



Carbon and Water Fluxes in an Exotic Buffelgrass Savanna[☆]



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ABSTRACT

Buffelgrass savanna is becoming widespread in aridland ecosystems around the world following invasion or deliberate land conversion for cattle forage. There is still a gap of information regarding functional and ecohydrological aspects such as carbon, water, and greenhouse gas exchanges in these highly productive novel ecosystems where buffelgrass is an exotic species. We measured net ecosystem CO₂ exchange (NEE), ecosystem respiration (R_{eco}), gross primary production (GPP), and evapotranspiration (ET) with eddy covariance techniques over a buffelgrass savanna established for cattle grazing, approximately 30 yr ago within the Sonoran Desert. The savanna was a net carbon sink (NEE = −230 g C/m²/yr) during both a year with above average and one with below-average precipitation (NEE = −84 g C/m²/yr). Water loss through evapotranspiration (ET) was similar to total annual rainfall input. Up to 62% of the annual fixed carbon and 75% of ET occurred during the summer monsoon season, when 72–86% of annual rainfall occurred and buffelgrass was active. ET from summer months explained 73% of variation in NEE, with an average ET of 50 mm H₂O/month needed to turn the ecosystem into a net carbon sink during this season. Other seasons in the year, when buffelgrass was dormant, contributed with up to 48% of annual fixed carbon but with higher water use efficiency (−NEE/ET). We discuss the importance of the seasonal variability in R_{eco}, GPP, and ET processes and the phenology of native plant species for the net carbon uptake through the year for this managed novel ecosystem.

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Introduction

Aridland ecosystems represent close to 50% of the earth's surface, and more than half of those have seen changes in vegetation that could impact ecosystem goods and services (Reynolds and Stafford-Smith, 2002). Shifts in land use and cover are the second most important components of global change in arid and semiarid lands worldwide (Lal, 2001; Hassan et al., 2005), following rangeland degradation for cattle production (Walker, 1979; Lambin et al., 2003). Since the middle of the past century, ecosystems dominated by perennial African grasses have been intentionally established in aridlands worldwide in order to increase vegetation cover, forage, and cattle production following arid rangeland degradation (Cox et al., 1988; Williams and Baruch, 2000; Belnap

et al., 2012). Understanding what governs the structure and function of these novel, widespread ecosystems is a key management concern.

Buffelgrass (*Cenchrus ciliaris* L.) was one of those grasses successfully introduced worldwide (Herbel, 1979; Cox et al., 1988). Buffelgrass-dominated ecosystems are intentionally established through land clearing of native vegetation and seeding cover from this grass. This results in savanna-like ecosystems when some native woody plants are maintained for shade or have recolonized the area. Extensive transformations to buffelgrass savannas have happened in the past 3 decades, especially in Australia and North America, where expansive buffelgrass savannas are now common (Arriaga et al., 2004; Miller et al., 2010; Marshall et al., 2012). In northwestern Mexico alone, it is estimated that between 1 and 1.8 million hectares of historically arid/semiarid shrublands and tropical deciduous forests have been transformed to buffelgrass savanna (Burquez et al., 1998; Castellanos et al., 2002; Bravo-Peña and Castellanos, 2013).

Most research on exotic buffelgrass-dominated ecosystems has focused on describing biodiversity implications of its establishment and its characteristics as invasive species (see Marshall et al., 2012). Regarding this, studies have described how buffelgrass accelerates the fire-return intervals (D'Antonio and Vitousek, 1992; Butler and Fairfax,

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2003; McDonald and McPherson, 2011), reduces plant species diversity (Saucedo-Monarque et al., 1997), intensifies competition (Eilts and Huxman, 2013), or suppresses regeneration (Morales-Romero and Molina-Freaner, 2008). However, there is still a gap of information regarding functional and ecohydrological aspects such as carbon, water, and greenhouse gas exchanges in these widespread buffelgrass-dominated ecosystems (Wilcox et al., 2012).

Estimates of biomass production in exotic buffelgrass savannas range from < 465 and up to 3,045 kg/ha (Martin et al., 1995; Rao et al., 1996). Many factors may be contributing to such variation in productivity, such as management schemes, seed viability and abundance, seedling establishment success, nutrient and water availability and use, and microclimatic conditions (Martín et al., 1999; Castellanos et al., 2002; Celaya-Michel et al., 2015). While biomass production is important in the context of range management and forage production, other production estimates such as whole ecosystem carbon dioxide (CO₂) flux and water use efficiency (the amount of carbon fixed per unit of water loss through evapotranspiration [ET]) can provide insight into ecosystem function. In northwestern Mexico and the southwestern United States, whole ecosystem fluxes may be influenced by its biseasonal rainfall pattern, where most annual rainfall occurs in summer months due to monsoon storms and from late fall and winter rains (Brito-Castillo et al., 2010). Given the range of values in the literature and the uncertainty associated with how environmental and biological variables drive productivity in buffelgrass savannas, continuous measurements of ecosystem carbon and water exchange may achieve substantial understanding to guide decision makers, especially where there are implications of carbon sequestration.

The eddy covariance (EC) technique provides a continuous measure of ecosystem productivity by estimating CO₂, water (H₂O), and energy fluxes between the land-surface and surrounding atmosphere (Baldocchi, 2003) and has been used at multiple ecosystems across the world (Baldocchi et al., 2001). In this study, we document carbon (CO₂ net ecosystem exchange [NEE], gross primary productivity, and ecosystem respiration) and water (ET) flux dynamics of an exotic buffelgrass savanna established through the transformation of an arid shrubland within the Sonoran Desert. We used EC technique to answer the following questions: 1) What are the dynamics of CO₂ and water fluxes in an exotic buffelgrass savanna? 2) How does the biseasonal

rainfall pattern from the Sonoran Desert region drive those CO₂ and water fluxes? and 3) How big are interannual seasonal differences in carbon and water fluxes? Data that address these questions will allow us to understand a baseline response of buffelgrass savanna biosphere/atmosphere exchanges in the context of seasonal and interannual environmental variability.

Materials and Methods

Study Site

Our study was initiated in the summer of 2011, and we include 2 1/2 yr of measurements. The site is located at La Colorada, Sonora in northwestern Mexico, at 28°42.672'N and -110°32.969'W at an altitude of 398 m, and is part of the Mexican EC network (MexFlux; Vargas et al., 2013) within a plain that extends several kilometers. Mean annual air temperature of 22.7°C and 343.8 mm annual rainfall were obtained from a nearby meteorological station (San José de Pimas, ≈ 10 km). Fall rainfall account for 70% of annual rainfall and another 20% from December to March (Servicio Meteorológico Nacional, <http://smn.cna.gob.mx>).

Cattle grazing and wildlife hunting activities are carried out at the site, located within the central region of Sonora, at the eastern edge of the Sonoran Desert boundary (Shreve and Wiggins, 1964). The site is a former subtropical desert shrubland (INEGI, 1988), which was transformed to buffelgrass savanna approximately 30 yr ago (Fig. 1). The buffelgrass savanna was established after scraping the land of its mostly woody vegetation, leaving only some dominant individual trees for shade. Actual vegetation cover consists of 54% summer active annual grass cover (i.e., *Bouteloua aristidoides*, *Bouteloua rothrockii*, *Cathastecum brevifolium*), 32% of exotic buffelgrass (*C. ciliaris*), 5% of deciduous shrubs (*Mimosa distachya* and *Jatropha cardiophylla*); lower cover (about 3%) was present for trees (*Olneya tesota*, *Prosopis velutina*) and bare soil (3%). While this site is extremely seasonal and most vegetation has extended dormant/leafless periods, some shrub and tree species (such as *Phaulothamnus spinescens*, *Encelia farinosa*, *O. tesota*, and *P. velutina*) can retain their leaves throughout the year should conditions be favorable. Although extremely variable, mean vegetation height was ≈ 0.78 m.

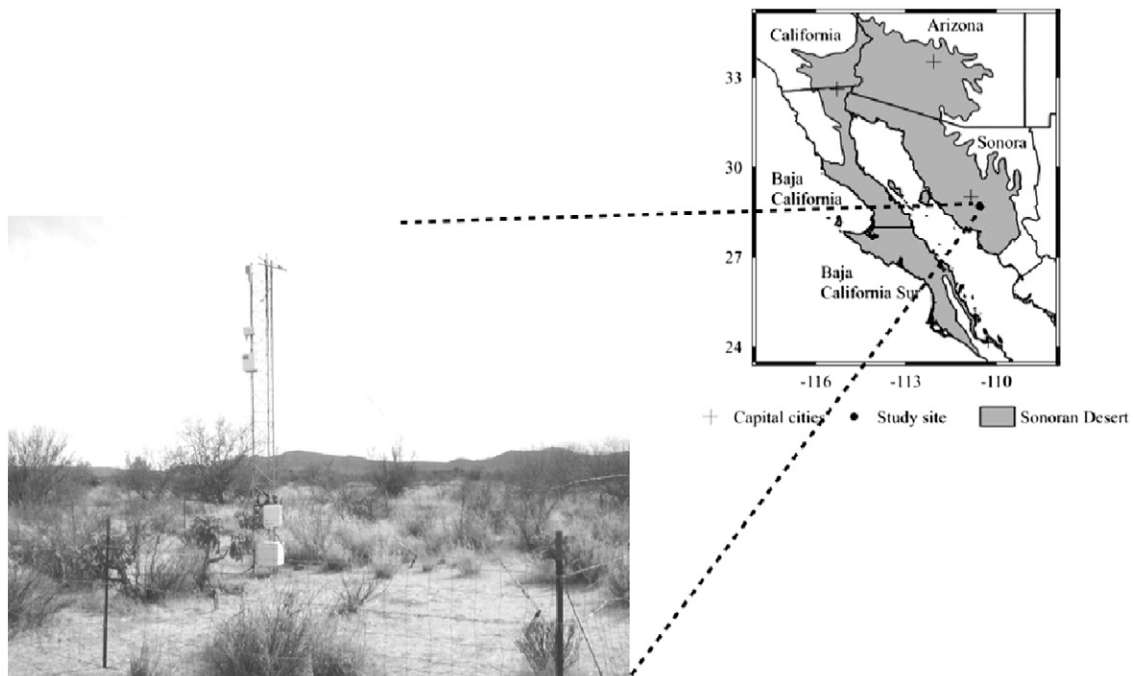


Figure 1. Study site localization and transformed Sonoran Desert shrubland to buffelgrass vegetation cover at La Colorada, Sonora, Mexico. Site location is 28°42.672'N and -110°32.969'W.

Measurement of CO₂, Water Fluxes, and Other Environmental Variables

A 6-m-high EC tower was installed at the site, and CO₂ and water fluxes were monitored from August 2011 until the end of 2013. The tower stands in the middle of the buffelgrass savanna with homogenous vegetation cover present in a 1-km radius, with the longer extent of consistent vegetation occurring in the southwest direction, which also was the direction of the prevailing winds. The flux tower is equipped with a three-dimensional sonic anemometer (CSAT-3, Campbell Scientific, Logan, UT) and a CO₂ and H₂O infrared gas analyzer (LI-7500, LI-COR Biosciences, Lincoln, NE) at the top (at 6-m height), both oriented to the direction of the prevailing winds (see Fig. 1). The top of the tower is instrumented with relative humidity and temperature sensors (HMP45C, Vaisala Inc., Vantaa, Finland) and a net radiometer (NR-Lite, Kipp and Zonen, Delft, The Netherlands). Near the base and at 10 cm depth, four soil heat flux plates (HFP01-L50, Campbell Scientific) and two thermocouples (TCAV, Campbell Scientific), as well as two moisture sensors (CS-616, Campbell Scientific), were distributed under intercanopy and buffelgrass soil conditions. Precipitation was measured with a TR-525USW-R3 (Texas Electronics, Dallas, TX) rain gauge. Sonic anemometer and gas analyzer data were recorded at a 10-Hz frequency; relative humidity, air temperature, and net radiometer were recorded every minute, while soil temperature, heat flux and moisture, and precipitation every 15 minutes using a CR3000 datalogger (Campbell Scientific).

With the 10-Hz frequency data, fluxes of NEE, ET, latent (LE), and sensible heat (H) were calculated in 30-minute blocks using EddyPro 4.0 (LI-COR Biosciences). Raw data were processed to assess their statistical quality including spike removal, amplitude resolution, and drop-outs, using parameters similar to Vickers and Mahrt (1997). Corrections performed on raw data included double axis rotation for sonic anemometer tilt correction and covariance maximization with circular correlation for time lag compensation between sonic anemometer and gas analyzer measurement (Wilczak et al., 2001). Fluxes obtained were then corrected for high- and low-frequency spectral attenuations (Moncrieff et al., 1997, 2004) and humidity effects on sonic temperature (van Dijk et al., 2004) and then compensated for air density fluctuations (Webb et al., 1980). The storage term for the NEE was determined with only CO₂ measurements at the top of the tower, as they provide a reasonable estimate for such term (Finnigan, 2006), using the already mentioned software.

We used the Mauder and Foken (2011) method for quality assessment of flux data. According to this method, values of 0 and 1 have acceptable quality, while values of 2 have bad quality and are eliminated, resulting in data gaps. Threshold values for friction velocity were determined to filter lower data using the online tool developed by the Max Planck Institute for Biogeochemistry (available at <http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php>). Flux data with acceptable quality represented 43.1%, 73.8%, and 74.2% for NEE, LE, and H data for the study period in 2011; 51.7%, 91.7%, and 91.8% for 2012; and 59.6%, 92.1%, and 92.1% for 2013. Data gap filling was performed with the same online tool following Reichstein et al. (2005) using net radiation, air temperature, and water vapor deficit data. NEE was partitioned in ecosystem respiration (R_{eco}) and gross primary productivity (GPP) using the Lloyd and Taylor (1994) regression model, available within the same online tool that uses an improved algorithm (Reichstein et al., 2005). We express CO₂ and H₂O fluxes from the atmosphere to the ecosystem (carbon uptake) as negative values, while fluxes from the ecosystem toward the atmosphere (carbon losses) are positive values. This way, GPP will always appear as negative, while R_{eco} and evapotranspiration (ET) appear as positive values.

Phenological changes were described for the site using the normalized difference vegetation index (NDVI). Data were obtained for 25 pixels (≈ 1.5 km²) within the buffelgrass savanna from 16-day composite satellite images from MODIS Land Product Subsets from Oak Ridge National Laboratory Distributed Archive Center (ORNL DAAC) at <http://daac.ornl.gov/MODIS/>.

Higher NDVI values indicate higher greenness and therefore higher ecosystem metabolic activity, while lower values represent a reduction in greenness and senescence of vegetation. NDVI may be influenced by phenological phases, primary productivity, and chlorophyll density (Huete et al., 2011). Additionally, species leaf phenology was tracked for dominant species (> 0.5% cover) in 10 individuals at different times during the year. A species was considered to have green leaves when > 60% of its individuals had some leaves present.

Data Analysis

Thirty-minute average CO₂ and evapotranspiration flux data were integrated to obtain daily values, and those were added to assess monthly, seasonal, and annual performance. Ecosystem water-use efficiency (WUE_e) was obtained from monthly, seasonal, and annual NEE-to-ET ratio:

$$WUE_e = -NEE/ET \quad (1)$$

Daily NEE, R_{eco}, GPP, ET, and WUE_e were compared between different months throughout the year using the Tukey HSD test. We obtained mean diurnal course values for every month to obtain a visualization of the seasonal responses driving diel patterns of GPP, R_{eco}, and ET over the study period. Energy budget closure for the site was assessed to validate flux measurements using daily data (Burba, 2013).

Results

During the study, annual rainfall at the site varied from below average (in 2011 and 2013 with 259 and 253 mm, respectively) to above the historic mean (in 2012 with 420 mm). Before the start of our flux measurements, the site had experienced an extended period of 9 months with no measurable rainfall (from September 2010 to June 2011). A large percentage of annual rainfall, 72–86%, was related to the summer monsoon (July to September; Fig. 2d), which varied from 190 to 200 mm in 2011 and 2013 and 364 mm in 2012.

The annual course of meteorological conditions is illustrated with data from 2012 (Fig. 2a–2d). The highest air temperatures (mean and maximum temperatures around 30°C and 37°C, respectively) of the year occurred in May and June and were associated with the foreshadowing dry period before the summer rainfall season and in late September with the drop in soil water content after the rainy season. The highest vapor pressure deficits (above 6 kPa) coincided with the highest peaks in air temperature. The lowest air temperatures and vapor pressure deficits of the year occurred during winter (mean temperature of 17°C and maximum vapor pressure deficit of 2.7 kPa).

The annual course of daily carbon fluxes is also illustrated with data from 2012 (Fig. 2f). During summer, a peak of net C efflux occurred with the start of the summer rains and initial canopy development, which lasted around 2 wk. After this peak, NEE was mostly negative throughout the summer but varied from +3 to –6 g C/m²/day with both positive and negative peaks corresponding to changes in soil water content (Fig. 2c and 2f). Coincident with this period of net carbon uptake during summer, a peak of canopy development occurred (NDVI above 0.4) where all species were active, and the highest GPP and R_{eco} of the year (up to –11 and 8 g C/m²/day, respectively). During the rest of the year NEE was relatively low with an interquartile range of –0.1 to –0.6 g C/m²/day while soil water was generally below 6%, although net carbon uptake of up to –1.5 g C/m²/day occurred during winter. According to our leaf phenology data, buffelgrass was mostly dormant from October to June while species such as *Encelia farinosa* retained green leaves until April and *O. tesota*, *P. velutina*, and *P. spinescens* throughout the whole year. The savanna was a carbon sink during most of the year (85% or 313 of days had negative NEE during 2012, and 71% or 261 days during 2013).

Mean daily values of NEE during a winter when prior late-fall rains occurred were comparable with those of the summer months (Fig. 3).

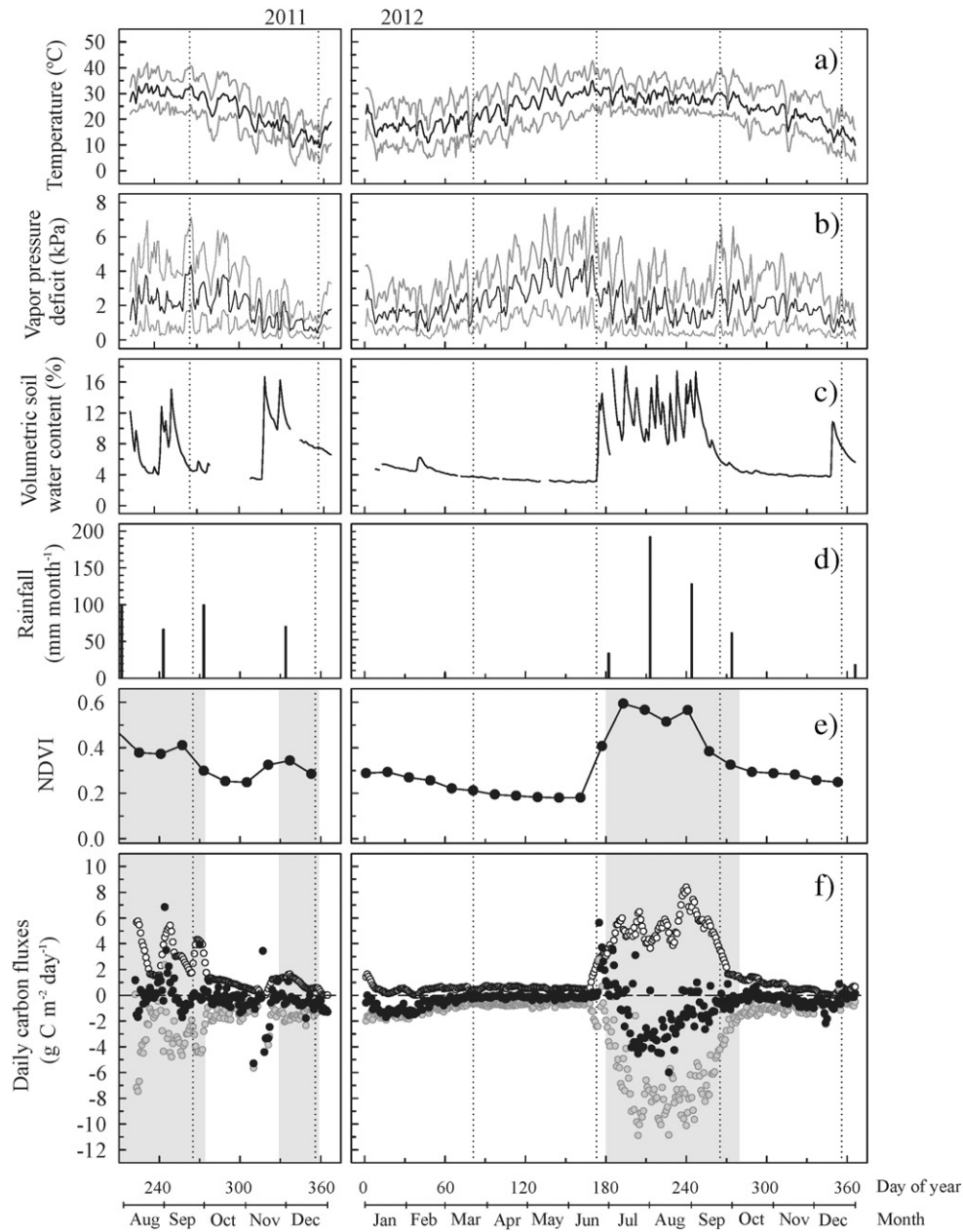


Figure 2. Annual course of a) air temperature; b) vapor pressure deficit; c) volumetric soil water content; d) monthly cumulative rainfall; e) 16-day composite normalized difference vegetation index NDVI; and f) daily net ecosystem exchange (NEE, black circles), ecosystem respiration (R_{eco} , open circles), and gross primary productivity (GPP, gray circles) in the buffelgrass savanna during 2011–2012. Vertical dotted lines mark the different seasons. Gray areas indicate approximate dates where buffelgrass had green leaves.

However, mean daily values of R_{eco} and GPP from winter were around 11 and 5 times lower than those from the summer. Instantaneous nighttime NEE during winter, as well as in the spring and fall seasons, was minimal (around $0.5 \mu\text{mol CO}_2/\text{m}^2/\text{s}$) as compared with summer (around $5 \mu\text{mol CO}_2/\text{m}^2/\text{s}$), which allowed carbon assimilation during the day (maximum NEE values of $1.5–5 \mu\text{mol CO}_2/\text{m}^2/\text{s}$) resulted in a daily net sink (Fig. 4).

Within-season and interannual variability in monthly fluxes and WUE_e from July to November is shown in Table 1. Monthly NEE for summer varied by an amount of $68–78 \text{ g C}/\text{m}^2$ each month in 2011, 2012, and 2013. The interannual variation in monthly fluxes was up to two-fold in R_{eco} , fivefold in GPP, and threefold in ET, which also resulted in variation in WUE_e . Monthly ET explains 73–87% of within-season and interannual variability in carbon fluxes (Fig. 5). The regression of

ET and NEE indicates that on average, 50 mm/month of ET were needed to shift the ecosystem from carbon source to sink during summer months (Fig. 5A).

Annual values of carbon and ET fluxes and WUE_e are shown in Table 2. The buffelgrass savanna was a net carbon sink during 2012 and 2013, with annual NEE values of -230 and $-84 \text{ g C}/\text{m}^2/\text{yr}$. Interestingly, overall annual WUE_e was 1.8 times higher in 2012 than 2013. Annual ET was similar to precipitation (P) for both years, with ET/P of 0.95 for 2012 and 1.04 for 2013. While summer months contributed with more than half of annual NEE and 64–76% of annual R_{eco} , GPP, and ET, the rest of the seasons also contributed importantly, especially for NEE contributing collectively with 38–48% (see Table 2). Regression of the energy budget closure for our site was $LE + H = 0.8179 \cdot (Rn + G) + 0.3839$ ($r^2 = 0.9374$, $P < 0.0001$), which slope falls around the mean of

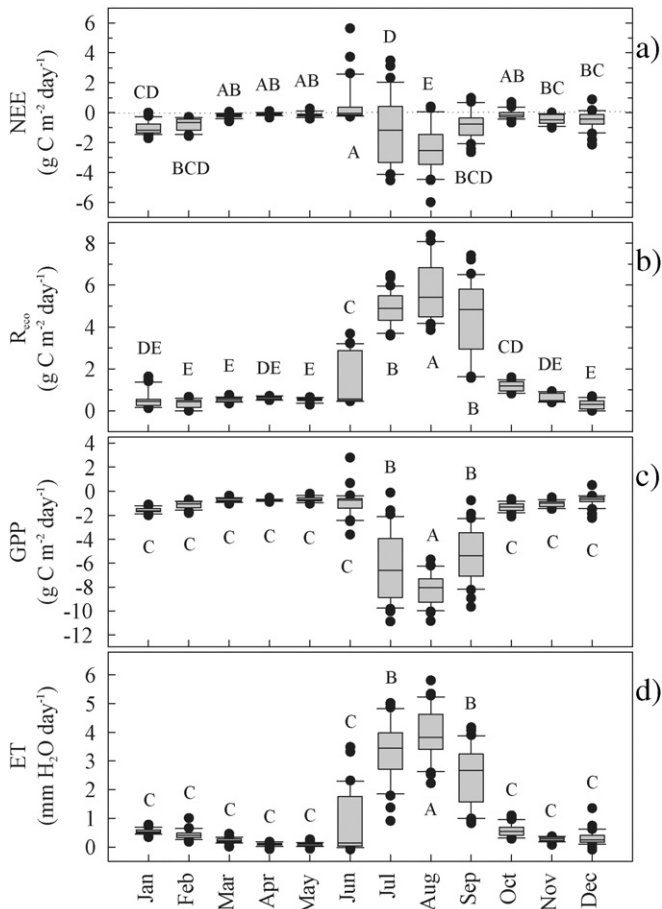


Figure 3. Mean daily carbon dioxide and evapotranspiration fluxes of the buffelgrass savanna during different months in 2012. Boxes represent the 25th, 50th, and 75th percentiles; whiskers are at the 10th and 90th percentiles; and dots represent extreme values outside whiskers. Letters represent statistically significant differences ($P < 0.05$).

the range reported (0.55–0.99) for FLUXNET sites (Wilson et al., 2002), giving confidence for our flux estimates for the buffelgrass savanna.

Discussion and Conclusions

In this paper we document the nature of biosphere/atmosphere CO_2 and water exchanges in an arid ecosystem that has been transformed into an exotic buffelgrass (*C. ciliaris*) savanna for cattle grazing management. While studies have previously documented carbon fluxes over buffelgrass-dominated ecosystems near the native range of this species (Lalrammawia and Paliwal, 2010; Hussain et al., 2015), here we document seasonality and interannual variation on ecosystem fluxes for a site where this species was introduced within the aridlands of North America. Given the increasing extent of human-influenced and degraded lands, documenting and understanding the nature ecosystem exchange dynamics within these novel ecosystems is of growing concern.

Annual and Seasonal Carbon Uptake

We found that the buffelgrass savanna was a net carbon sink. This was true for all years of study, even in years with below-average rainfall (2011, 2013; see Table 2). Other studies have found that arid ecosystems function as C sources in most years and only as net C sink during wet years (Scott et al., 2004; Scott et al., 2009; Bell et al., 2012). Annual NEE in a wet year at our savanna study site was about two to five times higher than those reported for North American deserts (Wohlfahrt et al., 2008; Bell et al., 2012) and within the high end of the range reported for semiarid grasslands in the southwestern United States (from 100 to $-300 \text{ g C/m}^2/\text{yr}$, Xu and Baldocchi, 2004; Scott et al., 2009; Scott et al., 2010; Scott et al., 2014; Wagle et al., 2015). Recent studies have shown that arid ecosystems can have important magnitudes of carbon fluxes at local (e.g., Luo et al., 2007; Wohlfahrt et al., 2008; Scott et al., 2014) and global scales (Poulter et al., 2014). Here we show that buffelgrass savanna's novel ecosystems, established in aridlands for increasing cattle grazing and management, can be important carbon sinks.

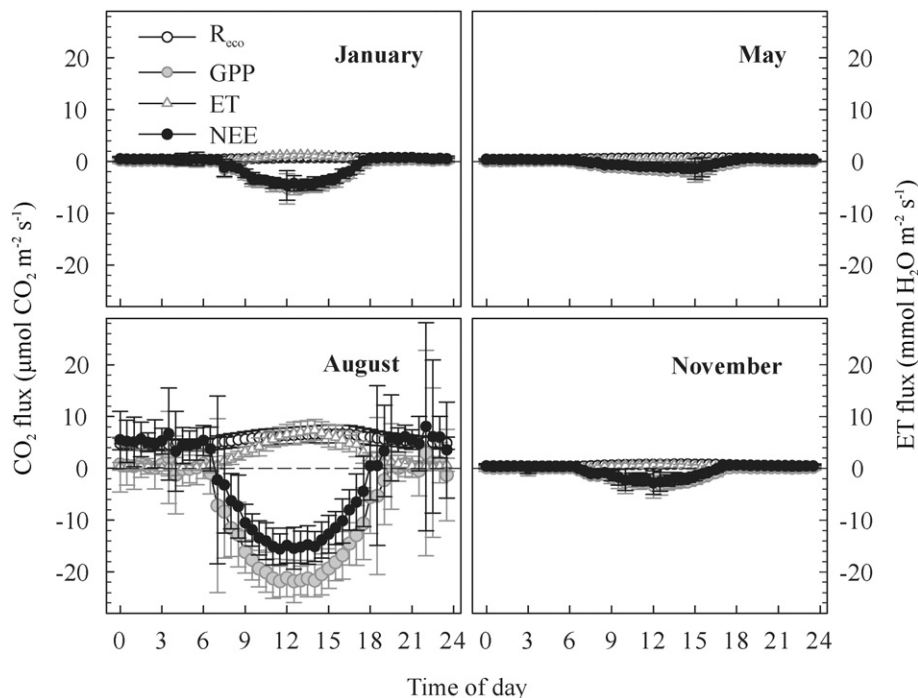


Figure 4. Average diurnal courses for CO_2 (R_{eco} , open; gross primary production [GPP], shaded; and net ecosystem exchange [NEE], black circles) and water fluxes (ET, triangles) of representative months and seasons in 2012.

Table 1

Interannual variation in carbon and evapotranspiration fluxes for summer and fall months. These months represent about seventy percent of total annual fluxes and rainfall in the buffelgrass savanna. First 10 days in August 2011 were filled with mean daily value for the month. Data for October 2011 were mostly filled with the online tool

Yr	Jul	Aug	Sep	Oct	Nov	Summer total
NEE (g C m⁻² month⁻¹)						
2011	*	-1.1	10.7	-7.8	-25.5	*
2012	-40.8	-78.6	-24.6	-3.5	-14	-144
2013	35.8	-22.7	-57	-9.7	-1	-43.9
R_{eco} (g C m⁻² month⁻¹)						
2011	*	92.1	104.6	33.8	21.1	*
2012	152.2	176.3	134.3	36.8	17.8	462.8
2013	73.7	91.3	117.7	40.1	17.9	282.8
GPP (g C m⁻² month⁻¹)						
2011	*	93.2	93.8	41.6	46.7	*
2012	193	254.9	158.9	40.3	31.7	606.8
2013	38	114	174.7	49.8	18.9	326.7
ET (mm H₂O month⁻¹)						
2011	*	10.1	12	4.9	6.9	*
2012	28.2	33.4	20.6	4.9	2.2	82.2
2013	13.4	15.3	21.7	6.1	3.5	50.4
WUE_e (g C kg⁻¹ H₂O)						
2011	*	0.1	-0.9	1.6	3.7	*
2012	1.4	2.4	1.2	0.7	6.2	1.8
2013	-2.7	1.5	2.6	1.6	0.3	0.9

The highest daily carbon and ET fluxes in the year were found during the summer monsoon season. Therefore, summer contributed with up to 62% of annual NEE and up to 75% of other carbon and ET fluxes. Importantly, ET explained the within-season and interannual variation

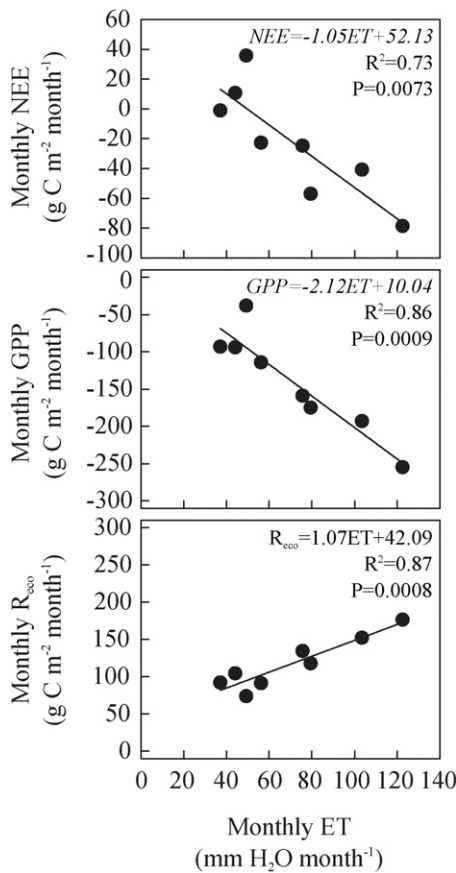


Figure 5. Linear relationships of accumulated monthly net ecosystem exchange, R_{eco}, and evapotranspiration for summer months (July, August, and September) from 3 different years (2011 – 2013).

in monthly NEE, R_{eco}, and GPP. ET has been recognized as a good measure of available water that drives arid ecosystem carbon exchanges (Biederman et al., 2016). Thus, within-season and interannual differences in summer carbon fluxes may reflect differences in water availability, which depends on meteorological (rainfall) and biological (e.g., phenology) activity in the ecosystem.

Winter season contribution to annual carbon fluxes changed from 27% during a year in which prior late-fall rainfall occurred (2012) to 16% during a year without significant rainfall in this season. Additionally, during the active winter (2012), mean daily NEE was comparable with some of the summer months (see Fig. 2). Such variability in carbon fluxes highlights the importance of the biseasonal rainfall pattern in the productivity of Sonoran Desert ecosystems (Jenerette et al., 2010) as constrained by the phenology of dominant species. In our study site, buffelgrass leaf phenology activity was constrained to the summer and was dormant from October to June. Thus, ecosystem fluxes may have been mostly driven by winter annuals, native trees, and shrubs species present at the savanna, the most important being *O. tesota* and *P. velutina*, which retain their leaves most of the year (Castellanos et al., 2010), and other opportunistic shrubs like *P. spinescens* and *E. farinosa*. Studies at the dry subtropical edges of the Sonoran Desert have found important contributions during autumn and winter seasons due to the extended activity of perennials and winter annuals when moisture conditions were favorable (Hastings et al., 2005; Bell et al., 2012). Our results suggest that, given the scenarios of global change in the region (Sprigg and Hinkley, 2000), both increasing temperature and precipitation in fall and winter seasons will allow plant species from the Sonoran Desert and of subtropical origin to extend their activity through the winter season. Buffelgrass is known to be limited by low temperatures, especially below 5°C (Cox et al., 1988), so it may be expected that buffelgrass will be able to extend its period of seasonal activity in the near future.

An important determinant of the total annual carbon sink of the buffelgrass savanna was that it had negative NEE values for 261 – 313 days (71 – 85% of the year). This is a longer period than most other sites reported in a recent grassland study along a climatic gradient in the United States (Wagle et al., 2015). A previous buffel grassland study in India had negative NEE values for about 210 days (7 months) while having rainfall events and soil moisture during 5 months (Lalrammawia and Paliwal, 2010). Those differences with our study arise due to the phenology of buffelgrass and the remaining native species and their effect on the seasonality in R_{eco} and GPP. During summer, positive NEE values (i.e., when R_{eco} dominates carbon exchange) occurred briefly at the start of the summer monsoon rains when canopy growth initiated, or when no rainfall occurred for prolonged periods, as has been observed in other seasonal ecosystems influenced by the Monsoon (e.g., Scott et al., 2010; Verdusco et al., 2015). When compared with that of summer, R_{eco} was minimal for most of the fall to spring seasons (see Figs. 3 and 4), limited by shallow soil moisture availability (Xu et al., 2004). A small R_{eco} allowed higher assimilation and GPP values of 0.7 – 1.3 g C/m²/day (interquartile range for fall to spring), which resulted in net carbon uptake even during the dry season.

We found WUE_e varying across seasons and years with contrasting rainfall regimes for the buffelgrass savanna. Lower WUE_e at summer months compared with other seasons may be associated with the vapor pressure deficits (up to 6 kPa) and air temperature (mean max 35°C) that occur during this season and the highest amount of leaf of the year (see Fig. 2). The highest WUE_e was found during fall and winter, where net C uptake occurred under lower vapor pressure deficits, air temperatures, and NDVI values than those of summer (see Fig. 2). In contrast, other studies in seasonal ecosystems have found higher WUE_e during the summer monsoon, as no net carbon uptake was found during the rest of the seasons (Perez-Ruiz et al., 2010). A higher increase in GPP than in R_{eco} between a dry (2013) and a wet (2012) year explains the 1.8-fold increase in annual WUE_e found at the buffelgrass savanna. In agreement with this, other studies have found

Table 2Seasonal water use efficiency (WUE_e) and percentage of contribution to total annual fluxes. Annual carbon fluxes are in g C/m²/yr. Annual and seasonal WUE_e are in g C/kg H₂O

	NEE		Reco		GPP		ET		WUE _e	
	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013
Annual sum	-230	-84	650	429	881	513	400	262	0.6	0.3
Winter (%)	27.0	16.3	6.8	8.7	12.1	10.0	9.1	7.6	6.8	1.8
Spring (%)	-3.5	21.1	12.3	7.9	8.1	10.1	6.6	2.6	-1.2	6.8
Summer (%)	62.5	52.2	71.2	65.9	68.9	63.6	75.3	70.5	1.9	0.6
Fall (%)	14.0	10.4	9.8	17.4	10.9	16.3	9.0	19.3	3.6	0.5

that increasing water availability, which promotes net carbon uptake, also increased annual WUE_e (Scott et al., 2015).

Management Implications

It is known that arid rangelands can provide a wide range of ecosystem goods and services, such as food, fiber, clean water, recreation, and sources of natural medicines (Havstad et al., 2007). Nonetheless, land use intensification can compromise a variety of goods and services, especially those that depend on biodiversity (Foley et al., 2005; Alkemade et al., 2012). That can be the case of arid ecosystems transformed to buffelgrass savanna, which represent an intensified use of the land by raising cattle for food production. In this study we have shown that intentionally established buffelgrass savannas can be substantial carbon sinks.

Our study site has comparable structural vegetation characteristics with other intentionally established or invaded buffelgrass-dominated ecosystems that have been studied within the Sonoran Desert region (e.g., De la Barrera, 2008; Franklin and Molina-Freaner, 2010; Abella et al., 2012; Celaya-Michel et al., 2015). However, most of the established buffelgrass savannas are found to be degraded or in bad condition (Castellanos et al., 2002). Management decisions driven by climatic variability and poor socioeconomic conditions can lead to degradation of these ecosystems (Bravo-Peña et al., 2010). Also, it has been commonly suggested that increasing buffelgrass cover results in increased fire risk (D'Antonio and Vitousek, 1992; Butler and Fairfax, 2003; McDonald and McPherson, 2011). All these factors can lead to decreased productivity, losses in carbon pools, or diminished capacity of these buffelgrass savannas for net carbon uptake.

Our data suggest important aspects that may promote the net carbon uptake within buffelgrass-dominated ecosystems. An important amount of buffelgrass foliage needs to be maintained during summer in order to favor net carbon uptake during this season. Management activities decreasing water availability during the summer should directly affect and diminish net carbon uptake, given the strong relationship between NEE and ET (see Fig. 5). We suggest that maintaining or promoting the establishment of native species with contrasting phenological and water use strategies to those of buffelgrass would favor carbon uptake during the fall, winter, and spring seasons.

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