Native shrubland and managed buffelgrass savanna in drylands: Implications for ecosystem carbon and water fluxes

César Hinojo-Hinojo, Alejandro E. Castellanos, Travis Huxman, Julio C. Rodriguez, Rodrigo Vargas, José R. Romo-León, Joel A. Biederman

A R T I C L E   I N F O

Keywords: Buffelgrass Cenchrus ciliaris Eddy covariance Land cover change Sonoran Desert Carbon and water fluxes Grass encroachment

A B S T R A C T

Land cover and land-use change (LCLUC) between woody- and grass-dominated ecosystems in drylands comprise one of the largest uncertainties in the land CO₂ sink. This is especially true for the widespread transition from shrublands to grasslands/savannas caused by the establishment of exotic C₄ grass species for grazing or through biological invasion of these species, where information about its impacts on ecosystem CO₂ fluxes is limited. For studying this, we used three years of eddy covariance measurements of net ecosystem production (NEP), gross primary production (GPP), ecosystem respiration (Reco) and evapotranspiration (ET) over a Sonoran Desert shrubland and an adjacent grazing savanna of buffelgrass (Cenchrus ciliaris L.), established 35 years ago. At monthly, seasonal and annual time scales, we assessed whether between-site differences in CO₂ fluxes were related to differences in ecosystem water use, measured as the fraction ET to precipitation, water use efficiency (WUE, i.e. the ratio between GPP and ET) and/or to the relation between Reco and GPP. Although the savanna had higher WUE than the shrubland, its summer NEP was limited by water use, due to limitations in leaf area index and likely rooting patterns. Conversely, the savanna had higher NEP than the shrubland during fall to spring due to increased WUE; possibly due to activity of buffelgrass and remaining woody species using (summer) water from deeper soil layers. However, differences across these seasons compensated each other at the inter-annual scale, and both sites had comparable net carbon sinks over the three-year study period. Further studies are needed to understand and reduce the uncertainty associated with carbon and water fluxes associated with LCLUC in dryland ecosystems.

1. Introduction

Dryland ecosystems have a key role in the trend and interannual variability of the global land carbon sink (Ahlstrom et al., 2015; Poulter et al., 2014). These globally distributed ecosystems have large temporal and spatial variability in net ecosystem production (NEP), and consequently in CO₂ uptake by gross primary production (GPP) and emissions to the atmosphere by ecosystem respiration (Reco) (Ahlstrom et al., 2015; Biederman et al., 2016, 2017). Furthermore, extensive land-cover and land-use change (LCLUC) has been documented across drylands (Safriel et al., 2005), which in turn directly influence the magnitude of these fluxes (Le Quéré et al., 2016; Baldocchi, 2008). In temperate forest ecosystems, which have traditionally been more studied than drylands, LCLUC typically results in net CO₂ emissions to the atmosphere due to biomass loss and decomposition (Le Quéré et al., 2016). Changes in the net carbon balance in drylands following LCLUC are still unclear and represent one of the largest uncertainties in the global carbon balance (Hayes et al., 2018; King et al., 2007).

Woody shrubs and grasses are dominant in drylands (Safriel et al., 2005). The transitions from woody- to grass-dominated ecosystems and vice versa are recognized as the most widespread LCLUC across drylands (Barger et al., 2011; Marshall et al., 2012; Sala and Maestre, 2014). The gradual change over decades from grass- to woody-dominated ecosystems is referred as woody encroachment, which is regulated by interactions among climate, vegetation, and management across drylands (Van Auken, 2009). In the opposite direction, a change...
from woody- (e.g., shrublands) to grass-dominated ecosystems could occur by the anthropogenic introduction of highly productive and drought-resistant African/Asian C₄ grass species to increase forage production (Castellanos et al., 2002, 2010; Marshall et al., 2012; Williams and Baruch, 2000). Vegetation structure may be dramatically changed within a season through land clearing of native vegetation and seeding of grass or more gradually through invasion of exotic grasses (Arriaga et al., 2004; Williams and Baruch, 2000). These bidirectional LCLUC transitions could have important consequences for regional-to-global carbon budgets, but large uncertainties remain (Barger et al., 2011; Houghton et al., 2012 Jackson et al., 2002; Pacala et al., 2001). Woody encroachment has been more extensively studied (Petrie et al., 2015; Scott et al., 2006, 2014), and because of the lack of information, larger uncertainties exist for the shrubland-to-grassland transition and particularly the consequences for whole-ecosystem stocks and annual fluxes (Bradley et al., 2006; Prater et al., 2006).

Woody encroachment increases whole-ecosystem carbon fluxes (NEP, Reco, GPP) in drylands because access to deeper soil and groundwater sources supports longer growing seasons (Scott et al., 2006, 2014; Petrie et al., 2015), and because encroaching woody species can physiologically outperform native grass species under a wide range of drought conditions (Barron-Gafford et al., 2012; Throop et al., 2012). Changes are expected in evapotranspiration (ET), the water flux of available soil moisture (SM) that remains after infiltration from precipitation (P), and losses to runoff (R) and drainage (D) beyond the rooting zone (Fig. 1). ET approximates the available water that drives carbon fluxes (Biederman et al., 2016), and ET/P represents the fraction of water used at the ecosystem scale. Two relations are particularly important and explain the variation of NEP in drylands, which can be modified by land cover: the relation of GPP with ET, and the relation of Reco with GPP (Biederman et al., 2016). ET/GPP describes how available water is used for photosynthesis, reflecting the ecosystem water-use efficiency. Meanwhile, Reco/GPP reflects how carbon availability drives ecosystem respiration, and is sensitive to changes in vegetation, carbon pools and allocation caused by LCLUC or disturbances (Baldocchi, 2008; Biederman et al., 2016). In this context, C₃ grasslands have higher water-use efficiency than woody-encroached ecosystems dominated by C₄ plants (Emmerich, 2007; Kuc and Small, 2007; Scott et al., 2014). This advantage is counteracted by an increased Reco/GPP, which is likely related to the high proportion of root biomass in grasses (Scott et al., 2014; Petrie et al., 2015). The balance between these relationships further contributes to explain the lower NEP of grasslands when compared to woody-encroached sites. It is unclear how a LCLUC in the opposite direction (i.e., shrublands converted into C₄ grasslands) influences NEP in dryland ecosystems. We could expect diminished NEP by reversing the typical results of woody encroachment. However exotic grass species have historically been selected for high productivity under limiting abiotic conditions (Cox et al., 1988) and could lead to a different outcome.

Buffelgrass (Cenchrus ciliaris L.) is one of the main C₄ exotic grass species used for converting xeric shrublands into more productive grasslands/savannas for cattle grazing over America and Australia (Cox et al., 1988; Marshall et al., 2012). Notably, the Sonoran Desert of Mexico and the US may be one of the region’s most heavily impacted by these practices (Bravo-Peña et al., 2010; Bravo-Peña and Castellanos, 2013; Castellanos et al., 2002, 2010; Marshall et al., 2012). This perennial bunchgrass has one of the highest photosynthesis rates (Castellanos et al., 2010; Larcher, 2014) and can physiologically outperform dominant C₃ woody species from the Sonoran Desert (Castellanos et al., 2010) enabling exotic buffelgrass savannas to be substantial carbon sinks (Hinojo-Hinojo et al., 2016). However, remote sensing estimates suggest that buffelgrass-dominated ecosystems have less above—ground biomass production than Sonoran Desert shrublands (Bravo-Peña and Castellanos, 2013; Franklin et al., 2006; Franklin and Molina-Freaner, 2010). Thus, research is needed to contribute to our understanding of shrubland—to—grassland transitions across dryland ecosystems.

In this study we compare three years of CO₂ and water fluxes over a shrubland and an adjacent ecosystem converted to exotic buffelgrass savanna “35 years ago to address the following questions: 1) Does the change from shrubland into an exotic buffelgrass savanna modifies carbon fluxes (e.g., NEP, GPP, and Reco) at seasonal and annual scales?; and if so, 2) are changes related to responses in water use (ET/P), water use efficiency (GEP/ET) and/or the relation between Reco/GPP? We hypothesize that the high-productivity potential and water-use efficiency of buffelgrass will compensate with a high Reco/GPP and lower water use in the savanna; which is characterized by a shallower rooting structure and allows this ecosystem to sustain similar or higher NEP than in the shrubland. Our ultimate aim is to contribute to the discussion about the bidirectional changes of wood-to-grass transitions across globally important drylands ecosystems.

2. Materials and methods

2.1. Study sites

Two adjacent sites representing a native shrubland and a buffelgrass savanna were selected for installing eddy covariance (EC) systems to measure ecosystem scale carbon dioxide (CO₂), water and energy fluxes. These sites are part of the Mexican eddy covariance network (MexFlux, Vargas et al., 2013) and are located in Sonora, Mexico, within the Southeastern portion of the Sonoran Desert, a heavily impacted region by LCLUC for buffelgrass since its introduction to Mexico in 1960’s (Bravo-Peña and Castellanos, 2013; Castellanos et al., 2002, 2010 Franklin et al., 2006). Both sites are located in El Churi, a private
ranch near La Colorada, Sonora, where rotational management of cattle grazing is the prevalent activity throughout the year. The sites are separated by 1.8 km, thus both are exposed to the same regional environmental conditions but with different vegetation cover.

The shrubland site (located at 28° 41′ 53.60″ N, 110° 32′ 20.59″ W, with 450 m elevation; Fig. 2) has a Sonoran Desert scrub vegetation characteristic of the Plains of Sonora (Brown, 1994). The vegetation cover is composed of 14% trees (Olneya tesota, Fouquieria macdougalii, Ipomoea arborescens, in descending order of importance) and 28% shrubs (Jatropha cardiophylla, Encelia farinosa, Mimosa laxiflora, Lycium berlandieri) (Celaya-Michel et al., 2015). During the study period, interspaces between trees and shrubs were mostly covered with summer-active herbs, grasses and litterfall. Vines can also have some cover during summer (about 10%). Mean vegetation height is nearly 1 m, but a few of the tallest trees can grow up to 7 m. The EC tower is located at the center of homogeneous vegetation for more than 1 km in every direction (Fig. 2, Footprint analysis in Supplementary material, Figure S1).

The buffelgrass savanna site (located at 28° 42′ 40.32″ N, 110° 32′ 58.14″ W, with 399 m elevation; Fig. 2) was a former Sonoran Desert scrub converted to savanna approximately 35 years ago through selective land clearing and re-cleared periodically, with only few of the dominant tree species left (J. Dueñas, oral communication, June 2009), and some shrub and other species that have partially recolonized the site since. The vegetation cover was 32% buffelgrass (Cenchrus ciliaris), 3% trees (Olneya tesota and Prosopis velutina), and 7% shrubs (mostly Mimosa laxiflora, and Jatropha cardiophylla). During the study period, interspaces between plants had a cover of summer active herbs, grasses and litterfall. Mean vegetation height is about 0.5 m, but a few trees grow up to 4 m.

Climate for these sites (30-year averages from nearby station 26268, San Jose de Pima, Servicio Meteorológico Nacional) is warm-semi-arid, with a mean annual precipitation of 476 mm, 70% of which occurs during the summer monsoon as thunderstorms. Mean annual temperature is 22.8 °C, with mean maximum in the hottest month (June) of 40.1 °C, and a mean minimum of 5.4 °C in the coldest month (January). Most plant species from both sites are deciduous with the major period of photosynthetic activity between July and September (period of monsoon rains), but some activity can occur during other seasons given sufficient precipitation (Hinojo-Hinojo et al., 2016). The species Olneya tesota, Prosopis velutina, Encelia farinosa and Lycium berlandieri can retain their leaves during most of the year when sufficient soil moisture remains in their rooting zone (Castellanos et al., 2016). Terrain is flat within the tower footprints with an average slope < 2% (Fig. 2). Soils are calcic regosol and haplic phaeozem with loamy sand texture with 0.6–2.6 % of organic matter content (Celaya-Michel et al., 2015).

2.2. Eddy covariance and meteorological measurements

The instrumentation installed in both sites allowed us to measure the net ecosystem CO2 exchange (NEE), evapotranspiration (ET), and energy fluxes between the ecosystems and the atmosphere using the eddy covariance technique (Aubinet et al., 2012) and to monitor the environmental conditions under which these fluxes occur. In this study we used six site—years of EC comparative data (from March 2013 to the end of 2015). At the buffelgrass site, the EC system on a 9 m tall tower consisted of a sonic anemometer (CSAT3, Campbell Scientific, Logan, UT, USA) for measuring 3D components of wind velocity and sonic temperature and an open path CO2/H2O gas analyzer (Li-7500, LI–COR, Lincoln, NE, USA), both sampling at 10 Hz. Also at the top of the tower, net radiation (NR Lite, Kipp & Zonen, Delft, The Netherlands) and air temperature and relative humidity (HMP45C, Vaisala Inc., Vantaa, Finland) were measured every minute. All other environmental sensors had a sampling rate of 15 min including a rain gauge (TR-525USW-R, Texas Electronics, Dallas, TX, USA) and two pairs of soil heat flux plates (HPF01-L50, Hukseflux, Delft, The Netherlands) located at 5 cm depth under buffelgrass cover and beneath open spaces (with annual herbs cover). All data were sampled and stored using a data-micrologger (CR3000, Campbell Scientific, Logan, UT, USA).

At the shrubland site, the EC system on a 9 m tall tower had a 3D sonic anemometer (Wind Master Pro, Gill Instruments) and an open path CO2/H2O gas analyzer (Li-7500 A, LI–COR, Lincoln, NE, USA) at the top, both taking measurements at 10 Hz. All other sensors measured...
at a sampling rate of 1 min. Also at the top, the tower has a net radiometer (NR Lite2, Kipp & Zonen, Delft, Netherlands), and at 6 m height an air temperature and relative humidity probe (HMP-155, Vaisala Inc., Vantaa, Finland). Rainfall was measured with a rain gauge (TR-525 M, Texas Electronics, Dallas, TX, USA). Soil heat flux was measured (HFP01SC, Hukseflut, Delft, The Netherlands) at 5 cm depth under tree, shrub and open space cover. All 1-minute frequency data was sampled with a datalogger (Xlite 9210, Sutron, Sterling, VA, USA) and 1 min and 10 Hz frequency data are stored in the interface unit (LI-7550, LI—COR, Lincoln, NE, USA) of the gas analyzer.

2.3. Data processing

The high frequency (10 Hz) raw data processing and flux calculation were performed on Eddy Pro software (v. 4-5, LICOR Biosciences) on 30-minute blocks. Displacement height and roughness length settings used on Eddy Pro were set to be a function of vegetation height at the sites (see Study sites section). Prior to flux calculation, the following processing was performed on raw data: despiking and other statistical quality tests (following Vickers and Mahr, 1997), time lags compensation due to instrument separation by maximizing covariance, and double axis rotation for wind components (Wilczak et al., 2001). Angle of attack correction (Nakai and Shimoyama, 2012) was performed on the shrubland anemometer data to compensate for errors in wind velocity data due to instrument design, whereas the anemometer used at the buffelgrass savanna is designed to minimize such errors, and this correction was not used. Turbulent fluxes of CO2 ET, sensible (H) and latent heat (LE) were calculated using the vertical component of wind velocity, CO2 and water vapor molar densities, and sonic temperature. These fluxes were corrected for frequency spectral attenuations (Moncrieff et al., 1997 and 2004), humidity effects on sonic temperature (van Dijk et al., 2004), and air density fluctuations (Webb et al., 1980).

As a quality control, we discarded data under the following conditions: 1) when data failed tests for steady state and sufficiently developed turbulence assumptions of the EC technique (Mauder and Foken, 2004), 2) fluxes measured below a friction velocity threshold to avoid keeping underestimated nighttime flux data at conditions of low air mixing, 3) during rain events, 4) when bird feces occluded the gas analyzer lenses dropping CO2 concentration below 350 ppm (which caused substantial overestimation of CO2 fluxes, personal observation). Friction velocity thresholds for the shrubland were 0.15–0.13 m/s while savanna thresholds were 0.1 m/s for all years. Quality control and system failure resulted in an annual NEE gap fraction of 37–51% for shrubland, and 40–51% for the savanna, depending on the year. The estimation of friction velocity thresholds, gap-filling and NEE flux partitioning into $R_{eco}$ and GPP were performed according to Reichstein et al. (2005) using the online tool available at www.bgc-jena.mpg.de/MDIwork/eddyproc/. We followed the ecosystem-centered nomenclature where Net Ecosystem Production (NEP = - NEE) positive values indicate net carbon uptake by the ecosystem and negative values indicating net carbon emission to the atmosphere (Chapin et al., 2006).

Monthly, summer and annual flux sums were obtained by adding up through time the half-hourly gap-filled data. We estimated uncertainty in flux sums derived from gapfilling processing (obtained from the online tool, following Reichstein et al., 2005) and from random errors and long gaps (following Richardson and Hollinger, 2007). We analyzed the energy balance closure for the sites as a way to assess the accuracy of the eddy covariance measurements (Supplementary material, Figure S2).

2.4. Comparison of carbon and water fluxes between sites

To answer our first research question, we compared seasonal and annual CO2 fluxes between the study sites. For this, a t-test was performed to compare mean daily flux values for the period of interest (either a single season or a single year). Given that the daily mean multiplied by the number of days equals the sum for a given period, any between-site difference detected at daily means could be interpreted as a potentially significant difference that influence flux sums. For the seasonal flux comparison, we split each year in two seasons; (a) summer from July to September, where most of the annual precipitation and the highest flux rates occur, and (b) the rest of the year including data from January to June and October to December where rainy events are uncommon and flux rates tend to be low.

2.5. Drivers of ecosystem carbon flux differences between-sites

Our second research question was about identifying whether between-site differences in ecosystem carbon fluxes were related to differences in the amount of water used by the ecosystem; in terms of water use efficiency or in the relation $R_{eco}$/GPP. Both monthly ET and seasonal ET/P were used as a measure of water use by the ecosystem, as both have been shown to represent well the available water that drives CO2 fluxes (Biederman et al., 2016, 2017). Water-use efficiency was assessed at the monthly scale in two ways: (a) as the linear relationship of GPP against ET, which gives an estimate of realized water-use efficiency at the ecosystem scale (WUE) (Emmerich, 2007); and (b) as the linear relationship of the product of GPP and vapor pressure deficit (VPD) against ET, which is an estimate of inherent water use efficiency (WUE), and better reflects changes in plant physiology by controlling for the effect of VPD (Beer et al., 2009). The linear relationship of monthly $R_{eco}$ against GPP was also assessed. To compare how sites differed in these relationships, we fit the data to a statistical model evaluating the effects of the independent variable (either ET or GPP), site, and independent variable*site interaction on the dependent variable. The site effect gives an estimate of mean displacement of the dependent variable between sites, when all other effects are controlled. The interaction effect gives an estimate of the amount of between-site change in slopes of the independent vs dependent variables. We interpret any statistically significant effect of site and/or interaction as a significant change in WUE, WUE, or $R_{eco}$/GPP.

2.6. Vegetation phenology

We followed vegetation phenology through remote sensing data and with field observations to assess whether changes in flux dynamics and relations could be related to changes in canopy development or phenology of dominant species. For remote sensing data, we used time series of 8-day composites of leaf area index (LAI) derived from MODIS (Moderate-Resolution Imaging Spectroradiometer, MODIS/A2, collection 5) for the same dates as flux measurements obtained from the webpage of Distributed Active Archive Center for Biogeocchemical Dynamics (http://daac.ornl.gov/MODIS/). Linear regression analysis was used to assess how LAI responded to seasonal rainfall and how LAI influenced CO2 fluxes at both sites. For field observations of leaf phenology, we qualitatively censed the presence of green leaves on 10 individuals and long gaps (following Richardson and Hollinger, 2007). We characterized the three years of study (Fig. 3a–c). In 2013, annual
rainfall (253 mm) was below the long-term average, mostly dominated (86%) by summer rains (Fig. 3a), which also had the coldest winter of the three years (Fig. 3d). In contrast, total annual precipitation in 2014 was 412 mm with a rainy summer but dry winter and spring (Fig. 3b-c), and in 2015, a wet year (505 mm), rains were spread throughout the year with above-average precipitation in winter and spring but below-average in summer (Fig. 3e). Temperature patterns were similar for years 2014 and 2015 (Fig. 3e-f), which drove daily mean air VPD highest during late spring (4 kPa), and 1–3 kPa for the rest of the seasons (Fig. 3g-i). Thus, the three years allowed us to compare CO2 and water fluxes over a wide range of conditions for the two sites, with weekly and monthly values providing a first approach for comparisons.

Important differences were detected in monthly fluxes and 8-day LAI dynamics between sites (Fig. 4). Except for the summer, buffalo grass savanna had higher monthly CO2 fluxes at other times during the three years (Fig. 4a-o), especially for GPP and NEP, but these were not exclusively related to buffalo grass activity in 2013 and 2014 (Fig. 4a-b). On-site phenological observations showed that buffalo grass had green leaves mainly during summer in 2013 and 2014, but rain patterns in 2015 allowed this species to maintain green leaves during seasons of the year that otherwise they would not have been active already (Fig. 4a-c). The shrubland had higher CO2 fluxes, ET and LAI than the buffalo grass savanna early in the summer seasons of 2014 and 2015, but were similar and highly variable for both sites during 2013 (Fig. 4).

### 3.2. Annual and growing season comparisons of ecosystem fluxes

Annual CO2 fluxes ranged from being carbon neutral to a sink during the years of study. Carbon and water fluxes for the years 2013 to 2015 ranged from being carbon neutral in the shrubland in 2013 (t-test against 0: t = 0.0544, P = 0.3524) to a sink in the buffalo grass savanna (year 2013). Both sites were carbon sinks during 2014 and 2015 and no statistically significant differences were found between-sites for both years. Flux uncertainties for annual NEP estimates were ± 65 to 68 g C m\(^{-2}\) for the shrubland and ± 66 to 78 g C m\(^{-2}\) for the buffalo grass savanna. When summed over the three years, both sites had similar NEP (393 and 414 g C m\(^{-2}\) year\(^{-1}\) for shrubland and savanna, respectively). \(R_{\text{eco}}\) at the savanna was 75–90 g C m\(^{-2}\) year\(^{-1}\) higher than the shrubland during 2013 and 2015, but GPP at the savanna compensated for those differences. Sites had similar ET during 2013, but the savanna had lower ET than the shrubland during 2014 and 2015 and lower ET/P ratios, which were evident both in the total annual and during the summer (Table 2).

The importance of summer fluxes to the total annual was always higher, although their magnitude and annual sums were different between years and sites. During the years with minimal rains in winter and spring (2013 and 2014), summer contribution to the total annual NEP was over a hundred percent in the shrubland, but only 59–89% in the buffalo grass savanna (Table 2). In those same years, summer contributed with 68–86% of the yearly fluxes of GPP, \(R_{\text{eco}}\) and ET at both sites, with about 7–18% higher contribution of carbon fluxes and 1–7% higher ET in the shrubland than the buffalo grass savanna. However, during the more widespread rainfalls of 2015 (with rains in winter, spring and summer), summer contribution to annual flux totals was 46 to 56% (ET and NEP respectively) in the buffalo grass savanna, and 46 (ET) to 72% (NEP) in the native shrubland.

Leaf area index was related to summer precipitation. We found 1.6 times higher slope between summer rainfall and LAI for the shrubland site than for the buffalo grass savanna (Fig. 6a), but no differences in the slope of the relationship between LAI and NEP were found (Fig. 6b).

### 3.3. Comparison of water use, water use efficiency and \(R_{\text{eco}}/\text{GPP}\)

Lower ET/P was always found at the buffalo grass savanna site. Annual ET/P was lower during the rainy years (2014 and 2015) and every summer season during our period of study in the buffalo grass savanna (Table 2). The buffalo grass savanna had also higher WUEI than the shrubland, either when buffalo grass was active or inactive (Fig. 5a). The savanna assimilated about 2.4 g C mm\(^{-1}\) H\(_2\)O month\(^{-1}\) and 188 g C hPa and had higher GPP*VPD for a given ET (marginally significant interaction effect and significant site effect in Table 1) than the shrubland. Our estimates indicate that the shrubland could only have higher NEP than the savanna if it diminished 5.5 mm month\(^{-1}\) ET or more (\(y = -5.8 + 1.06x\), Fig. 7), which only happened during summer months and few times in other seasons.

### 4. Discussion

#### 4.1. Comparison with current understanding of reverse LCLUC transitions from woody- to grass-dominated ecosystems

Our study supports the hypothesis that a LCLUC from shrubland to savanna dominated by a highly productive exotic C\(_4\) grass may result in an ecosystem that is as productive as the shrubland. This contradicts the prediction from the reverse transition, woody encroachment, where woody-dominated ecosystems tend to have higher NEP than grass-dominated ecosystems (Barger et al., 2011; Scott et al., 2006, 2014; Petrie et al., 2015). Our findings are supported by an experimental study that found increasing carbon pools in shrublands invaded by exotic grasses (Wolkovich et al., 2010). Here, we discuss mechanisms
and feedbacks operating in both ecosystems that could explain the observed pattern and possible implications of bidirectional woody-grassland transitions on dryland ecosystem carbon fluxes.

When compared, the buffelgrass savanna had either higher or similar annual NEP than the shrubland in the same year but summed over the study period (3 years) the sites were net carbon sinks and ended up with closely similar NEP. This contrasts with higher NEP expected from woody-dominated compared to grass-dominated ecosystems attributed to woody plants having access to deeper water sources, allowing higher ET/P ratio, longer growing seasons, and lower Reco/GPP (Huxman et al., 2005; Petrie et al., 2015; Scott et al., 2006, 2014). These expected changes did not operate in the same way at our sites. Growing season length was fairly similar between sites (as suggested by time series of NEP and GPP, Fig. 4) despite increased water availability at the shrubland (ET/P from Table 2), probably because vegetation at both sites is dominated by deciduous and highly seasonal species (Turner et al., 1995). Furthermore, the relationship between GPP and Reco did not differ between sites (Fig. 5b). Although Reco was higher at the savanna than shrubland during some years (2013, 2015), GPP throughout those years compensated such increases at both sites (Fig. 5b), which agrees with our hypothesis that the high productivity potential of buffelgrass would compensate the typical high Reco/GPP relation commonly reported for grass-dominated ecosystems. Alternatively, sites differed in their seasonal contributions to annual fluxes, making the shrubland NEP more dependent on the summer season than the buffelgrass savanna (Table 2, Fig. 7).

4.2. Water use and water use efficiency as drivers of seasonal differences in ecosystem fluxes

Although both sites had similar NEP sums over the three years, the underlying seasonal fluxes and water-carbon relationships differed among sites, specifically water use (ET/P, Table 2), and water-use efficiency (GPP*VPD/ET, Fig. 5). The buffelgrass savanna had higher WUE, than the shrubland throughout the year, supporting our hypothesis that at least part of this increase in WUE is due to the C4 physiology of buffelgrass, as has been found for other C4 dominated ecosystems.
the buffelgrass savanna site. However, the small proportion (\(
\) p < 0.05).

When no significant interaction effect is found, the independent variable effect corresponds to the overall slope.

When interaction effect is statistically significant, the independent variable effect corresponds to that of shrubland site and the independent variable \times Site effect correspond to the amount of change in the slope of the savanna in relation to that of the shrubland.

The Site (savanna) effect corresponds to the difference of the means of the dependent variable of the savanna in relation to that of the shrubland when the other factors are controlled.

Table 2

Annual and summer fluxes and seasonal contributions for the study years at shrubland and buffelgrass savanna sites. \( P \) values are for between-site \( t \)-test comparison for the same period.

<table>
<thead>
<tr>
<th></th>
<th>2013 #</th>
<th>2014</th>
<th>2015</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Net ecosystem production</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GPP (g C m(^{-2}))</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrubland</td>
<td>16</td>
<td>183</td>
<td>193</td>
</tr>
<tr>
<td>Savannah</td>
<td>75</td>
<td>140</td>
<td>199</td>
</tr>
<tr>
<td>( p )</td>
<td>0.029</td>
<td>0.318</td>
<td>0.843</td>
</tr>
<tr>
<td><strong>Ecosystem respiration</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GPP (g C m(^{-2}))</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrubland</td>
<td>326</td>
<td>561</td>
<td>674</td>
</tr>
<tr>
<td>Savannah</td>
<td>402</td>
<td>557</td>
<td>763</td>
</tr>
<tr>
<td>( p )</td>
<td>0.017</td>
<td>0.938</td>
<td>0.026</td>
</tr>
<tr>
<td><strong>Gross primary production</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GPP (g C m(^{-2}))</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrubland</td>
<td>343</td>
<td>744</td>
<td>867</td>
</tr>
<tr>
<td>Savannah</td>
<td>477</td>
<td>697</td>
<td>962</td>
</tr>
<tr>
<td>( p )</td>
<td>0.005</td>
<td>0.579</td>
<td>0.127</td>
</tr>
<tr>
<td><strong>Evapotranspiration</strong> (mm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrubland</td>
<td>236</td>
<td>400</td>
<td>582</td>
</tr>
<tr>
<td>Savannah</td>
<td>246</td>
<td>321</td>
<td>519</td>
</tr>
<tr>
<td>( p )</td>
<td>0.722</td>
<td>0.044</td>
<td>0.047</td>
</tr>
</tbody>
</table>

\# Data for winter 2013 is missing at the shrubland site. Thus, annual flux sums for 2013 at both sites were based on data from March 6 through the rest of the year. Omitting winter data may cause and error of around \( \pm 7 \) g C m\(^{-2}\) or less as this is the flux that we have registered during the winters at both sites for 2013 and 2014.
agreement with our hypothesis that buffelgrass activity would enhance WUE. Unexpectedly, WUE in the savanna was also higher during fall, winter and spring when buffelgrass was not active (e.g. winter and spring of 2013 and 2014). We suggest that water infiltration into deeper soil layers and subsequent use by native woody species that retain their leaves during most of the year, such as Prosopis and Olneya, increased GPP and thus WUE at the savanna. In agreement with this, water accumulation in soil at 1.5–2 m depth was found at the same savanna site after rainy summer and fall seasons, in which a decrease in soil water content at these depths during the drier months until the following summer gives evidence of its use (Castellanos et al., 2016; Celaya-Michel et al., 2015). Deep soil water accumulation could be expected in sites invaded with exotic grasses, as suggested by modeling studies of water balance in drylands (Wilcox et al., 2012). This evidence suggests that the high WUE and biological limitations at the savanna, because the buffelgrass C₄ physiology, cause a lower ET/P during summer rainy seasons and years (e.g., 2014 and 2015), and results in the observed water accumulation that feedbacks to the activity at the savanna during dry fall, winter and spring seasons (Fig. 8).

5. Concluding remarks

There is a long way ahead the scientific community to understand how LCLUC impacts NEP when woody shrublands change to C₄—grass—dominated ecosystems. The high productivity, photosynthesis rates, resource-use efficiency, and other traits of C₄ exotic grasses—dominated ecosystems, can make important differences in their impact and feedbacks of these transitions from those reported in woody encroachment studies (Huxman et al., 2005; Petrie et al., 2015; Scott et al., 2014; Wolkovich et al., 2010). By using the EC techniques over adjacent shrubland and buffelgrass savanna sites, we documented that such LCLUC altered the temporal dynamics of carbon fluxes, and were able to link these differences to changes in water use and WUE. The representation of photosynthetic pathway, rooting pattern, and differential canopy responses were the main factors responsible for such changes (Fig. 8), all of these characteristics greatly modified by LCLUC from shrublands to grass-dominated ecosystems. However, our findings suggest that the effects of temporal changes in water use and WUE on NEP compensated in time, either between seasons (e.g., 2014) or between years (e.g., 2013 vs 2014), to a similar NEP over the years despite the strong biotic, and vegetation-specific structural and functional differences in land cover. Further studies on LCLUC from woody-dominated to grass-dominated ecosystems should focus on understanding how the impact of biotic traits (photosynthetic pathway, rooting...
pattern, differential LAI canopy responses) affect water use, WUE and NEP over ecological gradients such as rainfall (amount and seasonality), vegetation (over different kinds of woody dominated ecosystems), and management conditions (low and high cover of exotic grasses, overgrazed, non-overgrazed). Such studies will help to reduce the uncertainty associated with LCLUC between woody- and grass-dominated ecosystems and their impacts on carbon processes.

Acknowledgments

This manuscript was much improved by the insightful suggestions from the editor (C.K. Thomas) and two anonymous reviewers. We greatly appreciate support from CONACYT (CB61865, INF2012-1-188387) to AEC and CB223525 to AEC and JRL and Universidad de Sonora. CHH acknowledges CONACYT and Posgrado en Biociencias for a PhD scholarship. RV acknowledges support from NASA Carbon Monitoring Systems (80NSSC18K0173). We thank H. Celaya-Michel, A. Ibarra, J. Llano and J.E. López-Piña for technical support in this study. We especially thank and deeply appreciate Mr. L. Sierra for allowing us to install the eddy covariance towers and carry out this study in his ranch property, and to J. D彪as for initial support in the field.

Appendix A. Supplementary data

Supplementary material related to this article can be found in the online version, at doi:https://doi.org/10.1016/j.agrformet.2019.01.030.

References


