (Ponton *et al.*, 2006), and differences in species composition (Emmerich, 2007; Monson *et al.*, 1986). Differences in vegetation structure can impact ecosystem scale  $\lambda$ , including contrasts between species (Monson *et al.*, 2010), growth forms (Beer *et al.*, 2009; Scott *et al.*, 2011; Hu *et al.*, 2008), or photosynthetic pathway (Drewry *et al.*, 2011; San Jose *et al.*, 2008).

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At the ecosystem scale,  $\lambda$  is generally calculated as the ratio between either net primary production, net ecosystem production, or gross primary production to water loss (Kuglitsch *et al.*, 2008). Measured at the ecosystem, variability in  $\lambda$  at longer timescales (months to years) may reflect changes in precipitation variability or temperature trends (Kuglitsch *et al.*, 2008; Flanagan and Adkinson, 2011). Seasonal and inter-annual variations in temperature and precipitation impact the ecosystem carbon balance (Flanagan *et al.*, 2002; Xu and Baldocchi, 2004; Polley *et al.*, 2010a, 2010b). Variability in  $\lambda$  during shorter timescales (i.e. daily) may be masked when considered at larger timescales (i.e. annual) (Beer *et al.* 2009). Describing the variability in  $\lambda$  at different timescales may provide insight into the drivers of carbon and water cycling over time.

Eddy covariance has been shown to be an effective method for measuring and assessing carbon and water cycling in grasslands (Suyker and Verma, 2001; Flanagan and Adkinson, 2011; Brummer *et al.*, 2012). The eddy covariance method allows direct measurement of the exchanges of carbon and water between the surface and the atmosphere (Baldocchi *et al.*, 2001), allowing  $\lambda$  to be evaluated directly at the ecosystem scale (Law *et al.*, 2002; Kuglitsch *et al.*, 2008). Because eddy covariance systems do not directly measure carbon assimilation, this value is derived from measurements of net ecosystem exchange (NEE) (Beer *et al.*, 2009).

In this study, we examined how land cover in North American mesic grasslands affects carbon and water cycling. Specifically, we addressed how  $\lambda$  varies across different land-cover types (i.e. vegetation composition), precipitation gradients, and by daily, monthly, seasonal, and inter-annual scales. We used the eddy covariance technique to (1) examine how  $\lambda$  varies between sites with homogeneous land-cover composition and sites experiencing woody encroachment; (2) examine the impact of land-cover variability on the relationship between  $\lambda$  and site-specific variables (e.g. soil moisture, temperature, and precipitation); and (3) assess how temporal variability of  $\lambda$  varies across land-cover types. Disentangling the responses of  $\lambda$  across a gradient of land cover and local environmental conditions will provide greater context for interpreting grassland responses in carbon and water cycling to future climate changes.

## METHODS

### *Site description*

The research was conducted on the western edge of mesic grasslands in North America, where growing season precipitation is a strong driver of  $C_4$  grass productivity. Three different grasslands in northeastern Kansas were used. The University of Kansas Field Station (KFS) study site

is located 8 km north of Lawrence, Kansas (39°N, 94°W) (Fitch and Kettle, 1988). KFS lies on the ecotone between the eastern edge of the tall grass prairie and the western edge of the eastern deciduous forestbiomes. The area experiences a mid-continental climate with a mean annual temperature of 13.3 °C. The site experiences an average growing season of 185 days and mean annual precipitation of 937 mm (Brunsell *et al.*, 2011). The tower is an AmeriFlux site and was established in 2007. The tower is located on restored prairie that was used extensively as agricultural land between the 1940s and the 1960s and was a hay field until 1987. Maintenance includes periodic burning approximately every 3 years and mowing. Currently, the study area contains a mixture of  $C_3$  and  $C_4$  grasses and is experiencing woody encroachment (Brunsell *et al.*, 2011).

The remaining two grasslands are located at the Konza Prairie Biological Station (KPBS), located approximately 8 km south of Manhattan, Kansas (39°N, 96°W) in the Flint Hills Ecoregion (Knapp *et al.*, 1998), approximately 115 km west of KFS. KPBS is a 3487-ha native tallgrass prairie located on the western edge of the historic range of the tallgrass ecoregion in North America. KPBS is characterized as having a mid-continental climate with a warm, wet growing season (April–September) (1982–2009: mean rainfall of 586 mm and an air temperature of 20.8 °C) and cool, dry dormant season (October–March) (mean rainfall of 224 mm and mean air temperature of 4.3 °C). The AmeriFlux site KON located at KPBS was used in this analysis. KON is located on an annually burned, non-grazed watershed in an upland topographic area. This location has rocky, thin soils of the Florence series. The KON site is primarily dominated by native  $C_4$  grasses (Nippert *et al.*, 2011) and has been burned annually since 1978 ([http://www.konza.ksu.edu/old\\_web/UltraDev/Search.asp?currMenu=57&depth=2](http://www.konza.ksu.edu/old_web/UltraDev/Search.asp?currMenu=57&depth=2)). The second study site (K4B) is also primarily dominated by native  $C_4$  grasses but is experiencing woody encroachment, primarily by the woody  $C_3$  species *Cornus drummondii* and *Rhus glabra* (Briggs *et al.*, 2005). Soil depth at the tower location is deeper, typically greater than 1.5 m, and of soils in the Tully series. From 1975 to 2009, the watershed had prescribed burns every 4 years but also experienced un-prescribed wildfires in 1994 and 2000 ([http://www.konza.ksu.edu/old\\_web/UltraDev/Search.asp?currMenu=57&depth=2](http://www.konza.ksu.edu/old_web/UltraDev/Search.asp?currMenu=57&depth=2)).

### *Field measurements*

Field measurements at all sites were conducted using the eddy covariance technique (Baldocchi *et al.*, 2001). Field measurements at KFS were taken from 21 June (DOY 167) 2007 to 31 December (DOY 365) 2009; KON measurements were conducted from 1 January 2007 to 31 December Day of Year (DOY 365) 2009, and K4B measurements were conducted from 7 May (DOY 127) 2007 to 31 December (DOY 365) 2009.

Net ecosystem exchange, water flux ( $LE$ ), and sensible heat ( $H$ ) measurements were conducted with a Campbell Scientific CSAT3 3D Sonic Anemometer and a LICOR 7500 open-path gas analyser. Both flux instruments were located on the tower 3.0 m above the surface. The sonic anemometer was used to measure wind direction and turbulent fluctuations of wind velocities and virtual temperature. The open-path gas analysers measured gas concentrations of  $CO_2$  and water vapour in the atmosphere and was inclined to  $15^\circ$  into the mean wind direction to reduce any radiation effects on the sensor (Ham and Heilman, 2003). Energy balance measurements included soil heat flux ( $G$ ) and net radiation ( $R_n$ ). For soil heat flux, soil heat flux plates were installed 8 cm below the surface, while thermal couples are installed above the soil heat flux plate at 2 and 6 cm soil depths. Net radiation measurements are conducted with a net radiometer, including a REBS Q7.1 net radiometer (KFS: DOY 167, 2007–DOY 324, 2009; KON: DOY 138, 2007–DOY 118, 2009; K4B: DOY 124, 2007–DOY 113, 2009), Kipp and Zonen CNR1 four-way net radiometer (KFS: DOY 324, 2009–present), and a Kipp and Zonen CNR2 four-way netradiometer (KON: DOY 118, 2009–present; K4B: DOY 113, 2009–present). All net radiometers were placed approximately 2 m above the surface. Net radiometer measurements are missing at KFS between 15 October 2007 and 14 November 2007 because of a bird attack on the sensor. Ancillary meteorological data also collected at these sites include precipitation, temperature and humidity, photosynthetic active radiation, and soil moisture (2.5 cm). Measurements were sampled and stored using Campbell Scientific dataloggers, including CR23X (KON, K4B), CR1000 (KON, K4B), and CR3000 (KFS). Turbulent measurements were collected at 20 Hz, while ancillary data were stored at 30 min averages.

#### Data processing

Several post-data collection processing methods were used on the 20 Hz data from each site. This methodology closely follows the data processing outlined in Baum *et al.* (2008) and Brunsell *et al.* (2011). All 20 Hz data collected from the eddy covariance towers were processed with the EdiRE software package ([www.geos.ed.ac.uk/abs/research/micromet/EdiRe/](http://www.geos.ed.ac.uk/abs/research/micromet/EdiRe/)). Corrections on the 20 Hz data included despiking, lag removal and planar-fit rotation (Paw U *et al.*, 2000), frequency-response corrections (Moore, 1986), sonic-temperature sensible heat flux corrections (Schotanus *et al.*, 1983), and density corrections for carbon and water fluxes (Webb *et al.*, 1980). EdiRe was used to calculate other parameters, such as Obukhov length ( $L$ ), stability parameters ( $z/L$ ), and friction velocity ( $u_*$ ) (Baum *et al.*, 2008). After data was processed with EdiRe, quality-control filtering was performed using R code ([www.r-project.org](http://www.r-project.org)). Quality-control

filtering methodologies similar to those outlined by Foken and Wichura (1996) and Hammerle *et al.* (2007) were conducted on the 20 Hz data collected from all sites. Two tests were used to filter data, including an integral turbulence test and a stationarity test (Hammerle *et al.*, 2007). An integral turbulence test is a comparison of the vertical windspeed to the friction velocity ( $\sigma_w/u_*$ ). Values greater than 30% were removed. For stationarity, the mean of six covariance intervals were calculated, and any interval that differed from the mean by  $\geq 60\%$  were removed (Foken and Wichura, 1996; Hammerle *et al.*, 2007). Filtered and missing data is gapfilled for continuous sets of data (Reichstein *et al.*, 2005).

#### Water-use efficiency

Water-use efficiency ( $\lambda$ ) reflects the ratio of net carbon gained in the system to the amount of water lost via transpiration or evaporation (Bal-docchi, 1994). To find  $\lambda$ , ecosystem respiration ( $R_{eco}$ ) must be calculated. To calculate  $R_{eco}$ , only night-time values are examined (Falge *et al.*, 2002). Stability parameters for night-time unstable conditions ( $z/L < 0.1$ ) and reasonable turbulence ( $u_* > 0.15$ ) were used to identify periods to be used to estimate respiration via a  $Q_{10}$  temperature coefficient (Lloyd and Taylor, 1994):

$$R_{eco} = R_{10}Q_{10}^{(T-10)/10} \quad (1)$$

where  $R_{10}$  is a coefficient of least squares regression, and  $T$  is air temperature in  $^\circ C$  (Falge *et al.*, 2002). This relationship is then applied to all half-hour periods at each site to calculate ecosystem respiration. Once half-hour  $R_{eco}$  values were determined, carbon assimilation ( $A$ ) was calculated as

$$A = NEE - R_{eco} \quad (2)$$

water-use efficiency can be found by determining the slope of a linear regression between  $A$  and  $LE$  (Bal-docchi *et al.*, 2001):

$$\lambda = dA/dLE \quad (3)$$

where the units of  $\lambda$  are [ $g C kg^{-1} H_2O$ ]. As plants assimilate carbon, negative values of  $NEE$  result in negative values of  $A$ . This means that as the ecosystem assimilates more carbon per unit of water,  $\lambda$  values increase in magnitude (become more negative). Positive values of  $\lambda$  would indicate periods of ecosystem respiration.

Values of  $\lambda$  were also calculated at multiple timescales. Daytime 30-min averages of  $LE$  and  $A$  were used to calculate daily, monthly, and annual averages of  $\lambda$  via linear regression. A 5-day window of  $LE$  and  $A$  values was used to calculate a 5-day moving average of  $\lambda$ .

#### Energy balance closure

The eddy covariance method allows independent measurements of all of the major flux components of the energy

balance (Wilson *et al.*, 2002; Twine *et al.*, 2000). The radiation balance is stated as

$$R_n = H + LE + G + S + Q \quad (4)$$

where  $S$  ( $\text{W m}^{-2}$ ) is the canopy heat storage, and  $Q$  ( $\text{W m}^{-2}$ ) is any additional energy sources or sinks.  $Q$  is generally neglected in grassland environments because of its small value (Wilson *et al.*, 2002). However, it has been found that these measurements do not hold to the conservation of energy (Wilson *et al.*, 2002; Twine *et al.*, 2000). The ratio of the turbulent fluxes to the available energy gives a measure of this imbalance, referred to as the Energy Balance Ratio (EBR):

$$EBR = (H + LE)/(R_n - G) \quad (5)$$

Perfect energy balance closure would consist of a ratio of  $EBR=1$ . Here, EBR was used to assess to what extent there was a relationship between closure in different land-cover regimes and water-use efficiency.

### RESULTS

Energy balance and scalar fluxes were analysed to assess the effect of land cover between the sites (Figure 1). Peak  $R_n$  values ( $\sim 700 \text{ W m}^{-2}$ ) appear to have little variation from site

to site. Peak latent heat flux values for both KON and K4B appear to be greater than the KFS site ( $\sim 800 \text{ W m}^{-2}$  vs  $\sim 600 \text{ W m}^{-2}$ ). KON and K4B received greater amounts of precipitation than KFS (Table I). From Table I, mean temperatures for KON and K4B were higher than KFS. Both higher annual precipitation and higher mean temperatures at KON and K4B help to explain the higher values in  $LE$ . This may also explain the higher peak  $H$  values that appear at both KON ( $\sim 420 \text{ W m}^{-2}$ ) and K4B ( $\sim 460 \text{ W m}^{-2}$ ) sites compared with KFS ( $\sim 343 \text{ W m}^{-2}$ ). Soil heat flux ( $G$ ) values appear to be higher at the KON site during the early spring months than at the other two sites. This appears to be in response to the annual burning that takes place at KON ( $\sim 125 \text{ W m}^{-2}$ ) in mid-late April. Burned biomass lowers surface albedo, which in turn increases  $G$ . Carbon flux values indicate that all sites were carbon sinks, although these values do not consider the carbon lost during burning. Both KON and K4B sites showed much more dramatic carbon uptake than the KFS site, which had consistently lower values of NEE during the growing seasons.

The effect of land cover on water-use efficiency was examined in relation to several variables, including soil moisture ( $\theta$ ) and energy balance closure. Figure 2(a) shows the 5-day mean  $\lambda$  as a function of the energy balance ratio. Energy balance closure was calculated at 5-day averages. Generally, for all sites, the majority of closure values fell

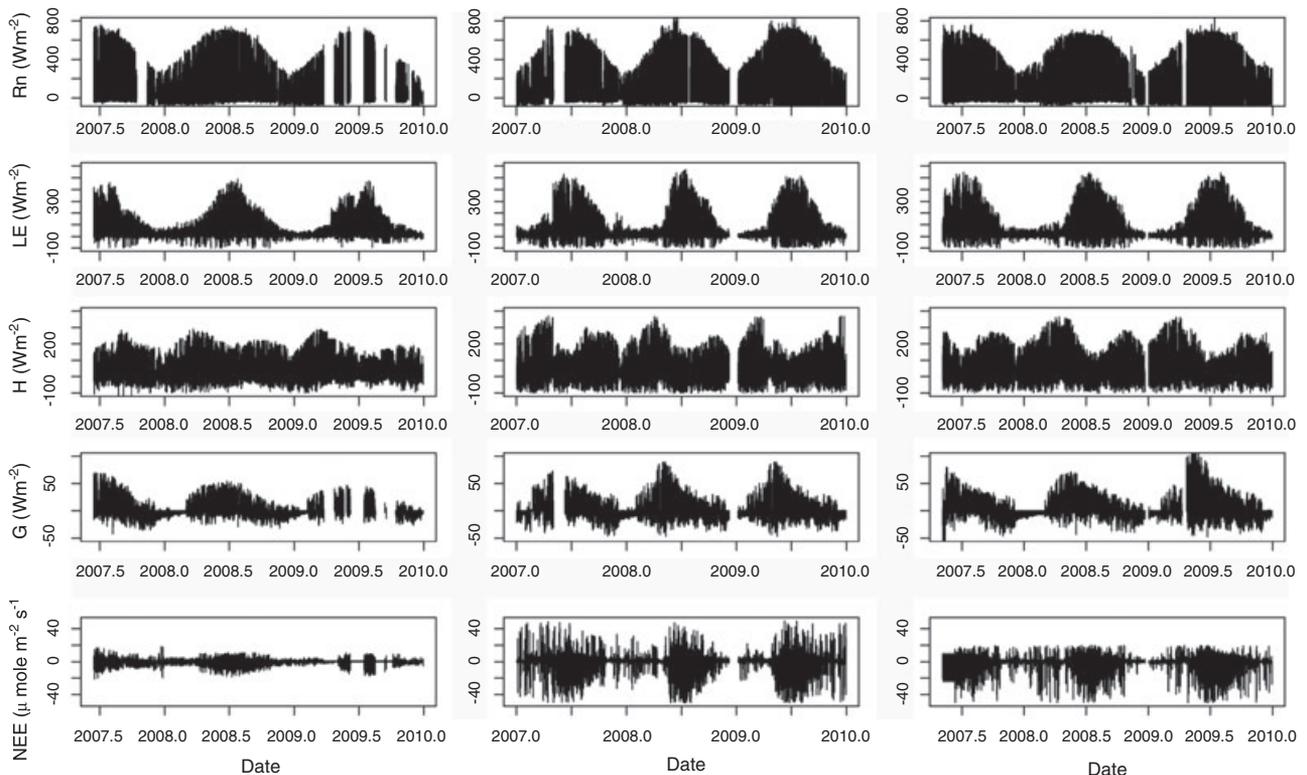


Figure 1. Time series of (in order from top to bottom) net radiation ( $R_n$ ), latent heat flux ( $LE$ ), sensible heat flux ( $H$ ), soil heat flux ( $G$ ), and net ecosystem exchange (NEE) for KFS (left column), KON (middle column), and K4B (right column) study sites.

Table I. Annual averages for the Kansas Field Station (KFS), the annually burned Konza Prairie Site (KON) and the Konza Prairie 4 year burn site (K4B).

	KFS			KON			K4B		
	2007	2008	2009	2007	2008	2009	2007	2008	2009
Temperature (–C)	13.3	12.8	12.2	14.9	13.8	14.0	14.9	13.8	14.0
Precipitation (mm)	982.6	1049.6	1062.2	992.6	1073.9	1054.6	992.6	1073.9	1054.6
Rn (W m <sup>-2</sup> )	109.1	88.8	73.2	100.9	92.9	92.1	113.4	102.3	86.2
LE (W m <sup>-2</sup> )	59.4	52.7	38.9	54.7	52.4	49.4	71.3	50.1	47.7
H (W m <sup>-2</sup> )	21.8	21.5	21.9	21.0	18.6	20.1	18.9	24.0	22.1
G (W m <sup>-2</sup> )	-1.65	-0.13	-1.85	-0.92	-0.75	-1.37	-0.75	-0.69	-2.05
NEE (μmol m <sup>-2</sup> s <sup>-1</sup> )	0.03	-0.35	-0.49	-0.60	-0.52	-0.72	-0.96	-0.95	-1.40
Bowen ratio	0.50	0.58	0.35	0.43	0.38	0.34	0.35	0.42	0.32
λ (g C kg <sup>-1</sup> H <sub>2</sub> O)	-0.72	-0.63	-1.19	-0.29	-0.25	-0.24	-0.38	-0.35	-0.28
Spring λ (g C kg <sup>-1</sup> H <sub>2</sub> O)	-0.93	-0.65	-0.81	-0.23	-0.22	-0.25	-0.35	-0.32	-0.20
Summer λ (H <sub>2</sub> O)	-0.69	-0.78	-0.30	-0.30	-0.26	-0.32	-0.50	-0.35	-0.39

KFS, Kansas Field Station; NEE, net ecosystem exchange.  
Annual mean temperature and precipitation are the same for KON and K4B.

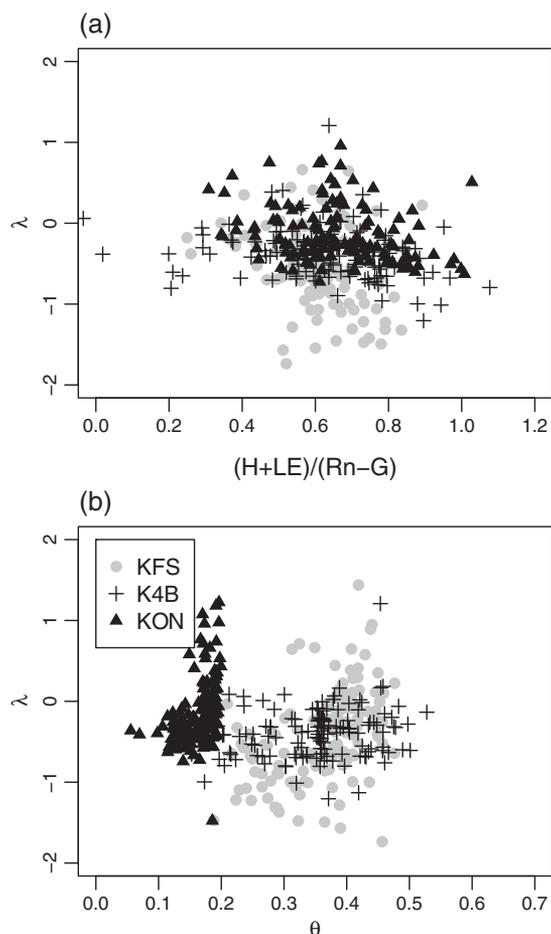


Figure 2. (a) Five-day mean water-use efficiency ( $\lambda$ ) as a function of energy balance closure and (b) 5-day mean water-use efficiency ( $\lambda$ ) as a function of 5-day mean soil moisture ( $\theta$ ).

between 0.5 and 1.0. KON and K4B both appeared to have a greater amount of closure (values closer to 1) than KFS. When comparing these two variables, there does not appear

to be a correlation between variability in energy balance closure and  $\lambda$  across differing land covers. Soil moisture values [Figure 2(b)] vary from 0.17 to 0.48 m<sup>3</sup> m<sup>-3</sup> at KFS, 0.18 to 0.57 m<sup>3</sup> m<sup>-3</sup> at KON, and 0.14 to 0.49 m<sup>3</sup> m<sup>-3</sup> at K4B. Interestingly, there appears to be no significant relationship between  $\lambda$  and  $\theta$ .

The impact of land cover on contributing source area was examined by using the footprint model of Hsieh *et al.* (2000). According to this model, footprint area is a function of atmospheric stability, measurement height, and surface roughness. Fetch distance was calculated for 70% flux source contribution. Greater fetch values were generally seen for the KON site, with most values ranging between 200 and 300 m. At KFS, most values ranged from 150 to 250 m and at K4B between 100 and 200 m. Fetch values were compared with  $\lambda$  to investigate whether there is a relationship between fetch distance and the water-use efficiency as related to the heterogeneity within the tower footprint. Although it appeared that homogeneous surfaces, such as KON, showed larger fetch distances and lower  $\lambda$  values, compared with the two other sites that contain more heterogeneous surfaces and higher  $\lambda$  values, there was not enough evidence to conclude a relationship (data not shown).

To assess the effect of seasonality on  $\lambda$ , mean values for daily, 5-day, monthly, spring, summer, and annual timescales were calculated. From daily and 5-day average  $\lambda$  values (Figure 3), seasonal variation of  $\lambda$  within the sites can be seen throughout the year. During the growing season,  $\lambda$  values become more negative until reaching a maximum magnitude in the summer months. This may be attributed to the fact that vegetation would be assimilating more carbon when photosynthesis is at its peak or that this may be a seasonal trend in  $LE$ , which would then affect the carbon assimilation rate in plants. Generally, less negative values of  $\lambda$  were observed at the KON site. Values of  $\lambda$  for

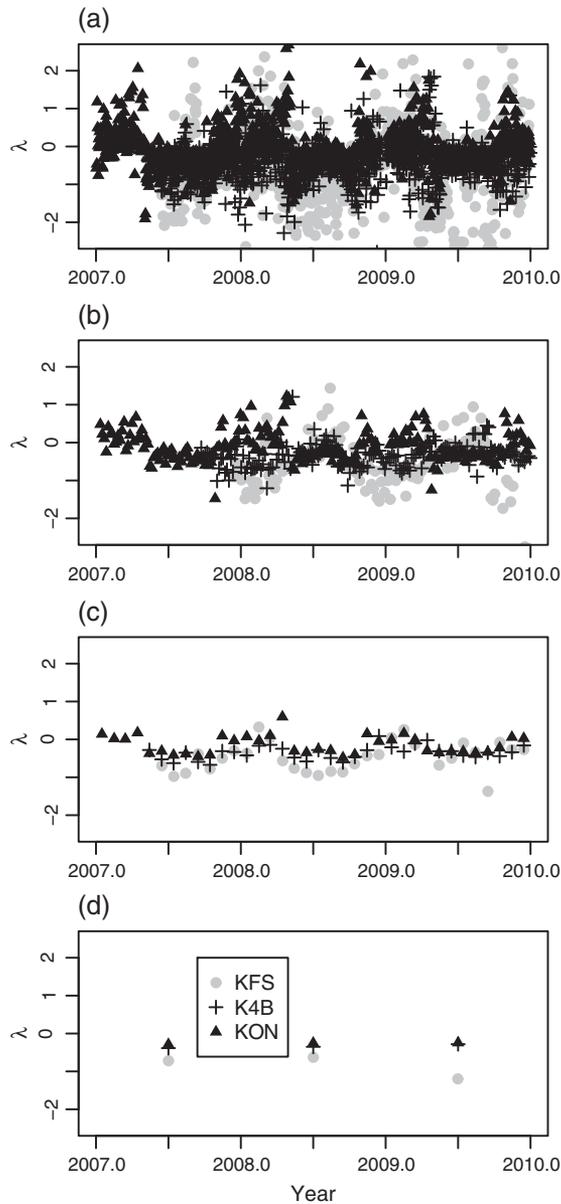


Figure 3. Comparison of the effect of timescale on water-use efficiency ( $\lambda$ ) for all sites. Panel (a), daily averages; panel (b), 5-day averages; panel (c), monthly averages; and panel (d), annual averages for 2007–2009.

KFS and K4B sites tend to be within the same proximity; however, KFS displays more negative values. This is especially pronounced when examining mean seasonal and annual values at KFS, which has lower  $\lambda$  values compared with KON and K4B (Table I).

Across all sites, there is an increase in  $\lambda$  (less negative values) when examining mean annual values (Figure 3, Table I) from 2007 to 2008. Mean annual values indicate an increase in  $\lambda$  at K4B continuing through 2009 (2007:  $-0.38$ ; 2008:  $-0.35$ ; and 2009:  $-0.28$ ), while KON values stay relatively constant (2007:  $-0.29$ ; 2008:  $-0.25$ ; and 2009:  $-0.24$ ). However, KFS showed a decrease in the mean annual  $\lambda$  from 2007 ( $-0.72$ ) to 2008 ( $-0.63$ ) and then an increase in  $\lambda$  in 2009 ( $-1.19$ ).

Mean spring and summer values are shown in Figure 4 as well as Table I. Spring values at KFS and KON show a decrease from 2007 to 2008 and then an increase in the magnitude of  $\lambda$  returning to approximately 2007 values in 2009. K4B shows a steady decrease in the magnitude through time ranging from  $-0.35$  in 2007 to  $-0.20$  in 2009. The two Konza sites show an increase in the value of  $\lambda$  from 2007 to 2008 summer values and then a decrease in 2009. KFS shows a decrease in 2007–2008 and then an increase in 2009, greatly reducing the magnitude from  $-0.78$  in the summer of 2008 to  $-0.30$  in the summer of 2009. The year 2009 was an interesting case because all three sites experienced prescribed burns (Figure 5). For a few months following the burn, KFS exhibits higher  $\lambda$  compared with previous years, while KON showed that values are on par with previous years, and K4B showed less negative values of  $\lambda$  compared with previous years.

In order to assess the impact of seasonality on energy partitioning between the sites, mean annual Bowen ratios ( $H/LE$ ) were evaluated (Figure 6). The KFS site displayed the highest mean annual Bowen ratio (Table I). K4B had low values in 2007 (0.35) and 2009 (0.32) with a slight increase in 2008 (0.42). KON generally had lower Bowen ratio values than the KFS site as well. Variability in precipitation appears to be the primary factor for variations in Bowen ratio due to vegetation composition, while inter-annual variations for KFS and K4B may be due to heterogeneous species composition.

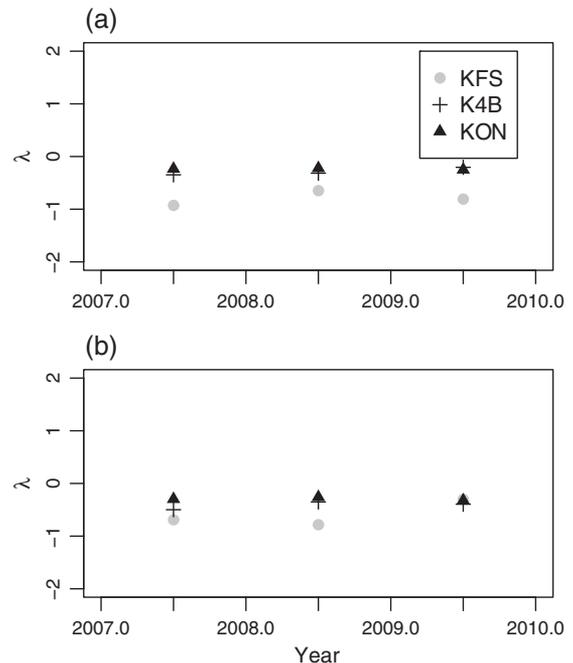


Figure 4. Comparison of the effect of seasonality on water-use efficiency ( $\lambda$ ) for all sites. Panel (a), averages for spring season, and panel (b), averages for summer season for 2007–2009.

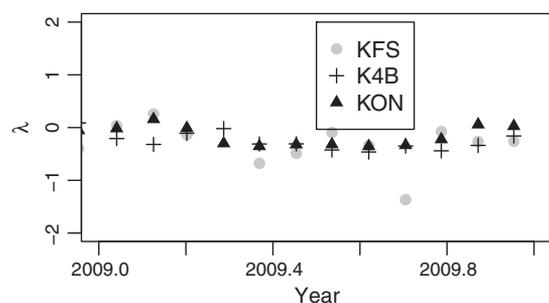


Figure 5. Mean monthly water-use efficiency ( $\lambda$ ) for 2009 for each site.

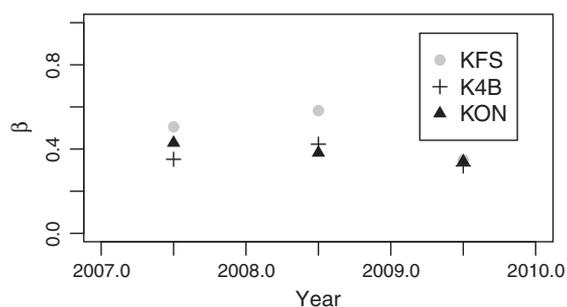


Figure 6. Mean annual Bowen ratio for all study sites during 2007–2009.

## DISCUSSION

### Impact of vegetation composition

While leaf-level water-use efficiency (WUE) is greater in  $C_4$  versus  $C_3$  plant species (Ehleringer and Monson, 1993), these results show that landscape patterns in  $\lambda$  can differ from physiological predictions and reflect heterogeneity in land cover and changing seasonal/inter-annual microclimates among the three mesic grassland types compared in this study. When  $\lambda$  values were examined at different timescales (Figure 3), KFS generally has the most negative values (highest WUE), followed by K4B, and finally KON with the least negative values (lowest WUE). These results do not seem to be a function of soil moisture, fetch distance, or energy balance closure. As Figure 1 shows, this is not necessarily due to variability in net radiation from site to site, because peak values were relatively similar. Differences in partitioning of  $LE$  and  $H$  could possibly affect values of  $\lambda$ . However, after examining the mean annual Bowen ratio for each site, there is little variation across the years. Although KON and K4B sites also exhibited higher  $LE$  and  $H$  values compared with KFS, this was most likely due to the greater amounts of precipitation and warmer temperature at these sites. Thus, the best explanation for variability in  $\lambda$  across these similar grassland sites is the influence of land cover and land use on landscape carbon and water exchange.

Sites experiencing woody encroachment (KFS and K4B) had higher water-use efficiency than sites not experiencing

woody encroachment (KON). It was previously shown that woody encroachment of mesic grassland in North America resulted in a  $\approx 3$ – $5$  times increase in aboveground Net Primary Productivity (ANPP) without concurrent changes in site-level rainfall, quadrupling the rainfall-use efficiency (Knapp *et al.*, 2008). Thus, the greater leaf area and leaf area index (LAI) in shrublands versus grasslands in a given location has dramatic consequences for the ecosystem carbon balance (Knapp *et al.*, 2008). Similar results were found by Scott *et al.* (2006), where grasslands experiencing woody encroachment had greater carbon assimilation per unit of water lost than comparable sites not undergoing encroachment. Differences among sites in Scott *et al.* (2006) reflected varying rooting depths among the community, as the woody vegetation was deeper rooted than the grasses, allowing woody vegetation to access deeper soil moisture or groundwater sources. When WUE was compared in varying size classes of woody encroaching species in Texas savanna, higher WUE was reported for *Prosopis glandulosa* trees with the greatest effective rooting depth (Eggemeier and Schwinning, 2009). Thus, the largest individuals had access to the deepest water available, facilitating higher rates and longer periods of carbon assimilation compared with smaller individuals and shallow-rooted woody species (Eggemeier and Schwinning, 2009). When physiological comparisons of WUE were made between the native  $C_4$  grass and an encroaching  $C_3$  shrub in Chihuahuan Desert grassland, the  $C_3$  shrub had higher rates of photosynthesis and lower leaf water stress despite a higher leaf-level WUE in the grass (Throop *et al.* 2012). Thus, when grasses and shrubs are decoupled from competition for the same water source, shrubs can have higher photosynthetic rates for a greater fraction of the total growing season compared with coexisting grasses (Throop *et al.* 2012).

Recently, Ratajczak *et al.* (2011) differentiated patterns of source water use among coexisting woody shrubs and  $C_4$  grasses at infrequently burned locations on Konza Prairie. The primary encroaching species at Konza Prairie (*Cornus drummondii*) used deeper water sources than the dominant  $C_4$  grass (*Andropogon gerardii*). Thus, the varying soil water niches by shrubs and grasses minimized resource overlap among these contrasting growth forms (Ratajczak *et al.*, 2011). The greater rooting depth and functional reliance on deeper soil water sources by woody vegetation contrasts with surface soil water reliance by the  $C_4$  grass community (Nippert and Knapp, 2007) and appears to be a primary driver of differences in  $\lambda$  among these sites. Soils greater than 0.5 m depth on Konza Prairie consistently have available soil moisture (Nippert *et al.*, 2011), and available soil moisture allows for longer period of carbon assimilation throughout the growing season by the woody shrub community. A similar relationship can be inferred at the KFS site, where rooting depth of woody vegetation exceeds that of grasses and resulted in more

negative  $\lambda$  values. Results from temperate steppe in northern China show similar results, as supplemental rainfall additions (and greater soil water availability) resulted in higher ecosystem WUE (Niu *et al.*, 2011). Thus, water additions stimulated carbon uptake across the growing more than the rate of water lost via transpiration when assessed at the ecosystem scale (Niu *et al.*, 2011).

Examining the seasonal and inter-annual variability in  $\lambda$  across the three grassland sites allowed us to infer changes in water and carbon cycling as a function of land cover and land use. At KON, annual prescribed burns inhibit woody encroachment (Briggs *et al.*, 2005). Therefore, KON is the most homogeneous of the sites compared and contains the most consistent species composition through time. Because of the close geographic proximity to the KON site, the K4B site experiences virtually the same energy balance partitioning and rainfall amounts and timing. However, K4B generally had greater water-use efficiency when compared with KON for the same periods. This discrepancy in  $\lambda$  between these two sites is most likely due to variation in surface heterogeneity and species composition. Greater variation in vegetative composition leads to more variability in the phenological patterns of species growth and senescence in response to seasonal environmental dynamics. Differences in vegetative composition may explain why variability in water-use efficiency is seen between sites that are experiencing woody encroachment and those that are not. In a modelling assessment of woody encroachment on carbon and water fluxes, O'Donnell and Caylor (2012) suggest that the combination of greater expansion of shrub roots in the soil matrix (laterally and by depth) as well as the higher LAI of shrub canopies may explain higher productivity and transpiration in grasslands following woody encroachment. Because K4B is experiencing woody encroachment, variability in  $\lambda$  is most likely due to growth-form differences (shrubs vs grasses), whereas KON reflects the inherent dependence of the C<sub>4</sub> grass community to current environmental conditions. KFS has also experienced woody encroachment, and heterogeneity in vegetation composition was the most likely factor driving temporal variability in  $\lambda$ . In addition, the higher values of  $\lambda$  at KFS may reflect the lower average annual temperature and thus lower latent energy exchange compared with the other two sites.

#### *Impact of seasonality*

Depending on the timescale analysed,  $\lambda$  varied for these mesic grassland sites. Evaluating mean seasonal (Figure 4) and annual values (Figure 3) for KON, there is little or no variability during the spring months and a slight decrease in water-use efficiency during the summer months. The K4B and KFS sites typically saw a general decrease in  $\lambda$  for summer and inter-annual scales. Between the 2007 and 2008 spring  $\lambda$  values, K4B experienced similar values of  $\lambda$

while KFS experienced a sharp decrease. However, in 2009 K4B saw a sharp decrease, while KFS showed an increase in  $\lambda$ . This phenomena was shown in the monthly averages of  $\lambda$  for 2009 in Figure 5. After the burn, KFS exhibits more negative values than the other sites, while K4B exhibited much lower values of water use compared with previous years. Possible explanations for this response is that unlike K4B, any woody vegetation left after burns at KFS are physically removed from the site, whereas K4B has experienced woody encroachment for a much longer time and remaining woody vegetation was not removed. Unlike the K4B site, the removal of the remaining unburned biomass at KFS allows for a greater opportunity for new vegetation to grow in its place. Hence, more carbon would be assimilated at KFS and therefore would show greater  $\lambda$  values.

The question exists as to whether the variability from partitioning fluxes between the sites provides a reasonable estimation of changes in  $Rn$ . In figure 3, we examined the relationship between energy balance closure and  $\lambda$  and showed that closure improved as  $\lambda$  values became more negative as well. This indicated that partitioning between  $LE$  and  $H$  may not be attributed to variability in  $\lambda$ . The relationship between soil moisture and  $\lambda$  showed that as soil moisture increased, there was little change in  $\lambda$ . Although increased  $LE$  values could be inferred with increasing soil moisture, these changes may also reflect the timing of rainfall in eastern Kansas, with most precipitation occurring early in the growing season (April–June). Thus, it is unlikely that variability in the partitioning of energy in  $Rn$  was the controlling factor on  $\lambda$  between the sites.

## CONCLUSIONS

Patterns of landscape water-use efficiency were compared among three mesic grassland ecosystems with various land use and land management. Site-specific variations in  $\lambda$  were more readily observed at seasonal and inter-annual timescales rather than daily and monthly averages. Grasslands not experiencing woody encroachment (homogenous C<sub>4</sub> grass cover) had lower magnitude  $\lambda$  values over this 3-year period compared with grassland sites experiencing woody encroachment. An explanation for this result may reflect that woody plants typically have deeper rooting depths and a greater proportion of root biomass at depth than grasses (Nippert *et al.*, 2012) with a greater functional reliance on deeper groundwater reserves (Craine and Nippert, 2013). The consequences of greater  $\lambda$  on ecosystem function is likely a dramatic increase in carbon gain, similar to predictions by Barger *et al.* (2011).

These results suggest that predicting future changes in water/carbon cycling in grassland ecosystems will likely need to consider the combination of environmental changes

(Petrie and Brunsell, 2012) as well as changes in community composition (Petrie *et al.*, 2012). As these grasslands experience greater woody encroachment, greater access to deeper soil water sources may support greater leaf area and carbon gain despite changes in precipitation patterns (Knapp *et al.* 2008). Reliance on a deeper water source by the woody community may buffer the negative consequences of forecast climate variability and drought, resulting in more negative values of  $\lambda$  and reduced susceptibility to water stress when compared with the coexisting grass species. It is not currently known how large-scale disturbance (climate extremes) including a multi-year drought or a change in groundwater ecohydrology will impact patterns of woody encroachment and corresponding changes in carbon and water cycling among these grassland sites or other water-limited grasslands (Knapp *et al.*, 2008).

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