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DIVISIÓN DE CIENCIAS BIOLÓGICAS Y DE LA SALUD
DEPARTAMENTO DE INVESTIGACIONES CIENTÍFICAS Y TECNOLÓGICAS

POSGRADO EN BIOCIENCIAS

ECOFISIOLOGÍA DE LA FOTOSÍNTESIS, PRODUCTIVIDAD NETA Y USO DE AGUA EN ECOSISTEMAS DESÉRTICOS Y TRANSFORMADOS A SABANA DE ZACATE BUFFEL EN SONORA.

TESIS

que para obtener el grado de:

DOCTOR EN BIOCIENCIAS

presenta:

CÉSAR HINOJO HINOJO

Hermosillo, Sonora, México 08 de diciembre del 2017

DERECHOS DE AUTOR

El presente trabajo de tesis se presenta como uno de los requisitos parciales para la obtención del grado de **Doctor en Biociencias** de la Universidad de Sonora.

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Hermosillo, Sonora, México Diciembre de 2017

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APROBACIÓN

Los miembros del Comité designado para revisar la tesis intitulada "Ecofisiología de la fotosíntesis, productividad neta y uso de agua en ecosistemas desérticos y transformados a sabana de zacate buffel en Sonora" presentada por César Hinojo Hinojo, la han encontrado satisfactoria y recomiendan que sea aceptada como requisito parcial para obtener el grado de Doctor en Biociencias.

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RESUMEN

La magnitud de los procesos ecológicos en ecosistemas áridos se ha explicado predominantemente por factores abióticos relacionados a la disponibilidad de agua. Sin embargo, la escasa información acerca de la influencia de los factores bióticos sobre estos procesos limita nuestro entendimiento sobre las consecuencias ecológicas que pudieran tener los cambios en la biota que están ocurriendo en los ecosistemas áridos del mundo. El presente trabajo pretende mejorar nuestro entendimiento acerca de cómo diferentes características bióticas de la vegetación influencian la magnitud y variabilidad de la productividad neta, mediante el estudio de: a) atributos ecofisiológicos relacionados a la fotosíntesis a nivel de hoja en algunas especies dominantes del Desierto Sonorense, y b) del intercambio gaseoso de CO_2 y agua a nivel ecosistema en un matorral y en un sitio adyacente cuya vegetación fue transformada a sabana de zacate buffel (*Cenchrus ciliaris*). A nivel de hoja, encontramos valores de velocidad de carboxilación máxima (V_{cmax}) y capacidad de transporte de electrones (J_{max}) mayores a los que típicamente se asumen para los diferentes tipos funcionales de plantas, en todas las especies de estudio. Estas características favorecen la captura de CO_2 por fotosíntesis, en condiciones favorables y de estrés moderado. A nivel ecosistema, el matorral y la sabana fueron sumideros de carbono similares, pero la transformación de la vegetación modificó la estacionalidad y disminuyo la variabilidad interanual de la productividad neta. Además, se muestra cómo estas características de la fotosíntesis, la perdida en diversidad y complementariedad, cambios en características y respuestas del dosel, y la fenología de las especies determinan la magnitud y causaron estos cambios en la dinámica temporal de la productividad neta, ya sea por efecto directo o al modificar el uso de agua del ecosistema cuando la vegetación es transformada.

ABSTRACT

The magnitude of ecological processes in arid ecosystems has been mainly explained by abiotic factors related to water availability. However, the scarce information about the influence of biotic factors upon these proceses limits our understanding about the ecological consequences that the changes in biota that are occurring in arid ecosystems of the world may have. This study addresses how different biotic characteristics of vegetation influence the magnitude and variability of net ecosystem production, by studying: a) ecophysiological traits related to leaf level photosynthesis in dominant species of the Sonoran Desert, and b) the gas exchange of CO_2 and water at ecosystem level in a shrubland and an adjacent site whose vegetation was transformed to exotic buffelgrass savanna (*Cenchrus ciliaris*). At leaf level, the values of maximum carboxilation velocity (V_{cmax}) and electron transport capacity (J_{max}) found for the studied species were higher than those typically assumed for the different plant functional types. These characteristics favors CO_2 capture by photosynthesis under favorable and moderate stress conditions. At ecosystem level, both shrubland and savanna were comparable carbon sinks, but the transformation of vegetation modified the seasonality and diminished inter-annual variation of net production. It is shown how these traits related to photosynthesis, the loss of plant diversity and complementarity, changes in canopy characteristics and responses, and species phenology, determine the magnitude and caused these changes in temporal dynamics of net production, either by direct effect or through modification of ecosystem water use when vegetation is transformed.

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I. INTRODUCCIÓN

La biota participa activamente en los procesos que determinan las características de la Tierra como sistema, moviendo mediante sus procesos vitales grandes cantidades de materia y energía entre organismos y el ambiente físico (Schlesinger y Bernhardt, 2013; Vernadsky, 1998). A estos procesos que resultan en flujos de materia y energía se les denomina funcionamiento del ecosistema (Chapin *et al.*, 2011; Reiss *et al.*, 2009). Producto de esta actividad biológica, los ecosistemas terrestres son capaces de capturar alrededor de 30% de las emisiones de antropogénicas de CO_2 a la atmósfera, uno de los principales gases de efecto invernadero (Le Queré *et al.*, 2016). Esta captura resulta en su mayor parte del balance de dos de los mayores flujos de CO_2 entre la biosfera y la atmósfera, la captura de CO_2 por la fotosíntesis o productividad primaria bruta (PPB) y la emisión de CO_2 por la respiración de los ecosistemas (R_{eco}) (Ciais *et al.*, 2013), y contribuye a regular la variación interanual del CO_2 atmosférico (Le Queré *et al.*, 2016). Al balance entre PPB y R_{eco} se le conoce como la productividad neta de los ecosistemas.

El funcionamiento de los ecosistemas, y con ello la magnitud de la productividad neta, es controlado por factores bióticos (biodiversidad, biota potencial, composición, estructura, tipos funcionales, atributos funcionales, respuestas y características fisiológicas) y abióticos (características geológicas y edafológicas, clima y microambiente, abundancia de recursos), los cuales a su vez pueden ser modificados por acción del hombre (Chapin *et al.*, 2011). Aunque los factores abióticos han dominado la explicación del funcionamiento de los ecosistemas, existe evidencia reciente que indica que los factores bióticos pueden tener un efecto comparable o incluso mayor que los abióticos (Hooper *et al.*, 2012; Maestre *et al.*, 2012a; Shao *et al.*, 2015; Tilman *et al.*, 2012). Sin embargo, el efecto de los factores bióticos se ha estudiado mayormente en ecosistemas experimentales, y su efecto en el funcionamiento de ecosistemas reales apenas recientemente se empezó a explorar.

Estudios en ecosistemas áridos normalmente han considerado a variables relacionadas con la disponibilidad del agua y otras variables abióticas como las principales limitantes y controladores de la magnitud de los flujos de CO_2, pero se le ha puesto poca atención a entender el papel que los factores bióticos tienen en esto. Por ejemplo, se ha documentado que a escala anual la magnitud de la productividad neta es controlada por la precipitación anual, la frecuencia de eventos de precipitación, la temperatura media anual y la evapotranspiración a escala anual (Bell *et al.*, 2012; Biederman *et al.,* 2016, 2017; Scott *et al.,* 2014); a escala mensual por la humedad del suelo (Bell *et al.,* 2012); y a menores escalas temporales es controlada por la temperatura (aire y suelo), humedad del suelo, deficit de presión de vapor, precipitación y radiación fotosintéticamente activa (Bell *et al.*, 2012; Kurc y Small, 2007; Scott *et al.,* 2014; Wohlfahrt *et al.,* 2008). Sin embargo, estudios recientes sugieren que el efecto de los factores bióticos sobre la variabilidad interanual de la productividad neta de los ecosistemas disminuye al aumentar la aridez, aunque aún muy pocos sitios de áridos se han incluido en estos estudios (Shao *et al.,* 2015). Aun la información es muy limitada sobre cómo diferentes factores bióticos son importantes, o bajo qué circunstancias lo son, para controlar la magnitud de la productividad neta de los ecosistemas áridos, y esto recientemente se ha empezado a explorar en algunos procesos (Maestre *et al.,* 2012a).

Tradicionalmente, las zonas áridas no se consideraban importantes en procesos biogeoquímicos globales tales como los flujos de CO_2, debido a su baja cantidad biomasa y cobertura vegetal, baja productividad primaria neta por encima del suelo, y sus condiciones climáticas extremas (Maestre *et al*., 2012b; Withford, 2002). Sin embargo, la evidencia actual sugiere que estos ecosistemas son de gran importancia para los procesos a nivel global, debido a su extensión (41.3% de la superficie terrestre, Hasan *et al.,* 2005), a la magnitud y variabilidad de los flujos de CO_2 y agua que se han medido a nivel ecosistema (Wholfahrt *et al.*, 2008; Bell *et al.,* 2012; Scott *et al*., 2014; Biederman *et al.,* 2017), y que análisis y modelos a nivel global indican que los flujos de ecosistemas áridos dominan la tendencia y la variación interanual en el sumidero de carbono terrestre (Ahlström *et al*., 2015; Poulter *et al*., 2014). Aunque esta importancia y magnitud de los flujos en zonas áridas ha sido cuestionada, y mas sobre los procesos biológicos que los generan (Schlesinger *et al*., 2009; Schlesinger *et al*., 2017), la evidencia que sustenta que la magnitud de los procesos en zonas áridas es importante a nivel local a global sigue en aumento (Biederman *et al.,* 2016; 2017; Ahlström *et al*., 2015; Poulter *et al*., 2014; Marcolla *et al.,* 2017). Por ejemplo, la productividad neta en regiones áridas tienen una magnitud muy variable (-350 a + 330 g C m^{-2} $año^{-1}$, Biederman *et al*., 2017), y que hay ecosistemas que consistentemente son sumideros, otros que consistentemente son fuente u otros que alternan año con año entre fuente o sumidero (Biederman *et al.,* 2017; Scott *et al*., 2015). Se ha encontrado que la variación en GPP y la cantidad de follaje tienen un papel dominante en explicar la variación en la productividad neta (Ahlström *et al*., 2015; Pulter *et al*., 2014). Estas características de sus flujos contrastan con otro tipo de biomas mésicos como los templados y tropicales (Baldocchi *et al*., 2001; Biederman *et al*., 2017). La biota de los ecosistemas áridos está cambiando por el cambio de uso del terreno, degradación y desertificación, uso y disponibilidad de agua, clima y otros agentes del cambio global (Hassan *et al.,* 2005; Maestre *et al*., 2012b). En la gran mayoría de los casos no se sabe cómo el cambio en la biota puede modificar las magnitudes y variabilidad de los flujos de carbono, ya sea por cambio en las respuestas del ecosistema a los factores abióticos o por influencia directa sobre los factores abióticos.

Para avanzar en entender la importancia de los factores bióticos en la productividad neta de los ecosistemas, se debe abordar este problema desde distintas perspectivas, escalas y aproximaciones:

- Se requiere tener más mediciones que permitan obtener información sobre cómo varían las características fisiológicas y atributos clave entre especies, y entre los principales tipos funcionales que habitan en los ecosistemas (Rogers, 2014). Esta información básica es insumo importante de modelos para entender y simular la productividad neta de los ecosistemas.
- Generar mediciones sobre flujos y factores controladores en sitios y tipos de ecosistemas aun subrepresentados. Ejemplos de esto son los diferentes tipos de matorrales, sitios bajo

prácticas de manejo, sitios dominados por especies invasoras, en sitios no prístinos en estados sucesionales o degradados, etc.

- Desarrollo de diseños experimentales en ecosistemas reales con condiciones biológicas contrastantes que permitan evaluar directamente el impacto de diferentes características biológicas (vías fotosintéticas, formas de crecimiento, perdida de diversidad, etc.) (Biederman *et al.,* 2016).

El presente estudio busca contribuir al conocimiento de la importancia de algunos de estos factores bióticos en los flujos, desde la hoja al ecosistema, en zonas áridas. A nivel hoja, se caracterizaron parámetros bioquímicos de la fotosíntesis que son importantes para modelar la fotosíntesis a diferentes escalas, y atributos foliares relacionados, para algunas especies dominantes del Desierto Sonorense. Con estos datos se obtuvo el rango de variación en estos parámetros y atributos en especies que representan una amplia gama de estrategias ecológicas y fenológicas. Además, se obtuvieron modelos estadísticos que pueden servir para derivar el valor de los parámetros bioquímicos para especies de zonas áridas usando atributos foliares para usarlos en modelos de fotosíntesis y productividad de los ecosistemas. A nivel ecosistema, se busca determinar el impacto de transformar la estructura y composición de la vegetación en la dinámica temporal de la productividad neta, a través de sitios pareados de eddy covariance. Tomamos como caso de estudio la transformación de matorrales a sabana de zacate buffel (*Cenchrus ciliaris*), que es un cambio de cobertura ampliamente distribuido en las zonas áridas del mundo, con fines ganaderos o por invasión biológica. Estos datos nos permitieron determinar maneras en los que el cambio en la representación en el ecosistema de las vías fotosintéticas, las formas de crecimiento y la simplificación de la diversidad puede modificar los controladores y la magnitud de los flujos de carbono en ecosistemas áridos. En las siguientes dos secciones se abundará un poco más acerca de estos dos temas: los parámetros bioquímicos de la fotosíntesis y la transformación de matorrales a ecosistemas dominados por zacate buffel.

I.1. Características bioquímicas relevantes para la modelación de la fotosíntesis

Existe muchos modelos que nos pueden ayudar a describir, entender y predecir la tasa de fotosíntesis de las plantas, desde modelos empíricos hasta semimecanísticos y mecanísticos (Jones, 2014; Thornley y France, 2007; Zhu *et al*., 2013). Uno de los más usados es el modelo bioquímico de la fotosíntesis C_3, que es un modelo semimecanístico originalmente formulado por Farquhar *et al*. (1980), y que ha seguido siendo desarrollado con el paso del tiempo (von Caemmerer, 2000). Este permite describir la tasa de fotosíntesis ante una gran gama de condiciones, y es parte fundamental en modelos a gran escala como los modelos del sistema terrestre. Según este modelo, la tasa fotosíntesis puede ser limitada por tres procesos principalmente (Ec. 1), por carboxilación o la actividad de la ribulosa-1,5-bifosato carboxilasa oxigenasa (Rubisco; Ec. 2), por regeneración de ribulosa-1,5-bifosfato (RuBP) y la tasa de transporte de electrones (Ec. 3 y 5), o por la velocidad de intercambio de triosas fosfato por fósforo inorgánico (Ec. 4) (Medlyn *et al*., 2002; von Caemmerer, 2000):

$$A_n = \min(A_c, A_j, A_p) - R_d \quad \text{(Ec. 1)}$$

$$A_c = \frac{V_{cmax}(C_i - \Gamma^*)}{\left[C_i + K_c\left(1 + \frac{O_i}{K_o}\right)\right]} \quad \text{(Ec. 2)}$$

$$A_j = \left(\frac{J}{4}\right) \cdot \frac{(C_i - \Gamma^*)}{(C_i + 2\Gamma^*)} \quad \text{(Ec. 3)}$$

$$A_p = 3 \cdot T_p \quad \text{(Ec. 4)}$$

$$J = \frac{\alpha Q + J_{max} - \sqrt{(\alpha Q + J_{max})^2 - 4\theta\alpha Q J_{max}}}{2\theta} \quad \text{(Ec. 5)}$$

donde A_n es la tasa de fotosíntesis neta, A_c es la tasa de fotosíntesis limitado por carboxilación, A_j es la tasa de fotosíntesis limitada por la regeneración de RuBP, A_p es la tasa de fotosíntesis limitada por la velocidad de intercambio triosas fosfato por fosforo inorgánico, R_d es la tasa de respiración mitocondrial, V_{cmax} es la actividad maxima de la Rubisco, C_i y O_i son las concentraciones de CO_2 y O_2 intercelular, K_c y K_o son los coeficientes de Michaelis-Menten para carboxilación y oxigenación por Rubisco, Γ^* es el punto de compensación de CO_2 en ausencia de respiración mitocondrial, J es la tasa de transporte de electrones y T_p es la tasa de exportación de triosas fosfato fuera del cloroplasto, α es el rendimiento cuántico del transporte de electrones, Q es la densidad de flujo de fotones de radiación fotosintéticamente activa incidente, J_{max} es la capacidad máxima de transporte de electrones, y θ es un parámetro de curvatura.

La mayoría de los parámetros que usa este modelo pueden ser asignados *a priori* (von Caemmerer, 2000), en especial todos los que caracterizan o dependen de la actividad enzimática (K_c, K_o, Γ^*) pues tienden a ser bastante conservados en las especies C_3, y existen valores típicos para algunos parámetros que caracterizan al transporte de electrones en las hojas (α, θ). Así, las principales incógnitas del modelo son los parámetros V_{cmax}, J_{max}, R_d y TPU (Walker *et al.*, 2014), que en este escrito nos referiremos a ellos como "parámetros bioquímicos" de la fotosíntesis. Estos parámetros se pueden derivar de mediciones de curvas de respuesta de la fotosíntesis a condiciones ambientales, principalmente al CO_2 (Long & Bernacchi, 2002; Duursma, 2015).

Se han realizado varios esfuerzos de síntesis para juntar la información disponible sobre estos parámetros en las especies de plantas, su variación entre tipos funcionales y principales atributos relacionados (Kattge *et al.*, 2009; Wullschleger *et al.*, 1993; Walker *et al.*, 2014). Se ha encontrado que estos parámetros pueden variar bastante entre especies, en especial V_{cmax} y J_{max} que varían hasta en 2 órdenes de magnitud (Wullschleger *et al.*, 1993; Walker *et al.*, 2014). Esta amplia variación se ha visto que está relacionada con el contenido de nitrógeno y fósforo por unidad de área foliar, y al área foliar específica (Kattge *et al.*, 2009; Walker *et al.*, 2014). Además, se sabe que diferentes tipos funcionales de plantas tienden a tener diferentes valores en estos parámetros, y pueden diferir incluso en sus relaciones con estos atributos (Kattge *et al.*, 2009).

Las estimaciones sobre flujos de carbono a gran escala son altamente sensibles a los parámetros bioquímicos, especialmente a V_{cmax} y J_{max} (Bonan et al., 2011). Sin embargo, la mayoría de los datos existentes sobre sus valores provienen de ecosistemas de bosques (templados o tropicales) o especies de cultivo. Diferentes modelos a gran escala (como los modelos del sistema terrestre) utilizan tablas con valores de fijos de estos parámetros por cada tipo funcional, y así parametrizar los modelos de manera sencilla (Rogers, 2014). Tanto las síntesis de datos como las tablas que usan los modelos aún tienen una muy pobre representación, si es que tienen alguna, de especies y tipos funcionales típicos de ecosistemas áridos (Rogers, 2014, Figura 1). Es probable que el conocimiento de los parámetros bioquímicos de la fotosíntesis para ecosistemas áridos, aparte de los pocos datos existentes, esté limitado además porque las mediciones son demandantes en tiempo y por lo general permite tener pocas replicas, y que son bastante comunes las condiciones estresantes para las plantas y por ello desfavorables para hacer mediciones. Esta poca disponibilidad de datos y poca representación de especies y tipos funcionales en las tablas de los modelos a gran escala puede implicar que la fotosíntesis aun es no está adecuadamente parametrizada para estos ecosistemas ampliamente distribuidos, y que las estimaciones pueden estar sesgadas, lo cual limita nuestro conocimiento sobre los procesos y flujos de carbono y sus controladores abióticos y bióticos.

I.2. Transformación de matorrales xerófilos a ecosistemas dominados por el zacate buffel

Desde el siglo XIX se han introducido especies de pastos exóticos, principalmente de origen africano, en los ecosistemas áridos del mundo para incrementar la productividad de sus agostaderos (Williams y Baruch, 2000). Algunos escritos señalan que las zonas áridas del mundo fueron afectadas por varios eventos de sequía severa que resulto en degradación del terreno a finales del siglo XIX y principios del XX, lo cual estimulo la búsqueda de especies de pasto altamente productivas y resistentes a la sequía con cuales rehabilitar los ecosistemas e incrementar su capacidad forrajera de (Cox, 1991). El zacate buffel fue tal vez la principal especie encontrada en esta búsqueda. Desde entonces ha sido introducido en diferentes eventos al menos en Australia, América del Norte y Sur (Marshall et al., 2012). En Estados Unidos fue introducido desde 1940 y en México desde 1970 (Marshall et al., 2012). Desde entonces, esta especie se ha vuelto dominante en grandes áreas donde no es nativo, por establecimiento intencional para incrementar la actividad ganadera, o por invasión, al colonizar áreas adyacentes de donde fue establecido. Se desconoce la extensión actual de los ecosistemas donde ahora es dominante. Algunas estimaciones indican que ocupa al menos 10 millones de hectáreas en el suroeste de Estados Unidos y el noroeste de México (Cox, 1991), y más de 1 millón de hectáreas solo en Sonora llegando tal vez a ocupar el 10% de la superficie estatal (Castellanos *et al.,* 2002; Burquez *et al.,* 1998; Bravo-Peña *et al.,* 2013). La introducción de estas especies exóticas en las zonas áridas del mundo, y en particular del zacate buffel, ha sido realizada sin considerar las posibles consecuencias ecológicas, las cuales en la actualidad aún no están bien entendidas.

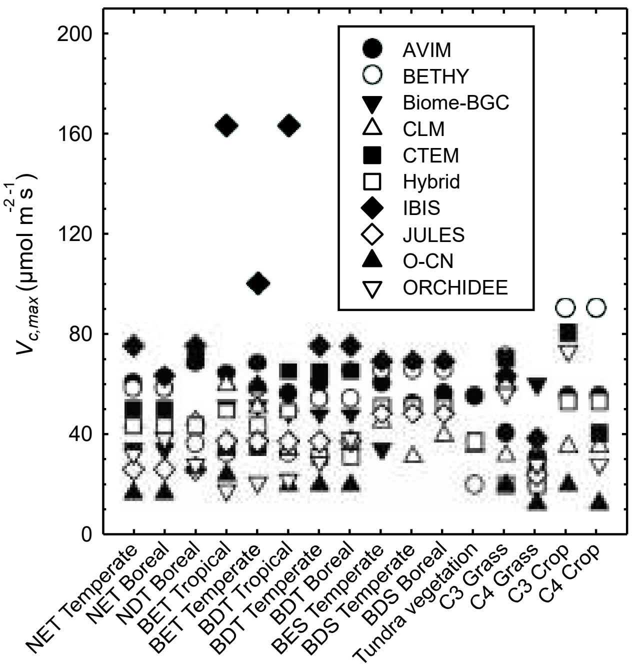

Figura 1: Algunos de los principales tipos funcionales usados por modelos del sistema terrestre y el valor que les asignan a V_{cmax}. Las siglas de los nombres de los tipos funcionales significan N: hoja acicular, B: latifoliado, E: siempreverde, D: caducifolio, T: árbol, S: arbusto, Temperate: templado, Tropical: tropical, y Boreal: boreal, C_3: via fotosintética C_3, C_4: via fotosintética C_4, Grass: zacate, Crop: cultivo. Los diferentes símbolos y los nombres en las leyendas hacen referencia a diferentes modelos del sistema terrestre. Tomada de Rogers (2014). Es de resaltar que no se pudiera considerar que estos tipos funcionales representan adecuadamente a los tipos funcionales típicos de zonas áridas.

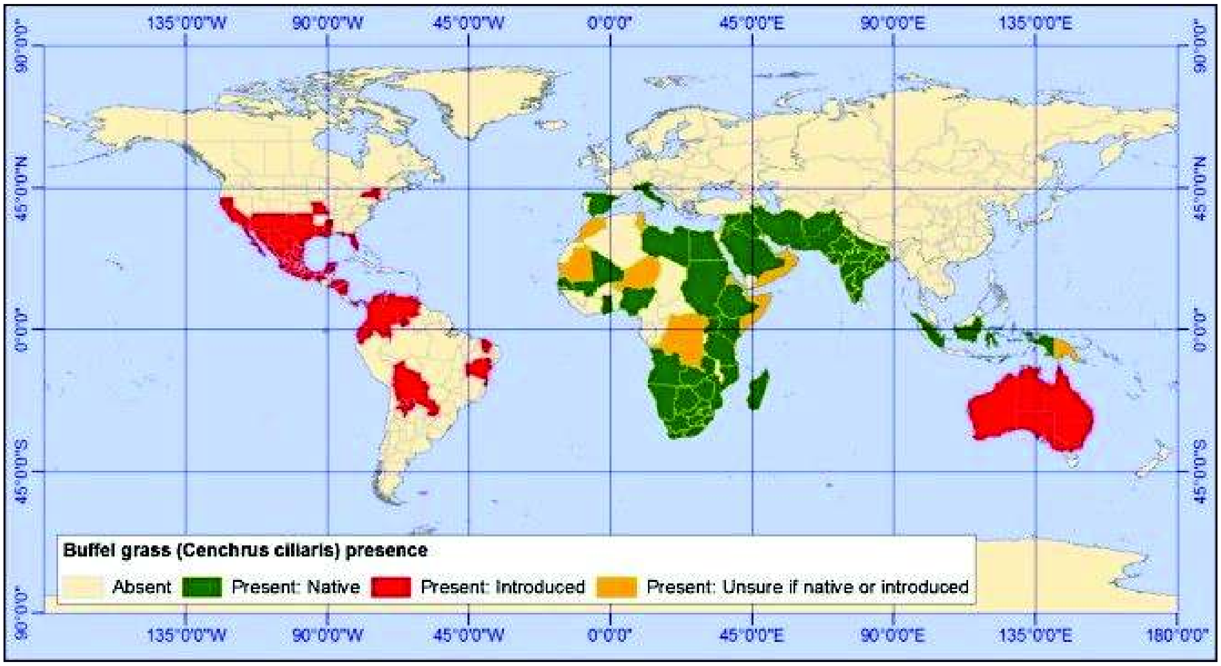

Figura 2: Distribución del zacate buffel en el mundo. Diferentes colores indican su estatus de nativo, introducido o incierto. Tomado de Marshall *et al.* (2012).

Por lo general, las prácticas para establecer zacate buffel implican la remoción total o casi total de la vegetación nativa mediante maquinaria y en su lugar sembrar cobertura esta especie. Por invasión, el zacate buffel incrementa su dominancia a expensas de las especies nativas, ya sea por inducir ciclos de fuego (McDonald y McPherson, 2013; McDonald y McPherson, 2011; Miller *et al*., 2010), por presión de propágulos (Brenner y Kanda, 2013; Fensham *et al.,* 2013), o por competencia (Olsson *et al.,* 2012). Además, la invasión del zacate buffel es favorecida por el disturbio e intensas lluvias después de periodos de sequía (Brenner y Kanda, 2013; Fensham *et al*., 2013). Ya sea por establecimiento o por invasión, esto causa cambios en la composición y estructura de los ecosistemas, que aunque algunos grupos de organismos pueden verse favorecidos, la mayoría de los grupos se ven afectados (Marshall *et al*., 2012). En especial para la vegetación, se ha detectado una perdida regional del 50% de la diversidad alpha, beta y gama, y una perdida hasta de 80% de la cobertura de plantas leñosas (Franklin y Molina-Freaner, 2010). Esto puede significar que la diversidad de estrategias ecológicas de las especies nativas (Hinojo-Hinojo *et al*., 2013) es reemplazada por las características del zacate buffel: altas tasas fotosintéticas, alta eficiencia de recursos (agua y nitrógeno) típica de la vía fotosintética C_4, y raíces superficiales (Ehleringer y Monson, 1993; Larcher, 2014; Mnif y Chaleb, 2009). Hay evidencia que indica que el impacto del zacate buffel sobre la diversidad y riqueza de especies aumenta con la cobertura de zacate buffel y el tiempo de su establecimiento (Olsson *et al*., 2012).

Estos cambios bióticos pueden tener consecuencias que aún no entendemos en la magnitud de los procesos ecológicos. La evidencia sugiere que la transformación de matorrales xerofilos a sabanas de zacate buffel causa pérdidas del nitrógeno y fósforo del suelo, y estas pérdidas aumentan con el tiempo transcurrido desde la transformación (Celaya *et al*., 2015; Morales-Romero *et al*., 2015), además de cambios en el almacenamiento de agua en el suelo (Celaya *et al*., 2015; Castellanos *et al.,* 2016). Sin embargo, las consecuencias en los procesos de productividad del ecosistema, flujos de CO_2 y agua aún se desconocen. ¿la perdida en diversidad, fertilidad y cambios en agua en ecosistema limitaran los flujos en un ecosistema de sabana? ¿o el aumento en la eficiencia de uso de recursos intrínseca a la vía C_4 en el buffel aumentara la productividad pero reducirá la evapotranspiración?.

Para analizar las consecuencias de la transformación de matorrales a sabanas de zacate buffel usamos la técnica de eddy covariance en sitios adyacentes con cobertura de matorral y de sabana de zacate buffel. La técnica de eddy covariance es en la actualidad la manera más directa de realizar mediciones de flujos de materia y energía entre los ecosistemas y la atmósfera (Figura 3). Así, este arreglo de sitios instrumentados para esta técnica nos permitió analizar el efecto del cambio en cobertura en estos procesos. Si la biota es un control importante de los procesos, esperaríamos cambios en estos flujos, o al menos en algunos años.

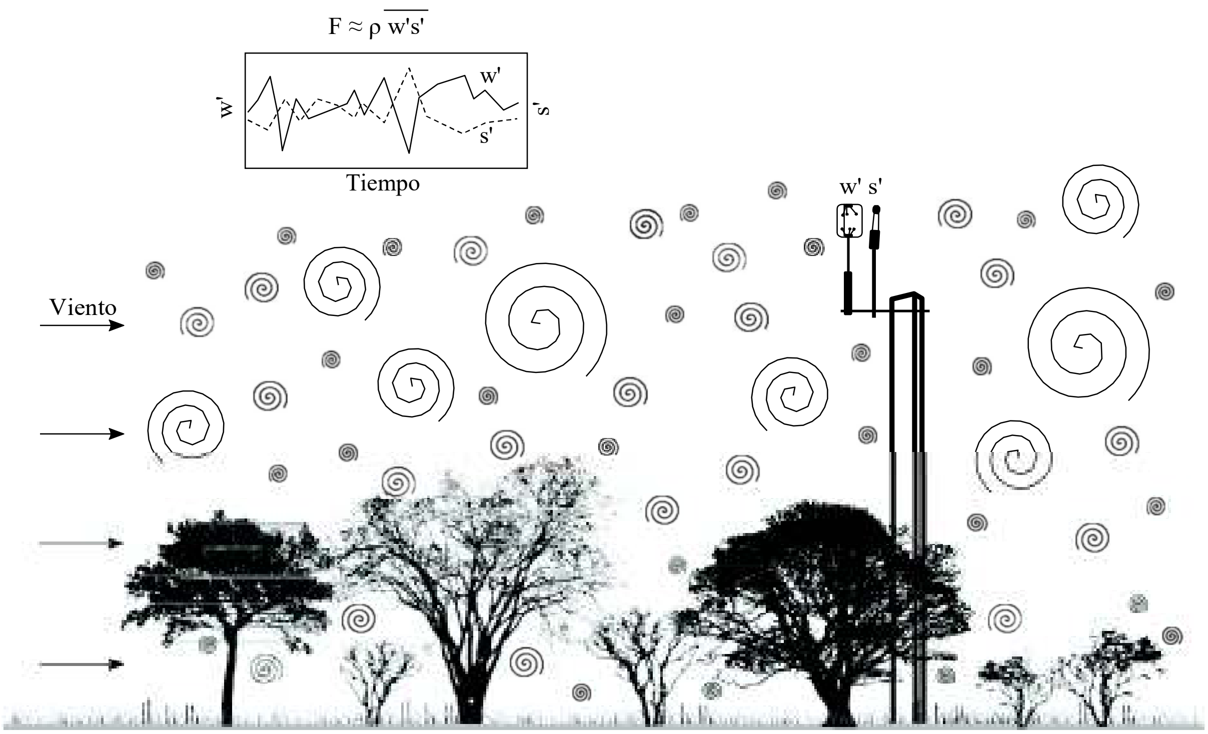

Figura 3: Esquema sobre las generalidades de la técnica de Eddy Covariance. La técnica se basa en que si podemos medir los vórtices (espirales) que componen al viento turbulento y la masa o energía que estos vórtices acarrean verticalmente, podemos tener una estimación de la magnitud de algún flujo de interés entre los ecosistemas y la atmósfera. Así, el flujo (F) se puede estimar como la covarianza de las fluctuaciones a alta frecuencia (a 10 o 20 Hz) de la velocidad vertical del viento (w') y algún escalar de interés (s', p ej. concentración de CO_2 o H_2O, temperatura, etc.) a través del tiempo, siempre y cuando se cumplan los supuestos de la técnica o los datos puedan corregirse para cumplirlos. Estos principales supuestos son que la densidad del aire es constante, que no hay gradientes horizontales que causen advección, lo cual ocurre cuando el terreno es horizontal, plano, homogéneo y de amplia extensión relativo al alcance de las mediciones, que la velocidad del viento media vertical y lateral sean cero, y que la atmósfera donde se realizan las mediciones se encuentra en estado estable. Las mediciones se realizan con sensores micrometeorológicos instalados sobre torres, y además por lo general se cuenta con sensores meteorológicos auxiliares para monitorear las condiciones ambientales.

II. OBJETIVOS

II.1. Objetivo general

Contribuir al conocimiento de la influencia de la vegetación en los flujos de CO_2 y agua en ecosistemas áridos mediante la caracterización de atributos ecofisiológicos de las especies y el análisis comparativo del intercambio gaseoso a nivel ecosistema en sitios con cobertura vegetal contrastante

II.2. Objetivos específicos

- Caracterizar atributos ecofisiológicos que determinan la tasa de fotosíntesis de las especies dominantes de ecosistemas del Desierto Sonorense
- Caracterizar la dinámica temporal y variación interanual de los flujos de carbono y agua en un ecosistema de sabana de zacate buffel
- Determinar el impacto de transformar un matorral nativo a sabana de zacate buffel en la productividad neta y uso de agua del ecosistema

III. PUBLICACIONES

High V_{cmax}, J_{max} and photosynthetic rates of Sonoran Desert species using nitrogen and specific leaf area traits as proxies in biochemical models

Este artículo fue sometido a la revista Journal of Arid Environments

En este artículo se caracterizaron los parámetros de V_{cmax} y J_{max} obtenidos usando curvas de respuesta de la fotosíntesis al CO_2, y atributos foliares potencialmente relacionados (area foliar específica y contenido de nitrógeno foliar), para 6 especies abundantes y ampliamente distribuidas en el Desierto Sonorense. En todas las especies estudiadas, encontramos valores mayores a los reportados para tipos funcionales relacionados (p ej. arbustos) en estudios de síntesis y los típicamente usados por los modelos del sistema terrestre. Los pocos valores para otras especies de ecosistemas áridos que existen en la literatura también tienen rangos altos en estos parámetros, lo cual pudiera indicar que este patrón es lo común en estos ecosistemas. La importancia de este trabajo radica en pudimos detectar que este patrón pudiera ser importante en favorecer la ganancia de carbono de las especies, y que es posible que los flujos y procesos fotosintéticos puedan no estar adecuadamente parametrizados para ecosistemas áridos en modelos a gran escala.

Carbon and water fluxes in an exotic buffelgrass savanna

Este artículo fue publicado en Journal of Rangeland Ecology and Management en el 2016, volumen 69, pp. 334-341.

Los ecosistemas dominados por especies exóticas cada vez ganan mayor extensión, ya sea por establecimiento intencional o por invasión. Sin embargo, aún conocemos muy poco sobre el funcionamiento de estos ecosistemas ahora ampliamente distribuidos. Para este estudio utilizamos los primeros 3 años de datos de mediciones de flujos en una sabana de zacate buffel para documentar por primera vez la estacionalidad y la variabilidad interanual de los flujos de CO_2 y agua de un ecosistema dominado por la especie exótica zacate buffel (*Cenchrus ciliaris*) fuera de su rango nativo. Encontramos que una sabana de buffel manejada adecuadamente puede ser un sumidero importante de CO_2, incluso durante años secos. Su potencial como sumidero está relacionado positivamente a la precipitación y disponibilidad de agua (medido como evapotranspiración). Además de estas variables relacionadas al agua, la fenología de las especies destacó como uno de los factores bióticos que pueden influir de manera importante en este potencial: la fenología contrastante del zacate buffel (activo principalmente en el verano) y de algunas especies nativas presentes en la sabana (activas durante la mayor parte del año) permitió al ecosistema tener una captura de CO_2 neta durante la mayor parte del año.

How land cover change from shrubland to exotic grass savanna influence ecosystem CO_2 and water fluxes: a study from adjacent eddy covariance sites

Este artículo fue sometido a la revista Global Change Biology en Junio del 2017

En este artículo usamos principalmente datos de los flujos de CO_2 y agua a nivel ecosistema obtenidos entre los años 2013-2015 en sitios adyacentes con cobertura de matorral y de sabana de zacate buffel. Estos datos nos permitieron explorar como la transformación de un matorral a sabana de zacate buffel puede modificar las magnitudes de los flujos y su respuesta a algunos de los factores controladores. Encontramos que la productividad neta del ecosistema durante el verano tiende a ser menor en la sabana durante el verano en comparación al matorral, pero la sabana tiende a tener mayor productividad neta que el matorral durante el resto de las estaciones. Sin embargo, a pesar de haber cambios estacionales, la productividad neta de los ecosistemas no se modificó a largo plazo (en los tres años de estudio), lo cual sugiere que estos cambios se compensan en el tiempo. El articulo resalta como el cambio en los factores bióticos modifican el uso de agua y eficiencia de uso de agua, lo cual puede resultar en cambios en la dinámica estacional en los flujos de CO_2 cuando ecosistemas dominados por leñosas se convierten a ecosistemas dominados por pastos exóticos C_4.

High V_{cmax}, J_{max} and photosynthetic rates of Sonoran Desert species using nitrogen and specific leaf area traits as proxies in biochemical models

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ABSTRACT

Dryland ecosystems play an important role in the inter-annual variability of the global carbon cycle. Unfortunately, there is a paucity of data on biochemical (V_{cmax} and J_{max}) parameters from species in these ecosystems that limits our capacity to model photosynthesis across scales. We studied six dominant C_3 shrub and tree species from the Sonoran Desert with different leaf traits and phenological strategies. We characterized maximum carboxylation velocity (V_{cmax25}) and rate of electron transport (J_{max25}) and combinations of traits were used as proxies for parameterizing biochemical photosynthetic models for each species. We found high values of V_{cmax25} and J_{max25} in all species using a combination of leaf nitrogen content (N_{area}) and specific leaf area (SLA) as proxies. High values of V_{cmax25} were comparable to those reported for herbs and crop species and higher than those reported for shrubs and other functional types in world databases. We found that the high values of V_{cmax25} and J_{max25} are important in enhancing photosynthetic water and nitrogen-use efficiencies and may favor carbon gain during stressful conditions. The relationships derived here, provide a novel explanation to findings of high N_{area} in arid species and improve the parameterization of photosynthesis models in dryland ecosystems.

Keywords: V_{cmax}; J_{max}; Photosynthesis biochemical models; Leaf N_{area}; Dryland species; leaf traits; N_2-fixers

INTRODUCTION

Photosynthesis is a fundamental biological process that influences the global carbon cycle, because is the main flux responsible for the inter-annual variability of the global terrestrial CO_2 sink (Ahlstrom *et al.*, 2015). Photosynthesis rates are widely described mechanistically (or semi-mechanistically), from sub-cellular to global scales (Farquhar *et al.*, 2001), using principles of the biochemical model originally developed by Farquhar *et al.* (1980). This model integrates knowledge about photosynthesis biochemistry, stoichiometry, and the kinetic properties of key enzymes and processes. While most parameters of the model are fairly constant among C_3 species, day respiration (R_d), the carboxylation capacity (V_{cmax}), electron transport capacity (J_{max}), and rate of triose phosphate utilization (TPU) can vary substantially among species (von Caemmerer, 2000). Of these parameters, R_d tends to be correlated with V_{cmax}, and TPU is usually not limiting under natural conditions; therefore, V_{cmax} and J_{max} can be considered the key parameters of the model (von Caemmerer, 2000). It is known that V_{cmax} and J_{max} can vary up to two orders of magnitude among species (Kattge *et al.*, 2009; Wullschleger, 1993), making large-scale estimates of photosynthesis highly sensitive to these parameters (Bonan *et al.*, 2011). Thus, large scale modeling of photosynthesis requires accurate characterization of V_{cmax} and J_{max} across a wide range of species and functional types and vegetation types.

Current Earth System Models use various approaches to parameterize the variation in V_{cmax} and J_{max} across the biosphere. The most common is the plant functional type approach, where functional types are broad categories of plants, vegetation types, or biomes, which are considered to have similar physiology and therefore similar values of V_{cmax} and J_{max} (Rogers, 2014). In this way, the variation across plant diversity in these parameters can be simplified to a single value for each functional type. The limitation on how well each parameter represents this variation depends on the number of different functional types that are considered, as well as the extent to which these parameters represent the average or most probable local-to-global value (depending on the scale of the study). Other approaches include covariation of V_{cmax} and J_{max} with different leaf traits, or by integrating biogeochemical cycles and leaf traits (Rogers, 2014). Measurement of V_{cmax} and J_{max} is laborious and time consuming, leaving a paucity of data when compared to other plant traits such as specific leaf area or leaf nitrogen content (Kattge *et al*., 2009; Kattge *et al*., 2011; Walker *et al*., 2014). Consequently, limited information on V_{cmax} and J_{max} challenge our capacity to represent the "real" variation of these parameters within models and lead to biases in regional and global estimates of carbon fluxes and net ecosystem productivity (Kattge *et al*., 2009).

Historically, dryland ecosystems have been underrepresented over the wealth of information available for tropical and temperate ecosystems. Consequently, Vcmax and Jmax parameters for plant functional types from temperate and tropical forest ecosystems overwhelmingly dominate the Earth System Models (Rogers, 2014). Recent evidence has shown that dryland ecosystems have a dominant contribution to the trend and inter-annual variation in the land CO_2 sink (Ahlstrom *et al*., 2015; Biederman *et al*., in press; Fu *et al*., 2017; Poulter *et al*., 2014). Typical functional types inhabiting dryland ecosystems are very diverse, including sclerophyll and deciduous trees and shrubs, stem-succulent deciduous trees and shrubs, non-succulent trees, herbs, and winter and summer active annuals among others (Shreve 1942). However only a handful of published data can be attributed to dryland species and functional types in extant syntheses of V_{cmax} and J_{max} parameters. For example, Wullschleger (1993) report data for three species of desert annuals and perennials (2.8% of total species), Kattge *et al*. (2009) included four desert evergreen and deciduous shrubs and annuals (unknown proportion), and Walker *et al*. (2014) reported six sclerophyll and deciduous tree species from open savannas (1.6% of total). It is evident that proper parameterization of V_{cmax} and J_{max} is important for understanding photosynthesis and modeling productivity, thus, information on these parameters from dryland species and functional types are needed and arguably effectively improve photosynthesis modeling efforts at different scales.

Even though there are few data V_{cmax} and J_{max} for dryland species and functional types, other leaf traits (that are linked to V_{cmax} and J_{max}) have been sampled more extensively and could provide valuable information. For example, the leaf traits such as specific leaf area

(SLA), area-based nitrogen (N_{area}), and phosphorus (P_{area}) content, which are known to be correlated with V_{cmax} and J_{max} (Domingues *et al.*, 2010; Kattge *et al.*, 2009; Walker *et al.*, 2014). Global syntheses indicate that increasing aridity tends to increase N_{area}, P_{area} and light-saturated net photosynthesis rates (A_{area}), but increasing aridity decrease SLA and nitrogen content on a mass basis (N_{mass}) (Bagouse-Pinguet *et al.*, 2016; Maire *et al.*, 2015; Wright *et al.*, 2005). In general, these observations could imply that conserving strategies such as low gas exchange rates and resource use predominate in drylands, or that dryland species have consistently high values of V_{cmax} and J_{max}.

Our overarching goal is to provide baseline information for key parameters relevant for modeling photosynthesis and provide a discussion of the physiological implications for dryland species. Previous studies have highlighted the large variability of plant functional types and leaf traits in dryland species but photosynthesis models are poorly represented for many of these. In this study, we characterized V_{cmax} and J_{max} from A-Ci response curves, SLA and nitrogen content for six dominant species from the Sonoran Desert representing a wide range of functional types and leaf phenology. We asked the following questions: which are the magnitudes and ranges of V_{cmax} and J_{max} across dominant species of the Sonoran Desert? What are the best proxies based on leaf traits to represent V_{cmax} and J_{max}? What are the implications of the magnitudes and ranges of V_{cmax} and J_{max} for photosynthesis in drylands?.

MATERIALS AND METHODS

Study site and species sampled

All gas exchange measurements and leaf material were obtained from plants growing under natural conditions at La Colorada, Sonora, Mexico. Field campaigns were conducted at locations associated with two sites participating with the Mexican eddy covariance network: Mexflux (Vargas *et al.*, 2013, Hinojo-Hinojo *et al.*, 2016), and which are representative of the Sourtheastern part of the Sonoran Desert. Predominant vegetation is a Sonoran Desert scrub characteristic of the Plains of Sonora composed by deciduous shrubs and low stature deciduous and evergreen trees (Shreve & Wiggins, 1964; Brown *et al.*, 1994). Long term annual rainfall is 345 mm, 70 % of which occurs during the summer monsoon, and mean annual temperature is 20.7 ºC (station 26046 La Colorada, Servicio Meteorológico Nacional). Soils are calcic regosol and haplic phaeozem with loamy sand texture with 0.6-2.6 % organic matter content (Celaya *et al.*, 2015).

The plant species have a wide distribution and are abundant throughout the Sonoran Desert and across other North American dryland regions. Species sampled included the more abundant C_3 perennial species of the sites including: *Olneya tesota* and *Prosopis velutina*, (leguminous evergreen trees); *Mimosa laxiflora (*drought deciduous leguminous shrub); *Encelia farinosa* (drought deciduous forb). We included other stem-succulents deciduous species with leaf phenology restricted to the summer: *Ipomoea arborescens* (a tree); and *Jatropha cardiophylla* (a shrub), most of them not represented within global leaf traits databases (Kattge & Knorr (2007).

Measurement of gas exchange and related leaf traits

We conducted gas exchange measurements at the study sites during multiple field campaigns for five consecutive years. All measurements were performed during the summer rainy seasons, from July to early October, in sun-exposed mature leaves. Gas exchange measurements were performed for: a) response curves of leaf net photosynthesis to intercellular CO_2 concentrations (A-C_i curves); b) surveys for maximum light saturated net photosynthesis rates; c) measurements where we manipulated light conditions; and d) diurnal courses of gas exchange. Light saturated net photosynthesis (Amax) measurements, as well as step changes using neutral filters, were made using a LCi system (ADC Bioscientific Ltd., Herts, England), and A-Ci curves and Amax measurements with a Li-6400XT (LICOR Scientific, Lincoln, Nebraska, USA). Both systems gave comparable data across species. We aimed to derive V_{cmax} and J_{max} parameters for the biochemical model of photosynthesis (A-Ci curves), to have measurements of photosynthetic rates under a wide range of natural environmental conditions, and baseline information to validate photosynthesis models.

A-Ci curves were measured in six to eleven individuals of each species with a Li-6400XT (LI-COR, Lincoln, NE, USA) following Long & Bernacchi (2001). Measurements were performed first time in the morning under saturating direct sunlight (PAR, photosynthetically active radiation flux density >1500 µmol m^{-2} s^{-1}) during clear, cloudless days. Leaf temperature was maintained close to the initial value as much as possible, although this value may had differ in different measurements. A-Ci curves were fitted using the "bilinear" method (see Duursma, 2015) with R software package "plantecophys" to obtain biochemical parameters (V_{cmax}, J_{max}, R_d and TPU) for the photosynthesis model. Temperature response functions and values were used for other parameters in the model (Medlyn *et al*., 2002). R_d and TPU were used to fit V_{cmax} and J_{max} accurately. Only photosynthesis curves from unstressed leaves (with stomatal conductance above 0.05 mol m^{-2} s^{-1}, see Flexas *et al*., 2006) were considered in our analyses and modeling as quality control.

V_{cmax} and J_{max} values were scaled to values at 25 ºC (V_{cmax25} and J_{max25}) following equations from Medlyn et al. (2002) using two sets of temperature response parameters, those from Bernacchi *et al*. (2001, 2003) and Kattge & Knorr (2007). The main difference between the two temperature responses is that activity keeps increasing with temperature in Bernacchi's model (BRc), and growth temperature (mean air temperature of the previous month) affect the temperature at which peak activity occurs in Kattge & Knorr model (KKr).

To perform leaf area corrections of gas exchange data, all leaf samples were collected after measurements, sealed in bags with moist paper and stored in dark and cold conditions. In the lab, leaves were scanned and area measured using ImageJ software (version 1.50i, Wayne Rasband, National Institutes of Health, USA). Leaves were oven dried at 70 ºC for two days and weighted. Specific leaf area (SLA) was estimated as the fresh area to dry weight ratio in each leaf. Total nitrogen content per mass was measured either by the phenate method for Kjeldahl nitrogen with a rapid flow analyzer (RFA300, ALPKEM Corporation, Clackamas, Oregon, USA) or with an elemental analyzer (2400, PerkinElmer Inc., Waltham, MA, USA). Nitrogen content per mass was expressed as nitrogen per area (N_{area}) using the SLA of the same leaf.

Data analysis and photosynthesis modeling

Single trait or trait combinations were assessed to determine the best proxy for the estimated V_{cmax} and J_{max}. For single leaf traits (SLA or N_{area}), simple linear regressions were performed for each parameter (V_{cmax} or J_{max}). The best statistical model for trait combinations was identified using backward and forward stepwise regression according to the minimal Akaike information criterion index, as follows: for V_{cmax25} we included SLA, N_{area}, and SLAxN_{area} interaction effects, and for J_{max25} we included SLA, N_{area}, V_{cmax25} and all interaction terms. Statistical analyses were performed on JMP software (version 9.0.1, SAS Institute, 2010).

The net photosynthetic rate was modeled using the V_{cmax25} and J_{max25} parameters (Farquhar *et al.*, 1980) and SLA and N_{area}, using the "plantecophys" package (Duursma, 2015). The following approaches were used to parametrize V_{cmax25} and J_{max25} for the model: average values obtained by the A-Ci curves for each species (species mean), average values obtained using the best models and all available trait values per species (trait mean), and calculating a V_{cmax25} and J_{max25} for each leaf using the best models and the trait values for each leaf (trait based). The first two approaches were to assess how well photosynthesis can be modeled by using a fixed value for V_{cmax} and J_{max}, and the third approach to assess whether allowing those parameters to vary with leaf traits enhances the accuracy of the model. Leaf temperature, photosynthetic photon flux density, and intercellular CO_2 concentration of each gas exchange measurement were entered into the model. The performance of each approach was evaluated using the mean absolute deviation of modeled versus measured data.

Light response curves of net photosynthesis rate for leaves under typical field conditions were simulated to determine the performance of leaves with the obtained values of V_{cmax25} and J_{max25}. Simulations were made for hypothetical leaves with contrasting trait values and for *J. cardiophylla* using parameters derived in this study, and those for shrubs from Kattge and Knorr (2009), despite their poor representation of dryland species.

RESULTS

V_{cmax}, J_{max} and leaf traits

We obtained data for V_{cmax} and J_{max} from two to five curves for each species. These curves yielded V_{cmax25} values between 86 and 212 µmol m^{-2} s^{-1} with BRc temperature parameters and 93 - 248 µmol m^{-2} s^{-1} with KKr temperature parameters. For J_{max25}, we found values of 83 - 312 µmol m^{-2} s^{-1} and 105 - 350 µmol m^{-2} s^{-1}, with BRc and KKr parameters respectively. V_{cmax25} and J_{max25} were on average 1.2 times higher with KKr than with BRc temperature parameters. The species with the lowest mean values for V_{cmax25} and J_{max25} parameters was *O. tesota*, and the species with the highest values *P. velutina*, both leguminous trees (Table 1). Nonetheless, there was a wide variation between individual values within each species.

V_{cmax25} and J_{max25} were well correlated to single foliar traits (Table 2). N_{area} was correlated with both V_{cmax25} and J_{max25} and explained 36-64% of the variance, and SLA was inversely related to J_{max25} and accounted for 18-21% of the variance. The N_{area} to V_{cmax25} relationship had a higher intercept compared to studies published in a recent global synthesis (Figure 1).

Combinations of traits in statistical models increased the explained variance of V_{cmax25} obtained with BRc parameters (Table 3). Only in this case, the stepwise regression showed that including the effects of SLA and N_{area} produced the best model and explained 10 % more variance than N_{area} alone. N_{area} explained similar amounts of variation for other parameters (J_{max25} with BRc parameters, and V_{cmax} and J_{max} with KKr parameters) than the best models (Table 2 and 3). Using the best models, we obtained a species average V_{cmax25} and J_{max25}, using all the data on SLA and N_{area} that we had available over the years (Table 4), which we could consider a more representative species average, if we ignore potential error biases of the models.

Photosynthesis modeling

The comparison between the species mean, trait mean and trait-based approaches for modeling photosynthesis on each species is shown in Table 5. The error obtained in *M. laxiflora* and *P.*

velutina species was substantially lowered with the trait-based approach, although the three approaches had similar errors (< 1 µmol m^{-2} s^{-1} of difference on its mean absolute deviation) in the remaining species (Table 5). Additionally, we found that models using V_{cmax25} and J_{max25} obtained with BRc temperature parameters had a better fit and lower error across all species (Table 5).

Modeled data tracked closely to most of our gas exchange measurements. Error diminished when observations with leaf temperatures above 40 ºC were discarded. Nonetheless, data modeled with BRc gave lower mean absolute deviation than data modeled with KKr when all data was considered, but had similar mean absolute deviation when data with leaf temperatures above 40 ºC were discarded.

To assess the effect of the values of V_{cmax25}, J_{max25}, and V_{cmax25} per N_{area} generated in this study, we simulated net photosynthetic rates under typical conditions that leaves experience in the field (Figure 3). Using our parameters, net photosynthesis rates were about 7-10 µmol m^{-2} s^{-1} higher than those obtained with parameters from a global database (Kattge et al., 2009) for hypothetical leaves at full sunlight, high leaf temperatures and high, mid or low stomatal conductances (see Figure 3). For *J. cardiophylla* leaves, our parametrization gave similar photosynthesis rates to our actual measurements, and had rates 7-13 µmol m^{-2} s^{-1} above those obtained with parametrizations from the global data base (Figure 3). Additionally, photosynthetic rates with the parameters obtained in this study saturated at higher irradiances (Figure 3).

DISCUSSION

Global databases and large-scale flux modeling schemes still have poor representation of key biochemical (V_{cmax} and J_{max}) parameters of photosynthesis for dryland plant species and functional types (Kattge *et al.*, 2009; Rogers, 2014; Wullschleger, 1993; Walker *et al.*, 2014). In this study, we characterized V_{cmax25} and J_{max25} parameters for six dominant and widely distributed species in the Sonoran Desert, representing a wide range of functional types, leaf phenological strategies, and leaf traits. By generating this set of biochemical parameters for dominant plant species and determining the relationship between these parameters and leaf traits, we aimed to contribute to more accurate parameterizations for modeling carbon fluxes in dryland ecosystems. The high values reported here for V_{cmax25} and J_{max25} in the studied species and the relationship between these biochemical parameters and leaf traits may have important implications for carbon flux models and plant species fitness in dryland environments.

High V_{cmax} and J_{max} for dryland species

Global databases report that plants have V_{cmax25} in the range of 10-200 μmol m^{-2} s^{-1} (Kattge *et al*., 2009; Walker *et al*., 2014), and the bulk of the data values are in the range of 35-63 μmol m^{-2} s^{-1} (interquartile range from Walker *et al*., 2014). According to Kattge *et al*. (2009) shrubs have on average V_{cmax25} of 15-25 μmol m^{-2} s^{-1}, which is lower than tropical (30-40 μmol m^{-2} s^{-1}), and temperate trees (40-60 μmol m^{-2} s^{-1}), although herbs and crops are known to range higher from 80 to 100 μmol m^{-2} s^{-1}, or even higher (100 to 150 μmol m^{-2} s^{-1}) on few other temperate broadleaved, coniferous, shrubs, herbs and crops species (Kattge *et al*., 2009). V_{cmax25} for the species in our study had a range of 86-212 μmol m^{-2} s^{-1} (BRc) and 93-248 μmol m^{-2} s^{-1} (KKr) depending on the temperature response dataset. These ranges indicate that all species in the study had values on the high end of those reported in the literature regardless of the method we used to obtain parameters. Other dryland species are reported to have high V_{cmax25} values of 60-130 μmol m^{-2} s^{-1} (Cernusak *et al*., 2011; Domingues *et al*., 2010; Ellsworth *et al*., 2004; Hamerlynk *et al*., 2002, and data from Wullschleger, 1993). Also, we found that most of our J_{max25} data were above the global median (89 μmol m^{-2} s^{-1}, Walker *et al*., 2014) and can also be considered somewhat high, although the J_{max25}:V_{cmax25} ratios in the species we studied had a range of 0.9-2.1 with an average of 1.4 which is similar to that previously reported (von Cammerer, 2000). The evidence summarized here indicate that high values of V_{cmax25} and J_{max25} are likely widespread across plant species from drylands. More importantly, this indicates that current global databases and modeling schemes (Kattge *et al*., 2009; Rogers, 2014; Walker *et al.*, 2014) may be underestimating the V_{cmax25} and J_{max25} of species and functional types in dryland ecosystems.

High V_{cmax25} and J_{max25} of dryland species may result from high N_{area} values, as shown in our analysis (Table 2 and 3). In all six species studied, we found values of N_{area} above the global median of 1.6 g N m^{-2} (from 12860 samples in Kattge *et al.*, 2011) with some above the global 97.5% quantile of 3.6 g N m^{-2} (Kattge *et al.*, 2011). The observation that N_{area} tends to increase with aridity (Bagouse-Pinguet *et al.*, 2016; Maire *et al.*, 2015; Wright *et al.*, 2005) supports the possibility that high values of V_{cmax25} and J_{max25} are widespread among dryland species and functional types. Our study shows a direct link between high N_{area} and high values of V_{cmax25} and J_{max25} in dryland species, which has not been previously reported.

High values of N_{area} in dryland species have several possible causes. Despite low nitrogen in the soil, species from these biomes tend to have similar (Killingbeck & Withford, 1996) or higher (Skujins 1981; West 1981; West & Skujins, 1978) nitrogen content on a mass basis (N_{mass}) compared to species from other biomes, such that higher N_{area} values should arise from combinations of N_{mass} and SLA values. For example, *O. tesota* had a mean N_{mass} of 2-3%. In this case, high N_{area} occurred due to relatively low SLA (10-15 m^2 kg^{-1}). Species with high N_{mass} (3-5%) and low SLA (5-15 m^2 kg^{-1}) such as *P. velutina* and *E. farinosa* had the highest N_{area}; and species with high SLA (15-30 m^2 kg^{-1}) need very high N_{mass} (3-6%) to achieve high N_{area}, as observed for *I. arborescens*, *J. cardiophylla* and *M. laxiflora*. Other mechanisms that may enable species to have high N_{area} are: 1) high efficiency of nutrient resorption (Killingbeck, 1993); 2) association with nitrogen-fixing symbionts, as in the three leguminous species *M. laxiflora, O. tesota and P. velutina*, which may increase nitrogen availability during the growing season, unless water or phosphorus is limited in the soil; 3) a relationship between non-nitrogen-fixing and nitrogen-fixing plant species in fertility islands (Garcia-Moya, 1974; Pugnaire *et al.*, 1996), and 4) the observation that nitrogen is not necessarily limiting in dryland ecosystems (LeBauer & Treseder, 2008).

We found high V_{cmax25} per N_{area} in our study species compared to typical values for shrubs and other functional types from a global database in which dryland species are poorly represented (Figure 1, Kattge *et al*., 2009). The relationship between V_{cmax25} and N_{area} described here is comparable to those reported for herbaceous and crop species (Kattge *et al*., 2009). This may indicate that the species in our study have a higher proportion of nitrogen allocated to photosynthetic enzymes compared to shrubs and other functional types from other ecosystems, yet similar to herbs and crop species. Niinemets & Tenhunen (1997) estimated the proportion of leaf nitrogen invested in the Rubisco enzyme and bioenergetics, based on V_{cmax25}, J_{max25}, N_{mass}, SLA and other intrinsic properties of enzymes. Our calculations show that Sonoran Desert species invest on average 36-46% of nitrogen in Rubisco which is higher than the typical 10-30% reported for C_3 plants (Evans, 1989; Evans & Seeman, 1989; Ghimire *et al*., in press). Nitrogen allocated to bioenergetics is 4.9-5.8% which is in the range that has been reported for shrubs and deciduous trees (Ghimire *et al.*, in press). These observations further support the high allocation of nitrogen to photosynthetic enzymes in the species under study which also may be true for other dryland species.

Implications for photosynthesis and productivity

Our data support the hypothesis that high N_{area} in species from low-rainfall sites results in an important strategy for water conservation, allowing an increase in net photosynthesis for any given stomatal conductance compared to species from high-rainfall sites (Field et al., 1983, Wright et al., 2001), and may result in high photosynthetic rates (Castellanos *et al.,* 2010). In addition, we suggest that high values V_{cmax25} and J_{max25} is a fundamental characteristic of dryland species that can: 1) enhance photosynthetic nitrogen-use efficiency to values comparable to herbs and crops; 2) have very high photosynthetic rates during periods of high resource availability (soil water, light, air humidity, air CO_2 concentration) (see Figure 3 at C_i of 290 μmol mol^{-1}); 3) enhance the carbon gain after periods of unfavorable conditions, during the short periods between rainfall pulses or at the end of the rainy season, when high leaf temperatures and vapor pressure deficits limit stomatal conductance (see Figure 3 at C_i of 180 μmol mol^{-1}); and 4) serve as photoprotective mechanism, decreasing photosynthesis limitations under high light environments rising the light saturation level of photosynthesis.

V_{cmax} and J_{max} derived here for dryland species may have important consequences for estimates of ecosystem production. Studies report that 70 - 90 % of annual net ecosystem productivity (NEP) in dryland ecosystems occur during relatively short periods when most of the annual rainfall is registered (Hinojo-Hinojo et al., 2016, Biederman et al. in press). Our V_{cmax25} and J_{max25} data were obtained during these periods. Dominant species have strategies which maximize the time when non-limiting conditions and the highest photosynthetic rates occur, by having deep roots and water redistribution (*O. tesota* and *P. velutina*), nitrogen-fixing (leguminous species), facilitation (*O. tesota* and *P. velutina*), storing water and nutrients in succulent stems or tuberous roots (*I. arborescens* and *J. cardiophylla*), and deciduous phenology (*I. arborescens*, *J. cardiophylla*, *M. laxiflora* and *E. farinosa*). Failing to incorporate high values of V_{cmax} and J_{max} for species with these strategies, will lead to important underestimation of dryland fluxes in large-scale Earth System Models and the global carbon cycle.

Calculation of V_{cmax} and J_{max} and limitations

V_{cmax25} and J_{max25} derived from a single-value average or leaf-specific values for SLA and N_{area} both described the net photosynthesis of each species. Since actual values for each leaf can be highly variable, estimating biochemical parameters for each leaf using leaf traits can result in errors which may be comparable to using a single average value. The ample range of biochemical and leaf N_{area} and SLA traits in our study may allow the calculation of V_{cmax25} and J_{max25} for a wider range of species in warm drylands communities.

Temperature response parameters (such as BRc and KKr) for crops and temperate species have been derived from measurements spanning 5 to 40 ºC leaf temperatures, as most photosynthesis rates are assumed to occur within this range (Bernnacchi *et al.*, 2001 and 2003; Kattge & Knorr, 2007; Medlyn *et al.*, 2002; Wohlfahrt *et al.*, 1999). The models in our study could not reproduce accurately photosynthesis rates at leaf temperatures above 40 ºC, although models using BRc parameters performed better than KKr at leaf temperatures above 40ºC (Table 5). As BRc parameters do not have a peak activity, this suggest that peak activity of

V_{cmax} and J_{max} occurred at higher temperatures than those assumed by functions for the acclimation to growth temperature in KKr parametrization. Given that leaf temperatures higher than 40 ºC may be common in dryland species and in our data, development of approaches that extend temperature response functions to higher temperatures should improve the performance of photosynthesis models in drylands.

Our approach may have had additional limitations. Mesophyll conductance and TPU can limit photosynthesis rates under drought conditions (Díaz-Espejo *et al.*, 2006; Flexas *et al.*, 2006). We did not include mesophyll conductance nor TPU limitation in our models due to the lack of widely tested parameters and functions on its response to environmental conditions, especially temperature. Also, increased availability of leaf phosphorus content data should help to further constrain estimates of V_{cmax25} and J_{max25} with leaf traits (Domingues *et al.*, 2010; Walker *et al.*, 2014). Lastly, simulating photosynthesis rates above 40 µmol m-2 s-1 was difficult, even using very high values of V_{cmax25} and J_{max25}, but photosynthesis rates that high have been reported for desert annuals and shrubs species (Ehleringer & Cook, 1984; Mooney *et al.*, 1976; Werk *et al.*, 1983). More data of V_{cmax25} and J_{max25}, and information of mesophyll conductance, TPU and phosphorus content for species and functional types from dryland ecosystems will increase their representation in global databases and improve modeling schemes for photosynthesis to better assess the role of drylands in the global carbon and water cycles.

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FIGURES:

Figure 1: Comparison of the relationship between V_{cmax25} and N_{area} found using Bernacchi's (BRc) temperature response parameters (thick solid lines) and those of Kattge and Knorr (KKr) (thick dashed line). Thin lines show N_{area} and V_{cmax25} for shrub and crop functional types, both from Kattge et al. (2009). Grey areas represent 95% confidence intervals.

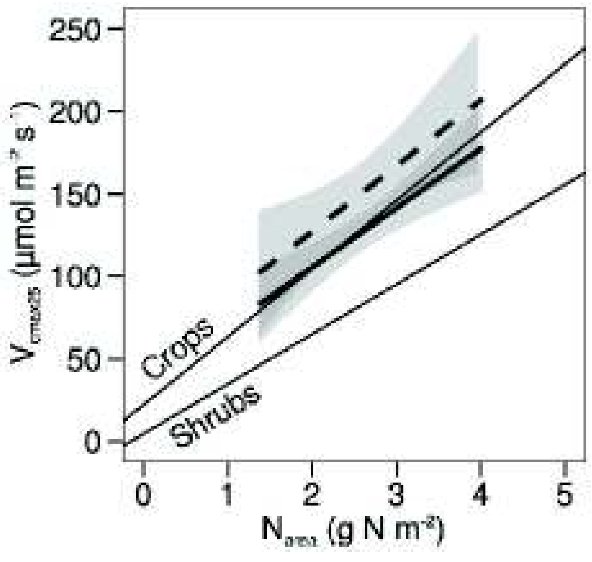


Figure 2: Modeled versus measured net photosynthesis rate for all available data and excluding data with leaf temperature > 40 ºC. Solid line corresponds to the 1:1 line. Photosynthesis rates were modeled using V_{cmax25} and J_{max25} for each leaf derived from our best models and trait values for each leaf (trait-based approach).

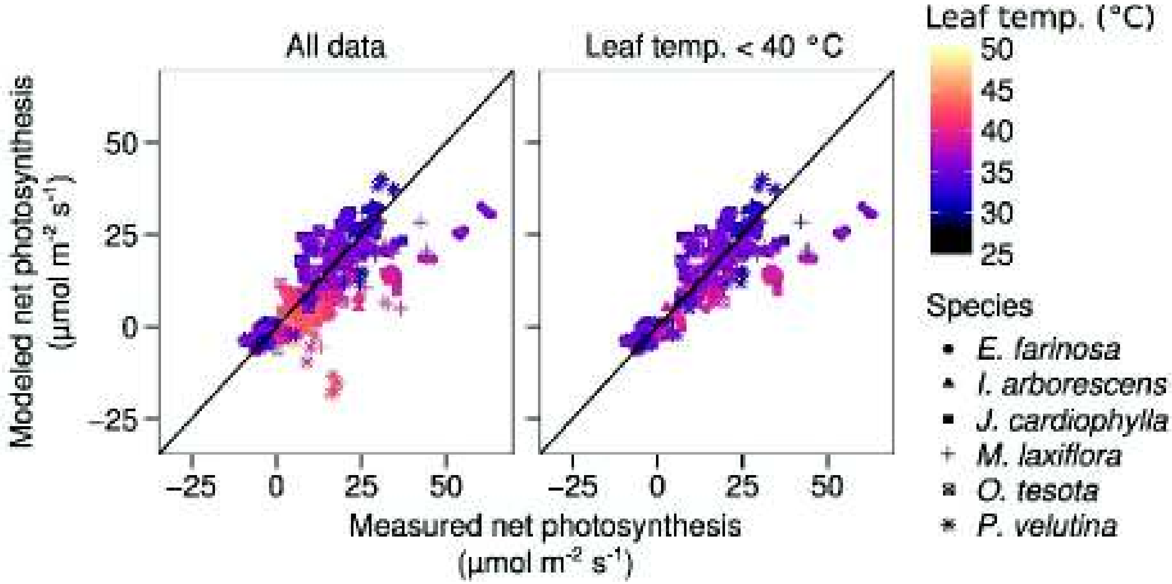
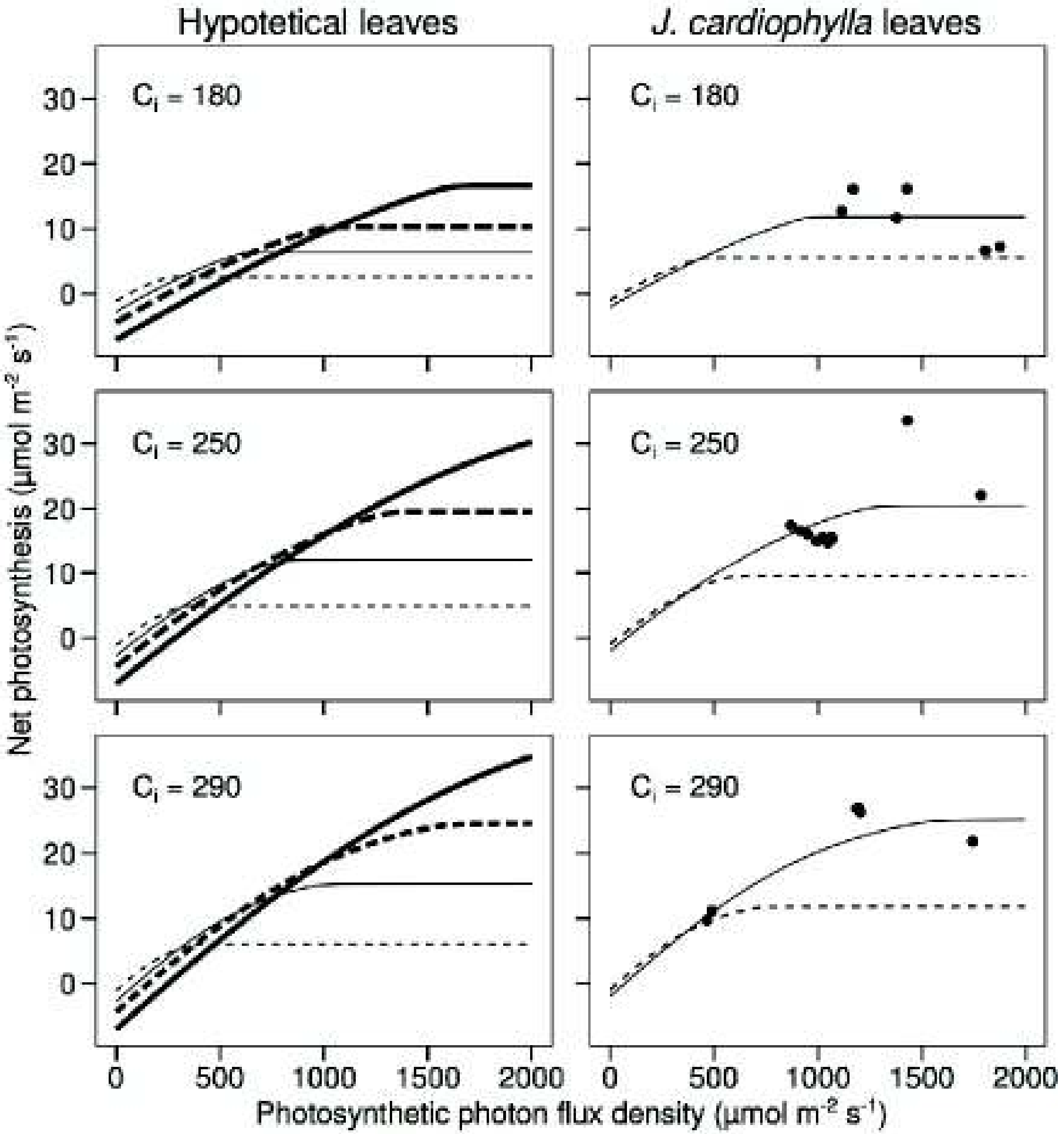


Figure 3: Comparison of simulated light response curves of net photosynthesis obtained using the parameterizations derived in this study for Sonoran Desert species (solid lines) and parametrizations for the shrub functional type from Kattge et al. (2009) (dashed lines). Simulations were performed for hypothetical leaves with high N_{area} (4.5 g N m^{-2}, thick lines) and low N_{area} (1 g N m^{-2}, thin lines) N_{area} and for *J. cardiophylla* leaves, under high leaf temperatures (37 ºC) and acclimated to typical July temperatures of our study locations. We used three levels of intercellular CO_2 concentration (C_i) corresponding to typical values found at low and high stomatal conductance: 180 µmol mol^{-1} for stomatal conductances of 0.1-0.2 mol m^{-2} s^{-1}, and 290 µmol mol^{-1} for stomatal conductances of 0.6-1 mol m^{-2} s^{-1}, respectively). Also included was a typical intercellular CO_2 concentration for C_3 species (250 µmol mol^{-1}) which is about the mean value of our data (Lambers et al. 2008). Data measured under similar conditions (dots) were included for *J. cardiophylla* leaves.


Hypotetical leaves
J. cardiophylla leaves
C_i = 180
C_i = 250
C_i = 290
Net photosynthesis (μmol m^{-2} s^{-1})
Photosynthetic photon flux density (μmol m^{-2} s^{-1})
0
10
20
30
0
500
1000
1500
2000

TABLES:

Table 1: V_{cmax25} and J_{max25} derived from response curves of net photosynthesis to intercellular CO_2 concentration. Values obtained with Bernacchi (BRc) and Kattge & Knorr (KKr) parameterizations are presented. n refers to the number of curves from which V_{cmax25} and J_{max25} were derived.

	V_{cmax25}			J_{max25}		
	n	Mean ± SD (μmol m^{2} s^{-1})		n	Mean ± SD (μmol m^{2}s^{-1})	
Species		Bernacchi	Kattge & Knorr		Bernacchi	Kattge & Knorr
Encelia farinosa	4	116 ± 16	156 ± 47	4	152 ± 45	197 ± 31
Ipomoea arborescens	5	112 ± 14	128 ± 19	4	145 ± 26	171 ± 21
Jatropha cardiophylla	3	115 ± 16	132 ± 10	5	138 ± 57	180 ± 31
Mimosa laxiflora	2	126 ± 29	188 ± 52	3	166 ± 61	176 ± 65
Olneya tesota	3	98 ± 11	108 ± 13	4	114 ± 17	124 ± 20
Prosopis velutina	3	190 ± 36	214 ± 50	4	268 ± 53	303 ± 49

Table 2: Results of linear regression analysis between parameters V_{cmax25} and J_{max25} and the leaf traits SLA and N_{area}, obtained with the two sets of temperature response parameters used (Bernacchi and Kattge & Knorr).

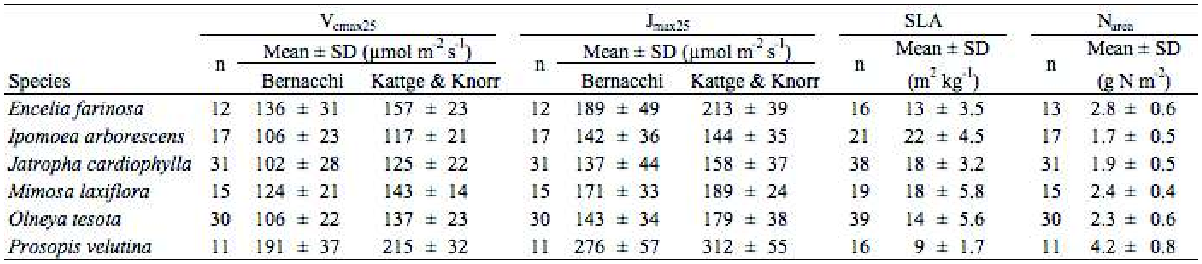
Biochemical parameter	SLA				N_{area}			
	Intercept	Slope	R^2	n	Intercept	Slope	R^2	n
Bernacchi								
V_{cmax25}	149.18*	-1.71	0.06	20	33.65	35.93*	0.55	19
J_{max25}	263.70*	-6.80*	0.21	24	5.13	59.05*	0.47	24
Kattge & Knorr								
V_{cmax25}	197.70*	-3.26	0.12	20	47.58	39.79*	0.35	19
J_{max25}	285.57*	-6.28*	0.18	24	20.87	64.25*	0.56	24

*$P < 0.05$

Table 3: Best models for describing the parameters V_{cmax25} and J_{max25} using combinations of leaf traits and two sets of temperature response parameters (Bernacchi and Kattge & Knorr). SE is the standard error.

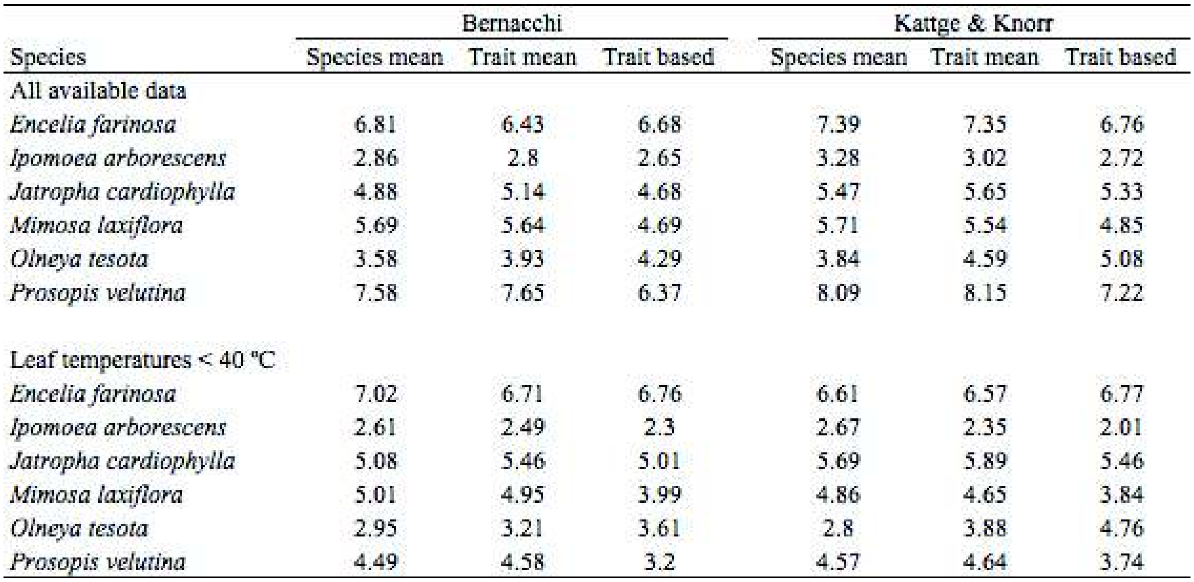
Biochemical parameter	Best model effects	Coefficient	SE	t	P	R^2
Bernacchi						
V_{cmax25}	Intercept	-56.28	46.58	-1.21	0.2445	0.65
	SLA	3.28	1.55	2.12	0.0503	
	N_{area}	51.92	10.43	4.98	0.0001	
J_{max25}	Intercept	-22.00	45.04	-0.49	0.6327	0.58
	V_{cmax25}	1.55	0.35	4.38	0.0006	
Kattge & Knorr						
V_{cmax25}	Intercept	47.58	34.70	1.37	0.1882	0.35
	N_{area}	39.79	13.07	3.04	0.0073	
J_{max25}	Intercept	-7.27	49.80	-0.15	0.8862	0.57
	N_{area}	39.28	19.10	2.06	0.0603	
	V_{cmax25}	0.71	0.31	2.32	0.0376	

Table 4: Species average V_{cmax25} and J_{max25} derived from using the best models and all available leaf trait values and two sets of temperature response parameters (Bernacchi and Kattge & Knorr). SD is the standard deviation.



	V_{cmax25}			J_{max25}			SLA		N_{area}	
	n	Mean ± SD ($\mu mol\ m^{-2}\ s^{-1}$)		n	Mean ± SD ($\mu mol\ m^{-2}\ s^{-1}$)		n	Mean ± SD ($m^2\ kg^{-1}$)	n	Mean ± SD ($g\ N\ m^{-2}$)
Species		Bernacchi	Kattge & Knorr		Bernacchi	Kattge & Knorr				
Encelia farinosa	12	136 ± 31	157 ± 23	12	189 ± 49	213 ± 39	16	13 ± 3.5	13	2.8 ± 0.6
Ipomoea arborescens	17	106 ± 23	117 ± 21	17	142 ± 36	144 ± 35	21	22 ± 4.5	17	1.7 ± 0.5
Jatropha cardiophylla	31	102 ± 28	125 ± 22	31	137 ± 44	158 ± 37	38	18 ± 3.2	31	1.9 ± 0.5
Mimosa laxiflora	15	124 ± 21	143 ± 14	15	171 ± 33	189 ± 24	19	18 ± 5.8	15	2.4 ± 0.4
Olneya tesota	30	106 ± 22	137 ± 23	30	143 ± 34	179 ± 38	39	14 ± 5.6	30	2.3 ± 0.6
Prosopis velutina	11	191 ± 37	215 ± 32	11	276 ± 57	312 ± 55	16	9 ± 1.7	11	4.2 ± 0.8

Table 5: Mean absolute deviation of modeled versus measured net photosynthesis rates using three approaches for obtaining V_{cmax25} and J_{max25} and two temperature response parameters datasets (BRc and KKr).



	Bernacchi			Kattge & Knorr		
Species	Species mean	Trait mean	Trait based	Species mean	Trait mean	Trait based
All available data						
Encelia farinosa	6.81	6.43	6.68	7.39	7.35	6.76
Ipomoea arborescens	2.86	2.8	2.65	3.28	3.02	2.72
Jatropha cardiophylla	4.88	5.14	4.68	5.47	5.65	5.33
Mimosa laxiflora	5.69	5.64	4.69	5.71	5.54	4.85
Olneya tesota	3.58	3.93	4.29	3.84	4.59	5.08
Prosopis velutina	7.58	7.65	6.37	8.09	8.15	7.22
Leaf temperatures < 40 °C						
Encelia farinosa	7.02	6.71	6.76	6.61	6.57	6.77
Ipomoea arborescens	2.61	2.49	2.3	2.67	2.35	2.01
Jatropha cardiophylla	5.08	5.46	5.01	5.69	5.89	5.46
Mimosa laxiflora	5.01	4.95	3.99	4.86	4.65	3.84
Olneya tesota	2.95	3.21	3.61	2.8	3.88	4.76
Prosopis velutina	4.49	4.58	3.2	4.57	4.64	3.74

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 CO_2 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 years ago within the Sonoran Desert. The savanna was a net carbon sink (NEE -230 g C m^{-2} yr^{-1}) both during a year with above average, as well as during one with below average precipitation (NEE -84 g C m^{-2} yr^{-1}). 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 H_2O $month^{-1}$ 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.

KEYWORDS:

Eddy covariance; Net ecosystem exchange; Evapotranspiration; *Cenchrus ciliaris;* Arid lands transformation

INTRODUCTION

Aridland ecosystems represent close to fifty percent 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 semi-arid lands worldwide (Hassan et al. 2005; Lal 2001), following rangeland degradation for cattle production (Lambin et al. 2003; Walker 1979). Since the middle of the last 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 (Belnap et al., 2012; Cox et al., 1988; Williams & Baruch, 2000;). Understanding what governs the structure and function of these novel, wide-spread ecosystems is a key management concern.

Buffelgrass (*Cenchrus ciliaris* L.) was one of those grasses successfully introduced worldwide (Cox et al. 1988; Herbel 1979). 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 three decades, especially in Australia and North America, where expansive Buffelgrass savannas are now common (Arriaga et al. 2004; Marshall et al. 2012; Miller et al. 2010). In northwestern Mexico alone, it is estimated that between one and 1.8 million hectares of historically arid / semi-arid shrublands and tropical deciduous forests has been transformed to Buffelgrass savanna (Bravo-Peña & Castellanos 2013, Castellanos et al. 2002; Búrquez-Montijo et al. 1998).

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., 2011). Regarding this, studies have described how buffelgrass accelerates the fire—return intervals (Butler and Fairfax 2003; D'Antonio and Vitousek 1992; 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 less than 465, and up to 3,045 kg ha^{-1} (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, and seedling establishment success, nutrient and water availability and use, and microclimatic conditions (Castellanos et al. 2002; Martín et al. 1999; Celaya-Michel & Castellanos 2015). While biomass production is important in the context of range management and forage production, other production estimates such as whole ecosystem carbon dioxide flux and water use efficiency (the amount of carbon fixed per unit of water loss through evapotranspiration) can provide insight into ecosystem function. In Northwestern Mexico and Southwestern US, whole ecosystem fluxes may be influenced by its bi-seasonal 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 carbon (CO_2), water (H_2O), and energy fluxes between the land-surface and the surrounding atmosphere (Baldocchi, 2003) and has been used at multiple ecosystems across the world (Baldocchi et al. 2001). In this study, we document carbon (CO_2 net ecosystem exchange, gross primary productivity and ecosystem respiration) and water (evapotranspiration) flux dynamics of an exotic Buffelgrass savanna established through the transformation of an arid shrubland within the Sonoran Desert. We used eddy covariance (EC) technique to answer the following questions: 1) What are the dynamics of carbon (CO_2) and water fluxes in an exotic Buffelgrass savanna?; 2) How does the bi-seasonal rainfall pattern from the Sonoran Desert region drive those CO_2 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 two and a half years 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 eddy covariance network (MexFlux; Vargas et al. 2013) within a plain that extend 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, approximately 10 km). Summer monsoon and fall account for 70% of annual rainfall and other 20% from December to March (Servicio Metereológico 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 years ago (Figure 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*, *Cathestecum brevifolium*), 32% of exotic Buffelgrass (*Cenchrus 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. While extremely variable, mean vegetation height was ~ 0.78 m.

Measurement of CO_2, water fluxes and other environmental variables

A six meter high Eddy Covariance (EC) tower was installed at the site, and CO_2 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 one kilometer 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 3D sonic anemometer (CSAT-3, Campbell Sci.), a CO_2 and H_2O infrared gas analyzer (LI-7500, LICOR Biosciences, Lincoln NE, USA) at the top (at 6 m height), both oriented to the direction of the prevailing winds (Figure 1). The top of the tower is instrumented with relative humidity and temperature sensors (HMP45C, Vaisala), and net radiometer (NR-Lite, Kipp and Zonen). Near the base and at 10 cm depth, four soil heat flux plates (HFP01-L50, Campbell Sci.) and two thermocouples (TCAV, Campbell Sci.), as well as two moisture sensors (CS-616, Campbell Sci.) were distributed under inter-canopy and Buffelgrass soil conditions. Precipitation was measured with a TR-525USW-R3 (Texas Electronics) rain gauge. Sonic anemometer and gas analyzer data were recorded with a 10 Hz frequency; relative humidity, air temperature, and net radiometer every minute, while soil temperature, heat flux and moisture, and precipitation every 15 minutes using a CR3000 datalogger (Campbell Sci., Logan UT, USA).

With the fast frequency data, fluxes of net ecosystem exchange (NEE), evapotranspiration (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, 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), humidity effects on sonic temperature (Van Dijk et al. 2004) and compensated for air density fluctuations (Webb et al. 1980). The storage term for the NEE was determined only with CO_2 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 were 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 of the study period on 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. Net ecosystem exchange (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 CO_2 and H_2O fluxes from the atmosphere to the ecosystem (carbon uptake) as negative values, while fluxes from the ecosystem towards the atmosphere (carbon losses) as positive values. This way, GPP will appear always 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 was obtained for 25 pixels (≈1.5 km^2) 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 more than sixty percent of its individuals had some leaves present.

Data analysis

Thirty-minute average CO_2 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 net ecosystem exchange (NEE) to evapotranspiration (ET) ratio:

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

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 nine months with no measurable rainfall (from September 2010 - June 2011). A large percentage of annual rainfall, 72 to 86 %, was related to the summer monsoon (July to September; Figure 2d), which varied from 190 - 200 mm in 2011 and 2013, and 364 mm in 2012.

The annual course of meteorological conditions is illustrated with data from 2012 (Figure 2a-d). The highest air temperatures (mean and maximum temperature around 30ºC and 37ºC, respectively) of the year occurred in May and June and were associated with the fore-summer dry period prior to 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 ºC and maximum vapor pressure deficit of 2.7 kPa).

The annual course of daily carbon fluxes is also illustrated with data from 2012 (Figure 2f). During summer, a peak of net C efflux occurred with the start of the summer rains and initial canopy development which lasted around two weeks. After this peak, NEE was mostly negative throughout the summer but varying from +3 to -6 g C m^{-2} day^{-1} with both positive and negative peaks corresponding to changes in soil water content (Figure 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 m^{-2} day^{-1}, respectively). During the rest of the year NEE was relatively low with an interquartile range of -0.1 to -0.6 g C m^{-2} day^{-1} while soil water was generally below 6%, although net carbon uptake of up to -1.5 g C m^{-2} day^{-1} 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 *Olneya tesota*, *Prosopis velutina* and *Phaulothamnus 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 to those of the summer months (Figure 3). However, mean daily values of R_{eco} and GPP from winter were around eleven and five times lower than those from the summer. Instantaneous nighttime NEE during winter, and also in spring and fall seasons, was minimal (around 0.5 μmol CO_2 m^{-2} s^{-1}) as compared to summer (around 5 μmol CO_2 m^{-2} s^{-1}), which allowed that carbon assimilation during the day (maximum NEE values of 1.5 to 5 μmol CO_2 m^{-2} s^{-1}) resulted in a daily net sink (Figure 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 g C m^{-2} each month between 2011, 2012, and 2013. The interannual variation in monthly fluxes was up to 2-fold in R_{eco}, 5-fold in GPP, and 3-fold in ET, which also resulted in variation in WUE_e. Monthly ET explains 73 to 87% of within-season and interannual variability in carbon fluxes (Figure 5). The regression of ET and NEE indicates that on average 50 mm $month^{-1}$ of ET were needed to shift the ecosystem from carbon source to sink during summer months (Figure 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 the years 2012 and 2013, with annual NEE values of -230 and -84 g C m^{-2} yr^{-1}. 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, specially for NEE contributing collectively with 38-48% (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 the range reported (0.55 to 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 carbon dioxide 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 (Hussain et al., 2015; Lalrammawia & Paliwal, 2010), 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; 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 (Bell et al. 2012; Scott et al. 2004; Scott et al. 2009). Annual NEE in a wet year at our savanna study site was about 2-5 times higher than those reported for North American deserts (Bell et al., 2012; Wohlfahrt et al. 2008), and within the high-end of the range reported for semi-arid grasslands in southwestern US (100 to -300 g C m^{-2} yr^{-1}, Scott et al., 2009; Scott et al., 2010; Scott et al., 2014; Wagle et al., 2015; Xu & Baldocchi, 2004). Recent studies have shown that arid ecosystems can have important magnitudes of carbon fluxes at local (e.g. Wohlfahrt et al., 2008; Luo et al., 2007; 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.

The highest daily carbon and ET fluxes in the year were found during the summer monsoon season, thereby 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 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 to some of the summer months (Figure 2). Such variability in carbon fluxes highlights the importance of the bi-seasonal 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 *Olneya tesota* and *Prosopis velutina*, which retain their leaves most of the year (Castellanos et al., 2010), and other oportunistic shrubs like *Phaulothamnus spinescens*, and *Encelia 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 (Bell et al. 2012; Hastings et al. 2005). 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 Sonoran Desert and subtropical origin to extend their activity through the winter season. Buffelgrass is known to be limited by low temperatures, especially below 5 ºC (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 US (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 & 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; Verduzco et al., 2015). When compared to that of summer, R_{eco} was minimal for most of fall to spring seasons (Figure 3 & 4), limited by shallow soil moisture availability (Xu et al., 2004). A small R_{eco} allowed higher assimilation and GPP values of 0.7 to 1.3 g C m^{-2} day^{-1} (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 to other seasons may be associated with the vapor pressure deficits (up to 6 kPa) and air temperature (mean max 35 ºC) which occur during this season and the highest amount of leaf of the year (Figure 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 (Figure 2). In contrast, other studies in seasonal ecosystems have found higher WUE_e during summer monsoon, as no net carbon uptake was found during the rest of the seasons (Pérez-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 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, sources of natural medicines, etc. (Havstad et al., 2007). Nonetheless, land use intensification can compromise a variety of goods and services, especially those that depends on biodiversity (Alkemade et al., 2012; Fooley et al., 2005). 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 buffegrass savannas can be substantial carbon sinks.

Our study site has comparable structural vegetation characteristics to other intentionally established or invaded buffelgrass dominated ecosystem which has been studied within the Sonoran Desert region (e.g. Abella et al., 2012; Celaya-Michel et al., 2015; de la Barrera, 2008; Franklin & Molina-Freaner, 2010). However, most of the established buffegrass savannas are found to be degraded or in bad condition (Castellanos et al., 2002). Management decisions driven by climatic variability and poor socio-economical 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 (Butler & Fairfax, 2003; D'Antonio and Vitousek 1992; McDonald & 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 which may promote the net carbon uptake within buffelgrass dominated ecosystems. An important amount of buffelgrass foliage need 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 (Figure 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 fall, winter and spring seasons.

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FIGURES

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

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 NDVI; and f) daily Net ecosystem exchange (NEE, black circles), ecosystem respiration (R_{eco}, open circles), and gross primary productivity (GPP, grey circles) in the Buffelgrass savanna during 2011 - 2012. Vertical doted lines mark the different seasons. Gray areas indicate approximate dates where buffelgrass had green leaves.

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

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

Figure 5. Linear relationships of accumulated monthly NEE, R_{eco} and ET for summer months (July, August and September) from three different years (2011 - 2013).

FIGURE 1.

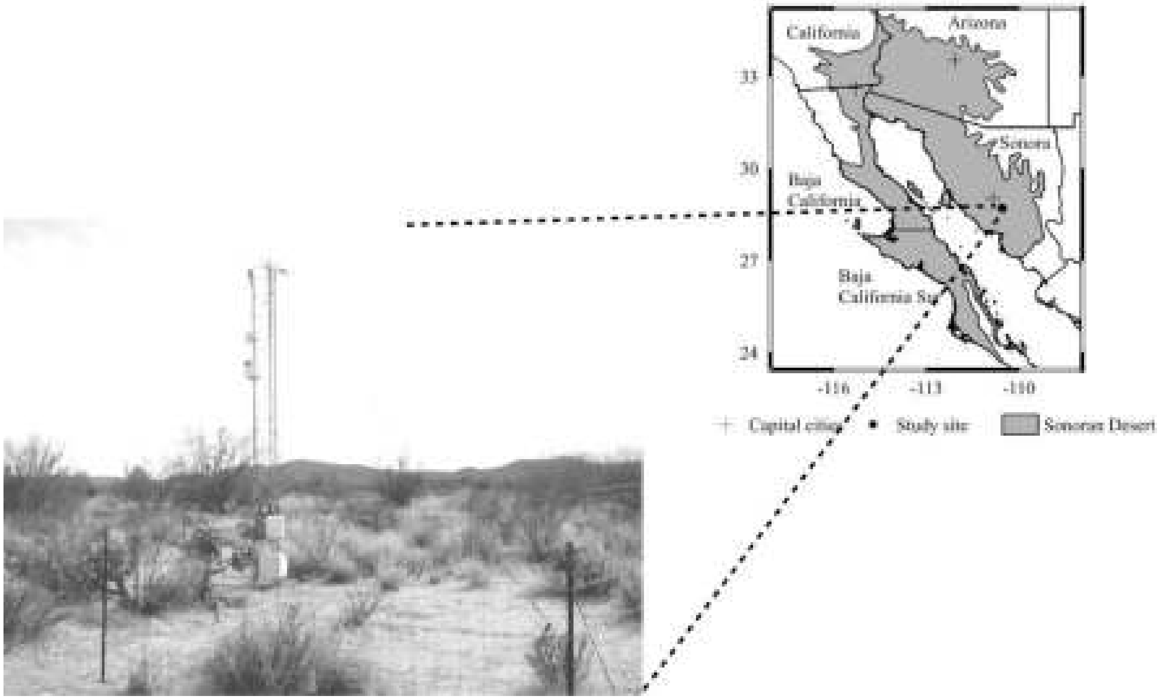
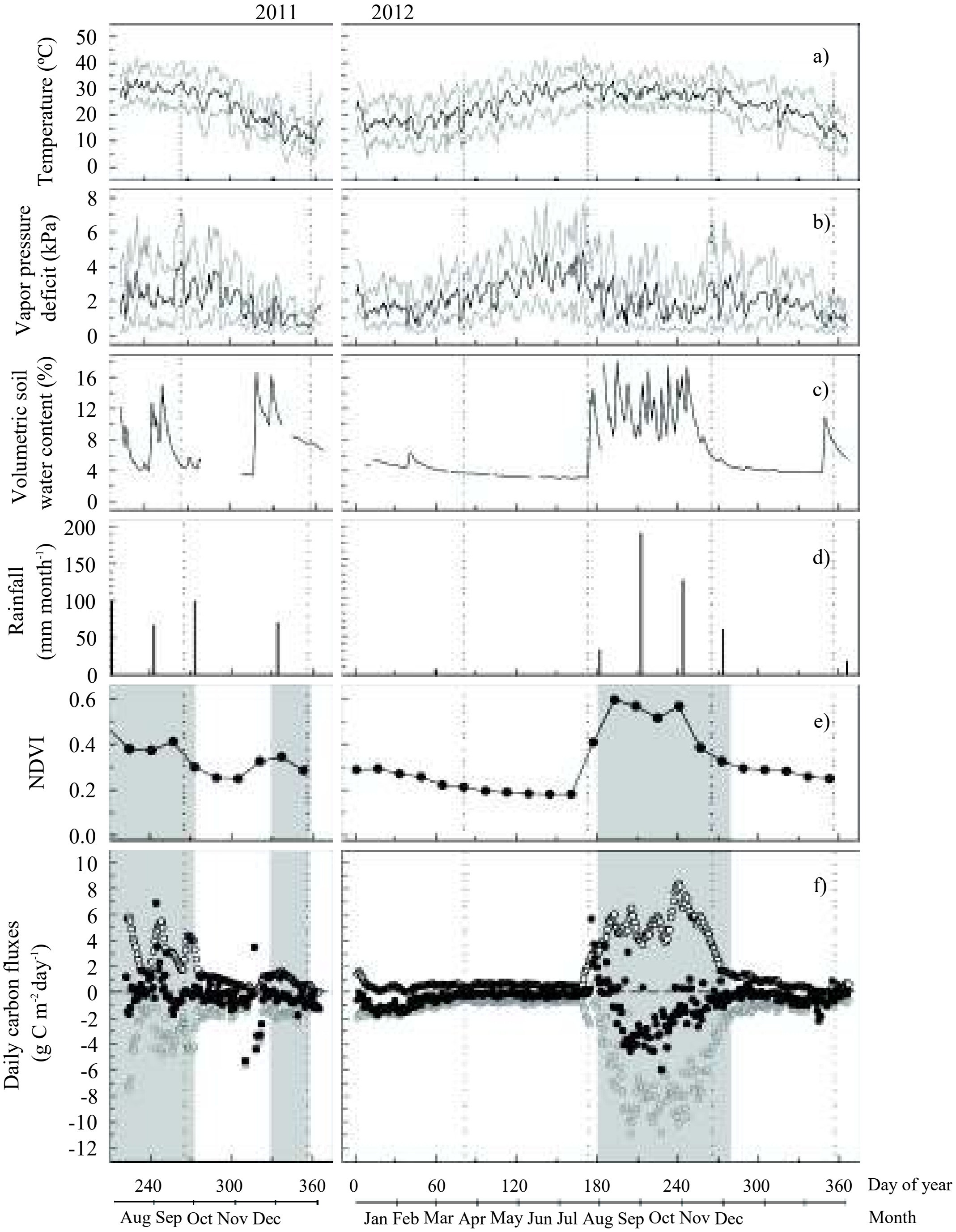
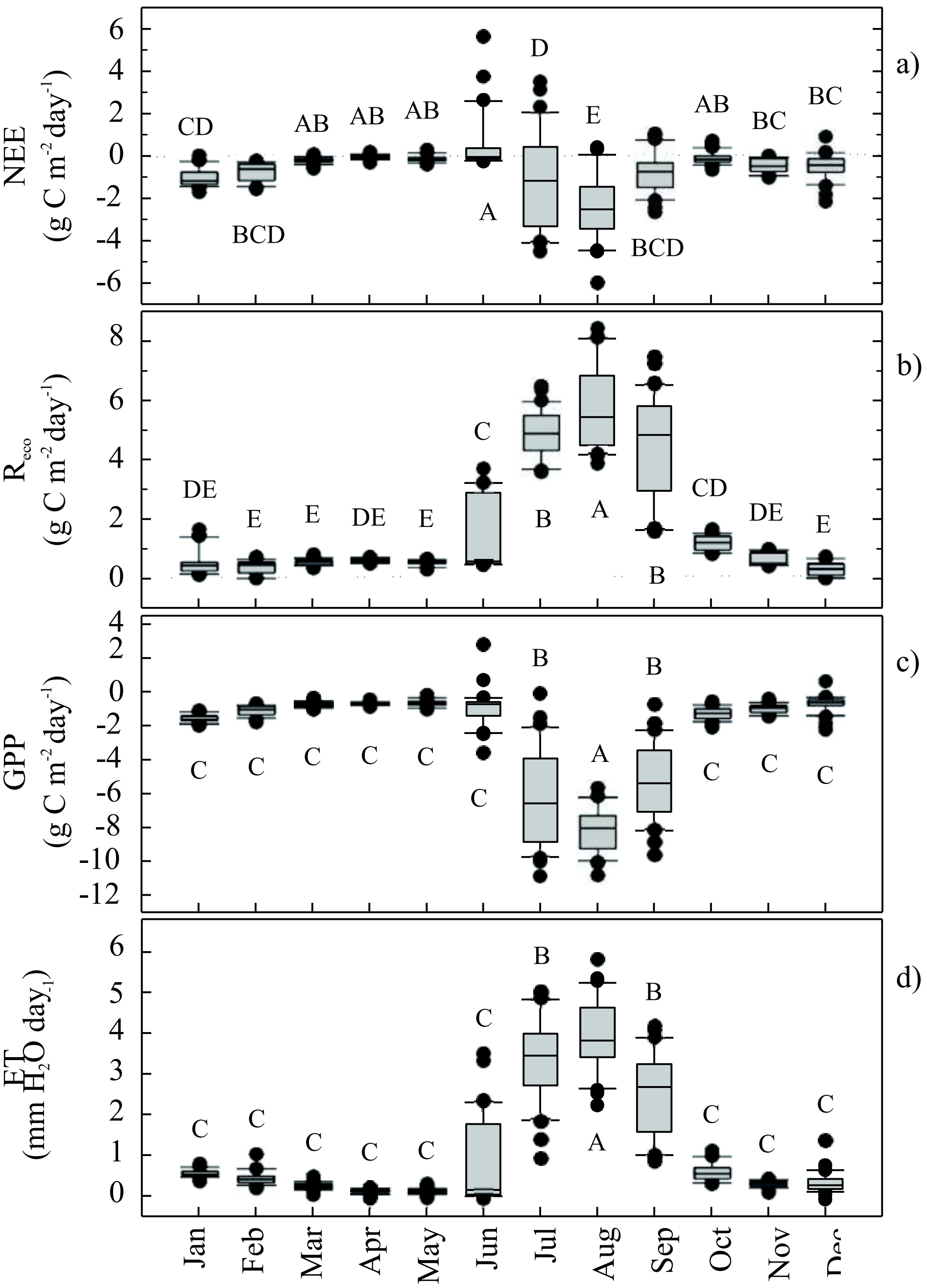

California
Arizona
Sonora
Baja California
Baja California Sur
33
30
27
24
-116
-113
-110
Capital cities
Study site
Sonoran Desert

Figure 2.



2011
2012
Temperature (ºC)
50
40
30
20
10
0
a)
Vapor pressure deficit (kPa)
8
6
4
2
0
b)
Volumetric soil water content (%)
16
12
8
4
0
c)
Rainfall (mm month-1)
200
150
100
50
0
d)
NDVI
0.6
0.4
0.2
0.0
e)
Daily carbon fluxes (g C m-2day-1)
10
8
6
4
2
0
-2
-4
-6
-8
-10
-12
f)
240
300
360
0
60
120
180
240
300
360
Day of year
Aug Sep Oct Nov Dec
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Month

Figure 3.



a)
NEE (g C m-2 day-1)
6
4
2
0
-2
-4
-6
CD
BCD
AB
AB
AB
A
D
E
BCD
AB
BC
BC
b)
Reco (g C m-2 day-1)
8
6
4
2
0
DE
E
E
DE
E
C
B
A
B
CD
DE
E
c)
GPP (g C m-2 day-1)
4
2
0
-2
-4
-6
-8
-10
-12
C
C
C
C
C
C
B
A
B
C
C
C
d)
ET (mm H2O day-1)
6
5
4
3
2
1
0
C
C
C
C
C
C
B
A
B
C
C
C
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figura 4.

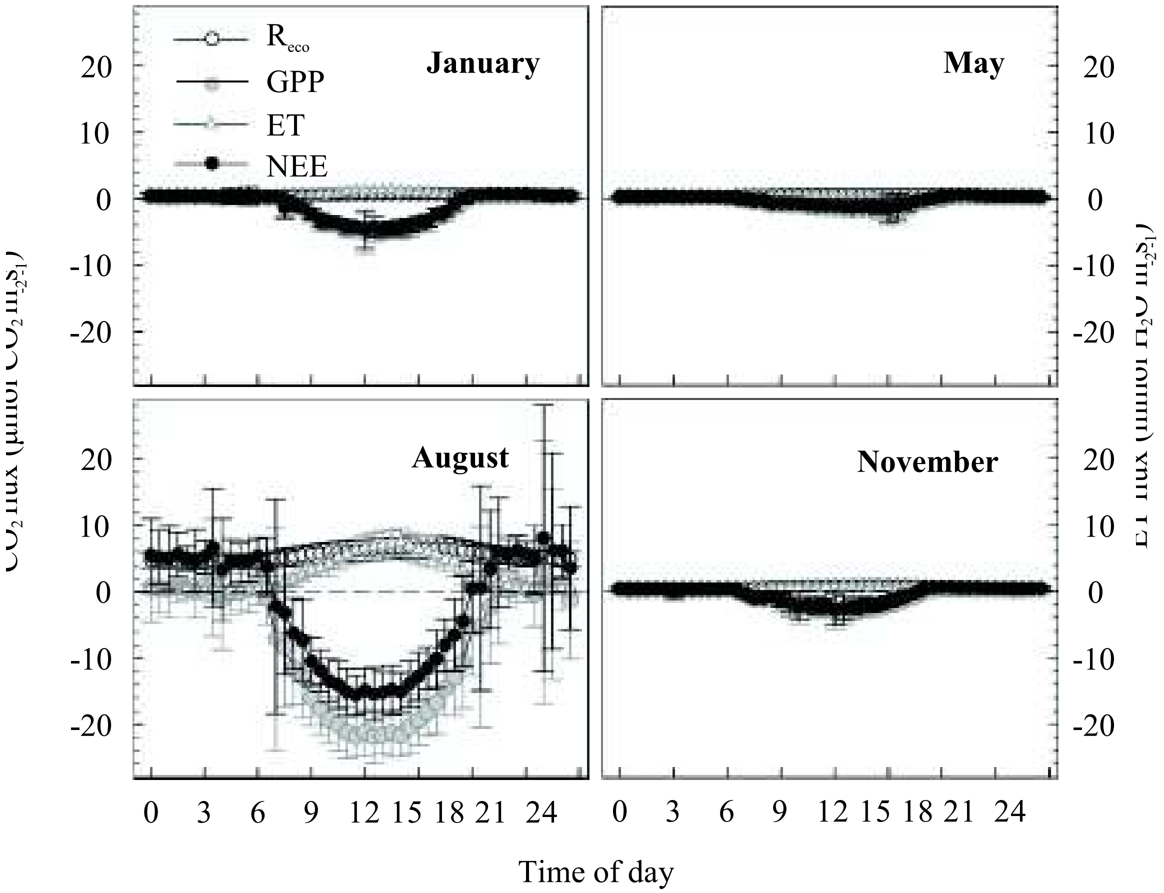
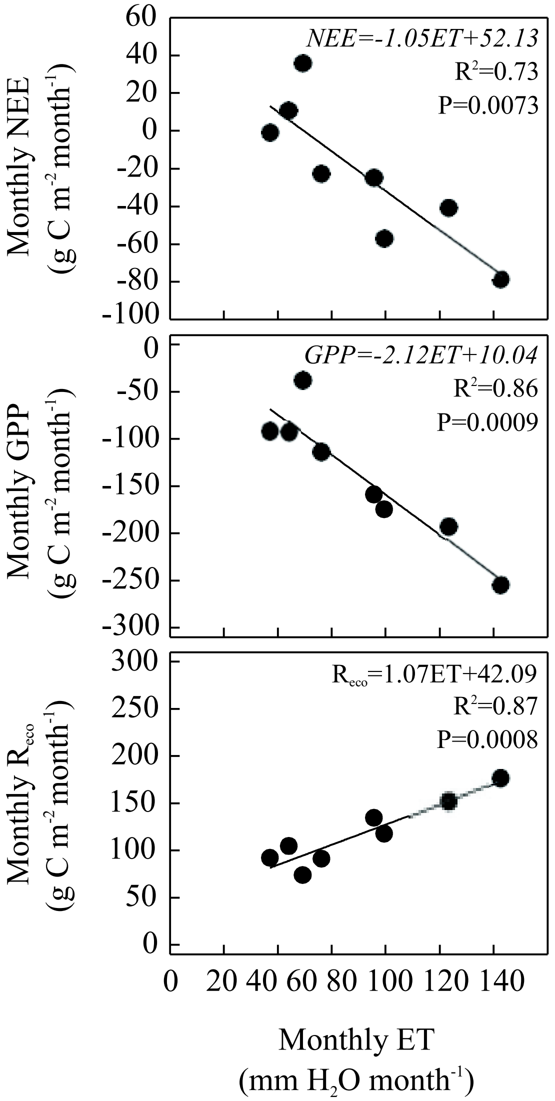

R_eco
GPP
ET
NEE
January
May
August
November
20
10
0
-10
-20
0 3 6 9 12 15 18 21 24
Time of day
CO2 flux (µmol CO2 m-2 s-1)
ET flux (mmol H2O m-2 s-1)

Figure 5.


NEE=-1.05ET+52.13
R2=0.73
P=0.0073
Monthly NEE
(g C m-2 month-1)
60
40
20
0
-20
-40
-60
-80
-100
GPP=-2.12ET+10.04
R2=0.86
P=0.0009
Monthly GPP
(g C m-2 month-1)
0
-50
-100
-150
-200
-250
-300
Reco=1.07ET+42.09
R2=0.87
P=0.0008
Monthly Reco
(g C m-2 month-1)
300
250
200
150
100
50
0
0
20
40
60
80
100
120
140
Monthly ET
(mm H2O month-1)

TABLES

Table 1. Inter-annual 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 ten days in August 2011 were filled with mean daily value for the month. Data for October 2011 were mostly filled with the online tool.

Table 2. Seasonal water use efficiency (WUEe) and percentage of contribution to total annual fluxes. Annual carbon fluxes are in g C m-2 yr-1. Annual and seasonal WUEe are in g C kg-1 H2O.

Table 1.

Year	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 H_2O $month^{-1}$)						
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} H_2O)						
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

Table 2.

	NEE		Reco		GPP		ET		WUE_e	
	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013
Annual sum	-230.4	-84.1	650.2	429.2	880.6	513.3	400.18	262.32	0.57582	0.32074
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

Net ecosystem production at adyacent shrubland and exotic buffelgrass savanna in the Sonoran Desert: interactions with water use and water-use efficiency

How land cover change from shrubland to exotic grass savanna influence ecosystem CO_2 and water fluxes: a study from adjacent eddy covariance sites

Shrubland transformation to exotic grass savanna in drylands: eddy fluxes in two adjacent sites

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

ABSTRACT

Land cover and land-use change between woody- and grass-dominated ecosystems in drylands comprise one of the largest uncertainties in the land CO_2 sink. This is especially true for the widespread transition from shrublands to grasslands/savannas caused by the establishment of exotic C_4 grass species for grazing or through biological invasion of these species, where information about its impacts on ecosystem CO_2 fluxes is limited. For studying this, we used three years of eddy covariance measurements of net ecosystem production (NEP), gross primary production (GPP) and ecosystem respiration (R_{eco}) over a shrubland and an adjacent exotic buffelgrass (*Cenchrus ciliaris* L.) savanna within the Sonoran Desert. We assessed whether between-site differences in CO_2 fluxes were explained by changes in water use, measured as evapotranspiration (ET), or by change in the relationships between GPP and ET (i.e., water-use efficiency, WUE) or between R_{eco} and GPP. Although the savanna had higher WUE than shrubland, its NEP was limited by water use during summer growing season, likely due to limitations of rooting pattern and leaf area index. Conversely, the savanna had higher NEP than the shrubland during fall to spring seasons due to increased WUE, likely related to buffelgrass when active, or to remaining native woody species using stored ground water when buffelgrass was inactive. However, these seasonal changes compensated over time, being both sites comparable carbon sinks over the study period. This study highlights changing mechanisms and feedbacks over ecosystem fluxes at shrubland to grassland/savanna transitions when highly productive, exotic C_4 grasses are involved.

INTRODUCTION

Dryland ecosystems have a key role on 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 CO_2 uptake by gross primary production (GPP) and emissions to the atmosphere by ecosystem respiration (R_{eco}) (Ahsltrom et al., 2015; Biederman et al., 2016; 2017). Furthermore, extensive land-cover and land-use change (LCLUC) has been documented across drylands (Hassan et al., 2005), which in turn directly influence the magnitude of these fluxes (Le Quere et al., 2016; Baldocchi et al., 2008). Traditionally, temperate forests ecosystems have been more studied than drylands, where LCLUC typically results in net carbon emissions to the atmosphere mainly due to a loss of living biomass (Le Queré et al., 2016). Changes in the net carbon balance in drylands following LULUC is still unclear and represent one of the largest uncertainties in the regional carbon balance (King et al., 2007).

Drylands are mainly grass-dominated and woody-dominated ecosystems (Hassan et al., 2005). The transitions from woody- to grass-dominated ecosystems and viceversa, are recognized as one of the most widespread LCLUC across drylands (Marshall et al., 2012; Sala & Maestre, 2014; Barger et al., 2011). The gradual change over decades from grass- to woody-dominated ecosystem is referred as woody encroachment, which is caused by interactions between 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 C_4 grass species to increase forage production (Castellanos et al., 2002, 2010; Marshall et al., 2012; Williams & Baruch, 2000). In this case, vegetation structure drastically changes within a season through land clearing of native vegetation and seeding, or more gradually through invasion of exotic grasses into adjacent areas from which they were established (Franklin & Molina-Freaner, 2010; Williams & Baruch, 2000). These LCLUC transitions in both directions could have important consequences for regional-to-global carbon budgets but large uncertainties still remain (Barger et al., 2011; Houghton, 2012; Jackson et al., 2002; Pacala et al., 2001). Arguably, larger uncertainties exist for the shrubland to grassland transition where there is limited information of carbon inventories and virtually no information regarding whole-ecosystem carbon fluxes that inform about changes in annual NEP (Bradley et al., 2006; Prater et al., 2006).

Most studies that have documented the effect of LCLUC on whole-ecosystem carbon fluxes in dryland ecosystems have focused on woody encroachment (Scott et al., 2006; 2014; Petrie et al., 2015). These studies have found that woodlands and shrublands have higher annual NEP than grasslands likely due to access to deep water and/or longer growing seasons (Scott et al., 2006; 2014; Petrie et al., 2015), and because encroached species can physiologically outperform grass species under a wide range of conditions (Barron-Gafford et al., 2012; Throop et al., 2012). Two relations are particularly interesting and explain the variation of NEP in drylands, which can be modified by land cover: the relation of GPP with evapotranspiration (ET), and the relation of R_{eco} with GPP (Biederman et al., 2016). The first one describes how available water is used for photosynthesis, reflecting the ecosystem water-use efficiency. The second one reflects how carbon availability drives ecosystem respiration, this relation being sensitive to changes in vegetation, carbon pools and allocation caused by LCLUC or disturbance (Baldocchi, 2008; Biederman et al., 2016). In this context, C_4 grasslands have higher water-use efficiency than woody-encroached ecosystems related to the physiology of C_4 grasses (Emmerich, 2007; Kurc & Small, 2007; Scott et al., 2014), but these advantage is surpassed by an increased R_{eco}/GPP likely related to the high proportion of root biomass in grasses (Scott et al., 2014; Petrie et al., 2015). This changes in relationships further contribute to explain the lower NEP of grasslands than woody-encroached sites. It is unclear how a LCLUC in the opposite direction (i.e., shrublands converted into C_4 grasslands) influence NEP in dryland ecosystems. We could expect a diminished NEP following the rationale for woody encroachment, but exotic grass species have been historically selected for being highly productive under limiting abiotic conditions (Cox, 1988) and could lead to a different outcome.

Buffelgrass (*Cenchrus ciliaris* L.) is one of the main C_4 exotic grass species used for converting xeric shrublands into more productive grasslands/savannas for cattle grazing over America and Australia (Cox et al., 1998; Marshall et al., 2012). Notably, the Sonoran Desert may be one of the most heavily impacted area by these practices (Castellanos et al., 2002; Franklin et al., 2006; Marshall et al., 2012). This perennial bunchgrass has one of the highest photosynthesis rates (Larcher, 2014) and can physiologically outperform dominant C_3 woody species from the Sonoran Desert (Castellanos et al., 2002), and exotic buffelgrass savannas can be a substantial carbon sink (Hinojo-Hinojo et al., 2016). However, remote sensing estimates suggest that buffelgrass dominated ecosystems have actually less above-ground biomass production than Sonoran Desert shurblands (Bravo and Castellanos, 2013; Franklin et al., 2006; Franklin et al., 2010). Thus, research is needed to contribute to our understanding of shrubland to grassland transitions in dryland ecosystems.

In this study we compare three years of information on CO_2 and water fluxes and their relationships over a shrubland and an adjacent exotic buffelgrass savanna in the southeastern Sonoran Desert. We asked the following scientific questions: Does the change from shrubland into a exotic buffelgrass savanna modifies NEP?; and if so, is this change related to seasonal changes on water use efficiency and/or R_{eco}/ GPP relation? We hypothetize that the high productivity potential and water-use efficiency of buffelgrass will compensate for the high R_{eco}/GPP of grasslands, leading to similar or higher NEP than a shrubland. Our ultimate aim is to contribute to the discussion about the bidirectional changes of wood-to-grass transitions across these globaly distributed ecosystems.

MATERIALS AND METHODS

Study sites

Two adjacent sites representing a native shrubland and a buffelgrass savanna were selected for installing eddy covariance systems to measure ecosystem scale carbon dioxide (CO_2), 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 and Castellanos, 2013; Castellanos et al., 2002, 2010; Franklin et al., 2006). Both sites are located in a private ranch near La Colorada, Sonora, where cattle grazing by rotational management is the prevalent activity through 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 28º 41' 53.60" N, 110º 32' 20.59" W, with 450 m elevation; Figure 1) has a Sonoran Desert scrub vegetation characteristic of the Plains of Sonora (Brown et al., 1994). The vegetation is composed by trees (*Olneya tesota*, *Fouquieria macdougalii*, *Ipomoea arborescens*, in descending order of importance) covering 14 % area, shrubs (*Jatropha cardiophylla*, *Encelia farinosa*, *Mimosa laxiflora*, *Lycium berlandieri*) covering 28 % area, and during the study period soil was covered mostly with summer active herbs and grasses and their remnants. Vines can also have some cover during summer (about 10%). Mean vegetation height is ≈ 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 (Figure 1).

The buffelgrass savanna site (located at 28º 42' 40.32" N, 110º 32' 58.14" W, with 399 m elevation; Figure 1) was a former Sonoran Desert scrub transformed to savanna through selective land clearing that left a few trees approximately 35 years ago (J. Dueñas, personal communication). Since then, some shrub and other species have slowly recolonized the site. The vegetation had 32 % cover of buffelgrass (*Cenchrus ciliaris*), 3 % cover of trees (*Olneya tesota* and *Prosopis velutina*), and 7% cover of shrubs (mostly *Mimosa laxiflora*, and *Jatropha cardiophylla*). During the study period, interspaces between plants had a cover of summer active herbs and grasses. Mean vegetation height is ≈ 0.5 m but few trees grow up to 4 m.

Climate on these sites (30 year averages from nearby station 26268 San Jose de Pima, Servicio Meteorológico Nacional) is warm-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 if there are events of 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 should conditions be favorable. Terrain is plain along the towers fetch with an average slope <2% (Figure 1). Soils are calcic regosol and haplic phaeozem with loamy sand texture with 0.6-2.6 % of organic matter content (Celaya et al., 2015).

Eddy covariance and meteorological measurements

The instrumentation installed in both sites allowed us to measure the net ecosystem CO_2 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 at which these fluxes occur. In this study we used three years of comparative data (from march 2013 to the end of 2015). The eddy covariance system at the buffelgras savanna was installed on a 6 m height tower. At the top of the tower, it has a sonic anemometer (CSAT3, Campbell Scientific, Logan, UT, USA) for measuring 3D components of wind velocity and sonic temperature, and an open path CO_2/H_2O 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 sensors had a sampling rate of 15 minutes. These include a rain gauge (TR-525USW-R, Texas Electronics, Dallas, TX, USA), and two soil heat flux plates (HFP01-L50, Hukseflux, Delft, The Netherlands) located at 5 cm depth under buffelgrass cover and two beneath open spaces (with annual herbs cover). All data were sampled and stored by a data-micrologger (CR3000, Campbell Scientific, Logan, UT, USA).

The eddy covariance system at the shrubland site was installed in a 9 m height tower. At the top of the tower (9.1 m) it has a 3D sonic anemometer (Wind Master Pro, Gill Instruments) and an open path CO_2/H_2O gas analyzer (Li-7500A, LI-COR, Lincoln, NE, USA), 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 6m height an air temperature and relative humidity probe (HMP-155, Vaisala Inc., Vantaa, Finland). Rainfall was measured with a rain gauge (TR-525M, Texas Electronics, Dallas, TX, USA). Soil heat flux was measured (HFP01SC, Hukseflux, 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 minute and 10 Hz frequency data are stored in the interface unit (Li-7550, LI-COR, Lincoln, NE, USA) of the gas analyzer.

Data processing

The high frequency (10 Hz) raw data processing and flux calculation were performed on Eddy Pro software (v. 4-5, LI-COR Biosciences) on 30-minute blocks. Prior to flux calculation, the following processing was made on raw data: despiking and other statistical quality tests (following Vickers & Mahrt, 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 & 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 CO_2, ET, sensible (H) and latent heat (LE) were calculated using the vertical component of wind velocity, CO_2 and water vapor molar densities, and sonic temperature. These fluxes were corrected for frequency spectral attenuations (Moncrieff et al., 1997 & 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 developed turbulence conditions (Mauder & Foken, 2004), 2) during rain events, 3) when bird feces occluded the gas analyzer lenses dropping CO_2 concentration below 350 ppm (which caused substantial overestimation of CO_2 fluxes, personal observation), 4) under low turbulence mixing according to a friction velocity threshold. Friction velocity thresholds for the shrubland were 0.15-0.13 while savanna thresholds were 0.1 for all years. Quality control and system failure resulted in a NEE gap fraction of 37-51% for shurbland, and 40-51 % for the savanna, depending on the year. Gap-filling and NEE flux partitioning into R_{eco} and GPP was performed according to Reichstein et al. (2005) using the online tool available at www.bgc-jena.mpg.de/~MDIwork/eddyproc/. The resulting calculated fluxes gave an overall daily energy closure of slope 0.87 and intercept of 0.46 MJ m-2 day-1 at the shrubland, and slope of 0.86 and intercept of 0.52 MJ m-2 day-1 at the savanna.

Daily, monthly, seasonal and annual flux sums were obtained by adding up through time the half-hourly gap-filled data. Seasons were considered as the three complete months where most of the seasons occur, i.e. January to March for winter, April to June for spring, July to September for summer, and October to December for fall. Uncertainty in flux sums were calculated as the squared root of squared uncertainties from gapfilling (from the online tool), from random errors and long gaps (following Richardson & Hollinger, 2007), and from systematic errors (assuming similar conditions to Wholfarht et al.,2008). We follow the ecosystem centered nomenclature where NEE values are taken as a measure of Net Ecosystem Production (NEP), where positive values indicate net carbon uptake by the ecosystem and negative values indicate net carbon emission to the atmosphere (Chapin et al., 2006).

Vegetation phenology

We followed vegetation leaf phenology through remote sensing data and with field observations. For remote sensing data, we use time series of 8 day composites of leaf area index obtained by the MODIS (Moderate-Resolution Imaging Spectroradiometer) product

MOD15A2 for the same dates as flux measurements. Data was obtained from the webpage of Distributed Active Archive Center for Biogeochemical Dynamics at http://daac.ornl.gov/ MODIS/. Additionally, species leaf phenology was recorded approximately every three to four weeks in 10 individuals of the dominant species (> 0.5% cover) at both sites, during the three years. A species was considered to have green leaves when more than sixty percent of its individuals had some leaves present.

Statistical analyses

We used t-test and simple linear regression analyses to detect between-site differences on monthly, seasonal and annual data. For seasonal and annual flux sum comparisons, we compared mean daily flux of the period of interest with the t test given that the mean multiplied by the number of days equals the sum. Welch ANOVA for unequal variances was also performed, but none comparison differed on its conclusions to those of the t test; thus, we only present the results for the t test. In the linear regression analysis, we used any statistically significant divergence from slope = 1 and/or intercept = 0 in the relation between monthly data for one site against the other to describe general trends in the difference on carbon and water fluxes between sites.

Water-use efficiency was assessed at monthly scale in two ways: as the relationship of GPP against ET, which gives an estimate of realized water-use efficiency (WUE); and as the relationship of the product of GPP and vapor pressure deficit (VPD) against ET as an estimate of inherent water use efficiency (WUE_i), which reflect changes in WUE due to plant physiology by controlling the effect of VPD (Beer et al., 2009). The relationship of monthly R_{eco} against GPP was also assessed. To compare how sites differed on 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 over 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 took any significant effect of site and/or interaction as a significant change in WUE, WUE_i or R_{eco}/GPP relationship. All these statistical analyses were performed in the statistical package JMP version 9.0.1 (SAS Institute, Inc, 2010) or R version 3.2.2 GUI 1.66 (R Foundation for Statistical Computing, 2014).

RESULTS

The three years under study differed markedly on its rainfall conditions (Figure 2a-c). Rainfall during 2013 (253 mm) was below the long term average, mostly dominated by summer rains (Figure 2a), while this year had the coldest winter of the three years (Figure 2d). Year 2014 (412 mm) had a rainy summer but dry winter and spring (Figure 2b-c), and 2015 (505 mm) had rains throughout the year with rainy winter and spring seasons, but below average rainfall in summer (Figure 2c). Temperature was similar for 2014 and 2015 (Figure 2e-f). Mean daily air vapor pressure deficit was highest during late spring on all years reaching about 4 kPa, and the rest of the seasons had values fluctuating around 1-3 kPa (Figure 2g-i). Thus, the three years allowed us to compare carbon and water fluxes between sites over a wide range of conditions.

Some between-site differences could be detected on the daily dynamics of fluxes and LAI (Figure 3). Buffelgrass savanna had consistently higher daily carbon fluxes on winter and spring during the three years (Figure 3g-o), but this was not related to buffelgrass activity during years 2013 and 2014 (Figure 3a-b). Buffelgrass main activity occurred during summer, but remained active during most of 2015 (Figure 3a-c). Shurbland had higher carbon fluxes, ET and LAI during the summer seasons of 2014 and 2015, especially early in the summer, but comparable and highly variable during 2013. However, daily fluxes have a large variability during summer, which difficult its comparison and generalizations at these time scales.

According to our relationships with monthly data, the buffelgrass savanna had higher WUE_i than the shrubland, either when buffelgrass was active or inactive (Figure 4a). The savanna had 2.4 g C mm^{-1} H_2O $month^{-1}$ and 188 g C hPa higher GPP*VPD for a given ET (marginally significant interaction effect and significant site effect in Table 1). However, sites did not differ on its R_{eco}/GPP relationship (Figure 4b, Table 1). In addition, we found that between-site differences in leaf area index increased with total summer rainfall, the shrubland having up to 1.6 times the values at the savanna site, and that leaf area index affected similarly the NEP of both sites (Figure 5). Our estimates indicate that for the shrubland to have a higher NEP than the savanna it has to lose as evapotranpiration 5.5 mm month^{-1} or higher than the savanna (y=-5.8+1.06x, Figure 6), which occurred mostly during summer months and few months from other seasons.

Annual carbon and water flux sums for the years 2013 to 2015 and between-site comparison are presented on Table 2. During 2013, the shrubland was carbon neutral (t-test against 0: $t = 0.0544$, $P = 0.3524$) and the buffelgrass savanna was a carbon sink. Both sites were carbon sinks during 2014 and 2015 and no between-site statistically significant differences were found for both years. Although we based our annual flux comparison on daily flux variability, uncertainties for annual NEP estimates gave a total of about ± 65 to 68 g C m^{-2} year^{-1} for the shrubland and ± 66 to 78 g C m^{-2} year^{-1} for the savanna. When summed over the three years, both sites had a very similar amount of NEP (393 and 414 g C m^{-2} year^{-1} for shrubland and savanna, respectively). R_{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 such differences. Sites had similar ET during 2013, but lower ET at the savanna site during 2014 and 2015 resulted in lower ET/P relations, which was evident at annual scale and during summer (Table 2).

Sites differed on their summer contribution to annual fluxes. During the years with no 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 to 89 % in the buffelgrass savanna (Table 2). In those same years, summer contributed with 68 to 86 % of the yearly fluxes of GPP, R_{eco} and ET at both sites, with this contribution being about 7 to 18 % higher for carbon fluxes and 1 to 7 % higher for ET in the shrubland than the buffelgrass savanna. However, during the rainy 2015 (with rains in winter and spring) summer contribution to annual flux totals was 46 -

56% (ET and NEP respectively) in the buffelgrass savanna, and 46 (ET) to 72% (NEP) in the native shrubland.

DISCUSSION

The information in this study does support our hypothesis that a LCLUC from shrubland into a grass-dominated ecosystem where a highly productive exotic C_4 grass is involved result in an ecosystem that can be as productive as the shrubland. This contradicts the common finding from the reverse transition, the woody encroachment, where woody-dominated ecosystems tend have higher NEP than grass-dominated ecosystems (Barger et al., 2011; Scott et al., 2006; 2014; Petrie et al., 2015). However, our findings are in line with an experimental study that has found increased carbon sequestration through measurements of carbon pools on shrublands invaded by exotic grasses than an un-invaded shrublands (Wolkovich et al., 2010). Here we discuss mechanisms and feedbacks operating at both ecosystems which lead to the observed pattern, and possible implications of bidirectional woody-grassland transitions on carbon fluxes of ecosystems.

The buffelgrass savanna had similar or higher annual NEP than the shrubland in comparisons for the same year, but summed over the study period (3 years) both sites ended with similar NEP, being net carbon sinks. The higher NEP that other studies found in woody-dominated compared to grass-dominated ecosystems has been explained by increased access to deep water (higher ET/P ratio), longer growing seasons, and higher R_{eco}/GPP at graslands (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 in our sites (as suggested by time series of NEP and GPP, Figure 3), and not affected by the increased water availability at shrubland (ET/P from Table 2), probably because vegetation at both sites is highly seasonal. Furthermore, the relationship between GPP and R_{eco} did not change between sites. Although R_{eco} was higher at the savanna than shurbland during some years (2013, 2015), GPP throughout those years compensated such increases, which agrees with our hypothesis (Table 2). Alternatively, sites differed on the seasonal contributions to annual fluxes, being the shrubland more dependent on the summer season than the buffelgrass savanna (Table 2). Thus, although both sites get to similar amount of NEP over the years, the processes that led to these similar NEP differed among sites, specifically, those related to water use and water-use efficiency.

The buffelgrass savanna had higher WUE_i than the shrubland throughout the year, which support that at least part of this increase in WUE is due to the C_4 physiology of buffelgrass, as has been found for other C_4 dominated grasslands when compared to C_3 dominated shrublands (Ehleringer & Monson, 1993; Emmerich, 2007; Scott et al., 2014; 2015). However, the savanna had lower NEP and ET than shrubland during most summer months (Figure 6) despite having higher WUE, which suggest water limitations. Two biotic mechanisms appear to be limiting water use and NEP at the savanna during summer. First, the conversion of a shrubland into a buffelgrass savanna greatly reduce the cover of most plant functional types, especially woody species with deep roots (Saucedo-Monarque et al., 1997; Castellanos et al., 2002, 2010; Franklin & Molina-Freaner, 2010). At the savanna site deep-rooted woody species cover less than 10%, and buffelgrass and annual plants are known to have roots within 0-60 cm depth (Forseth et al., 1984; Mnif & Chaleb, 2009), thus, most plant cover at the savanna is dependant on shallow soil water availability. In the shrubland, at least 30 % of its cover are deep-rooted woody plants and there is an important proportion of herbs and shrubs with shallow roots, thus allowing this site for better exploiting the water throughout the soil profile during summer and thus allowing higher transpiration (Castellanos et al. 2016; Celaya et al. 2015; Huxman et al., 2005).

Secondly, we found that LAI at both sites was similar at the lowest range of total summer rainfall, but differences in leaf area index increased as summer rainfall increased, having the shrubland up 1.6 times higher leaf area index than the savanna (Figure 5). Knapp et al. (2008) reported similar patterns and suggest that grasses may have an intrinsic limitation in LAI due to its architecture with meristematic disposition only closely at or below the soil surface, while the branching and meristem arrangement of shrubs allow for greater canopy deployment with high values of leaf area index. Because leaf area index is one of the parameters that greatly determine carbon and water fluxes over ecosystems (Allen et al., 1998; Bonan, 1993), these differences in canopy responses contribute to explain between-site differences on summer fluxes. Taking both limitations into account, when the shrubland increases its ET by more than 5 mm month^{-1} above the savanna, the effect of ET over NEP in the shrubland can surpass the advantage of higher WUE of the buffelgrass savana (Figure 6).

During the seasons of fall, winter and spring, the buffelgrass savanna had higher NEP than shrubland, mostly related to increased GPP as a consequence of increased WUE (Figure 3 and 4). The higher GPP and WUE could be attributed to the physiology of C_4 photosynthesis when buffelgrass was active (e.g. winter and spring of 2015). When buffelgrass was not active (e.g. winter and spring of 2013 and 2014), increased GPP at the savanna could be fueled by water accumulation at deep soil and subsequent use by native woody species that retain their leaves during most of the year, such as *Prosopis* and *Olneya*. In agreement with this, water accumulation in soil at 1.5-2 m depth was found at the same savanna site following rainy summer and fall seasons, while a decrease in soil water content at these depths until summer gives evidence of the use of this water, which did not occur at the shrubland site (Castellanos et al., 2016, Celaya et al., 2015). 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 suggest that the high WUE and biological limitations at the buffelgrass savanna cause a lower ET/P than that of the shrubland, especially at rainy seasons and years (e.g., 2014 and 2015), can results in the observed water accumulation and feedbacks activity at the savanna during dry fall to spring seasons.

Currently, the information about impacts on NEP from LCLUC from woody-dominated to grass-dominated ecosystems is very limited. The high productivity, photosynthesis rates, resource-use efficiency, and other traits of C_4 exotic grasses used for cattle management and invasive grasses, can make the impact and feedbacks of these transitions differ 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 eddy covariance technique 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 water-use effciency. The representation of photosynthetic pathway, rooting pattern, and differential canopy responses were the main factors responsible for such changes (Figure 7), all of these characteristics greatly modified by LCLUC from shrublands to grass-dominated ecosystems. However, our findings suggest that the effects of such temporal changes in water use and water-use efficiency on NEP can compensate in time, either between seasons (e.g. 2014) or between years (e.g. 2013 vs 2014), resulting in a similar NEP over the years despite the strong biotic changes in vegetation. Further studies on LCLUC from woody-dominated to grass-dominated ecosystems should focus on understanding how the impact of these biotic traits (photosynthetic pathway, rooting pattern, differential canopy responses) over water use, water use efficiency and NEP vary over ecological gradients, such as rainfall gradients (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 its impacts on carbon processes.

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FIGURES:

Figure 1: Location of the study area within the Sonoran Desert and of the eddy covariance (EC) towers in the landscape.

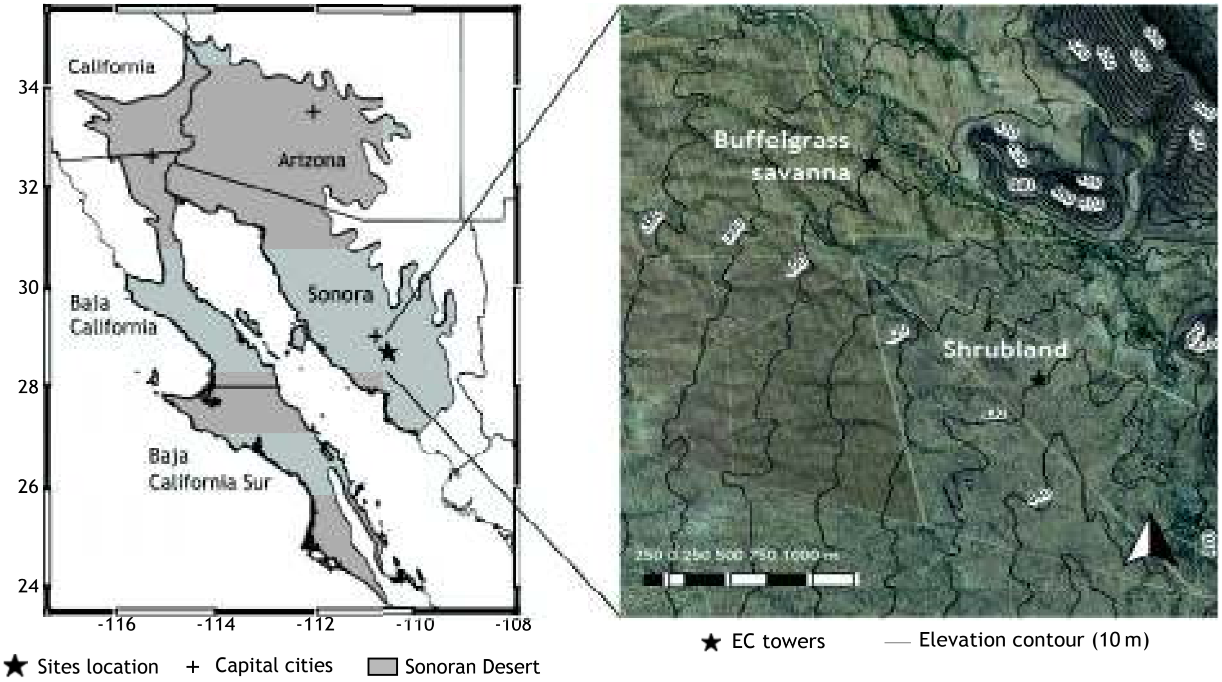

Figure 2: Annual course of monthly rainfall (a-c), mean daily air temperature (d-f), and vapor pressure deficit (g-i) at the shrubland (black symbols) and buffelgrass (gray symbols) savanna sites during the study period. In a-c, bars represent monthly rainfall during the study period and lines represent long-term average monthly rainfall.

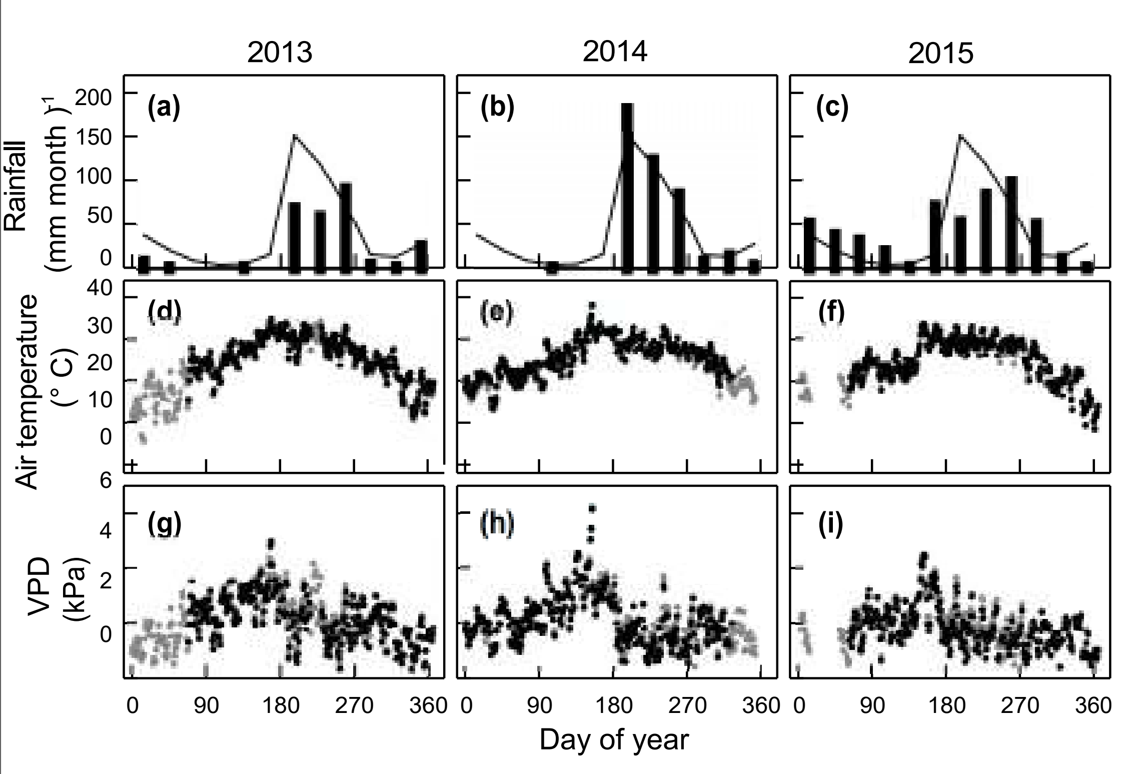

Figure 3: Annual course of a-c) leaf area index, d-f) daily evapotranspiration (ET), g-i) net ecosystem production (NEP), j-i) ecosystem respiration ($R_{eco,}$) and m-o) gross primary production (GPP) for the shrubland (black symbols) and buffelgrass savana (grey symbols) sites. Horizontal grey bars in a-c) indicate periods green leaf phenology of buffelgrass.

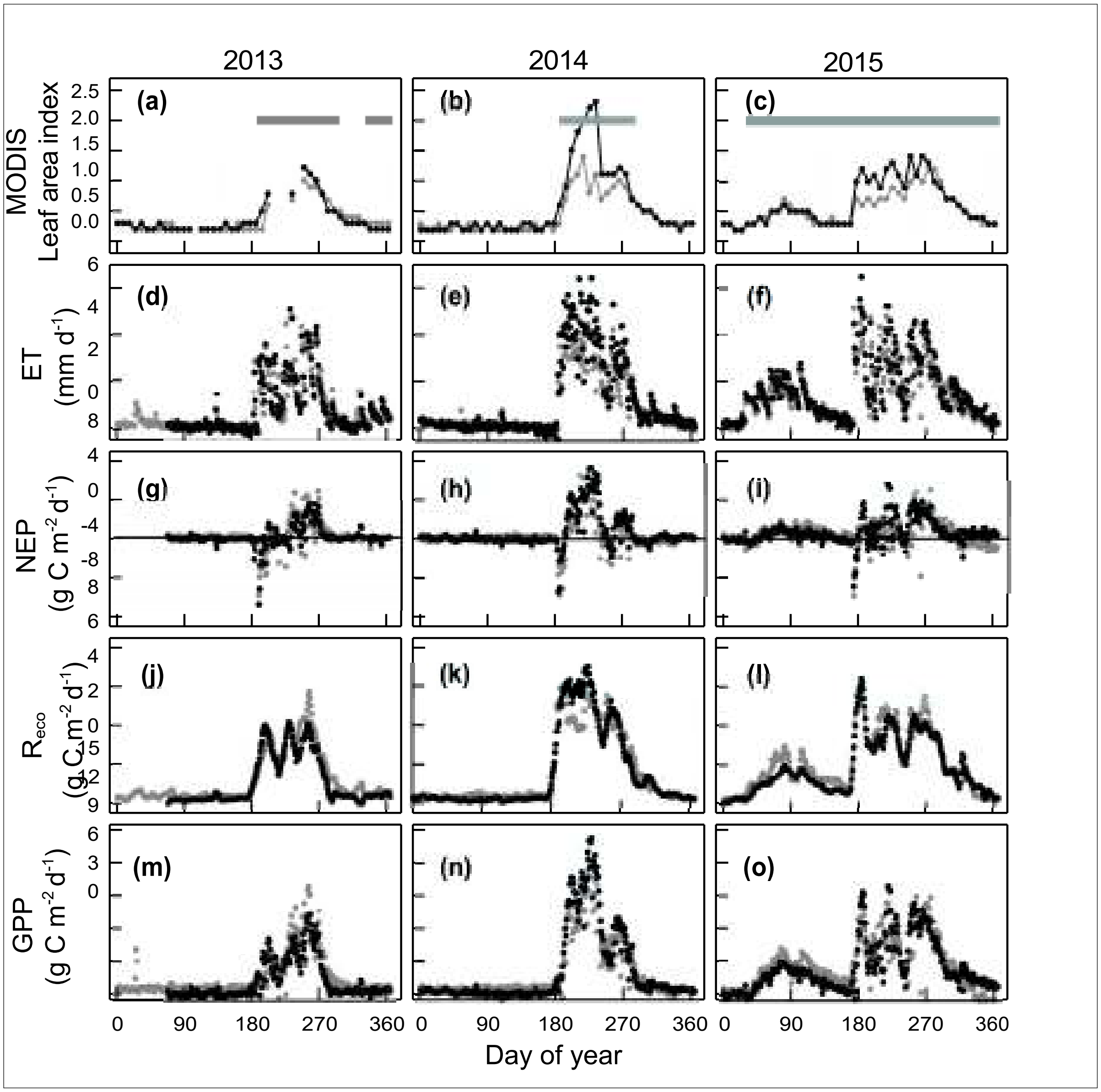

Figure 4: a) Water-use efficiency and b) R_{eco}/GPP relationship for the shrubland (black symbols) and buffelgrass savanna (open symbols) sites. Star symbols represent months when buffelgrass was active, and lines are linear regressions for each site.

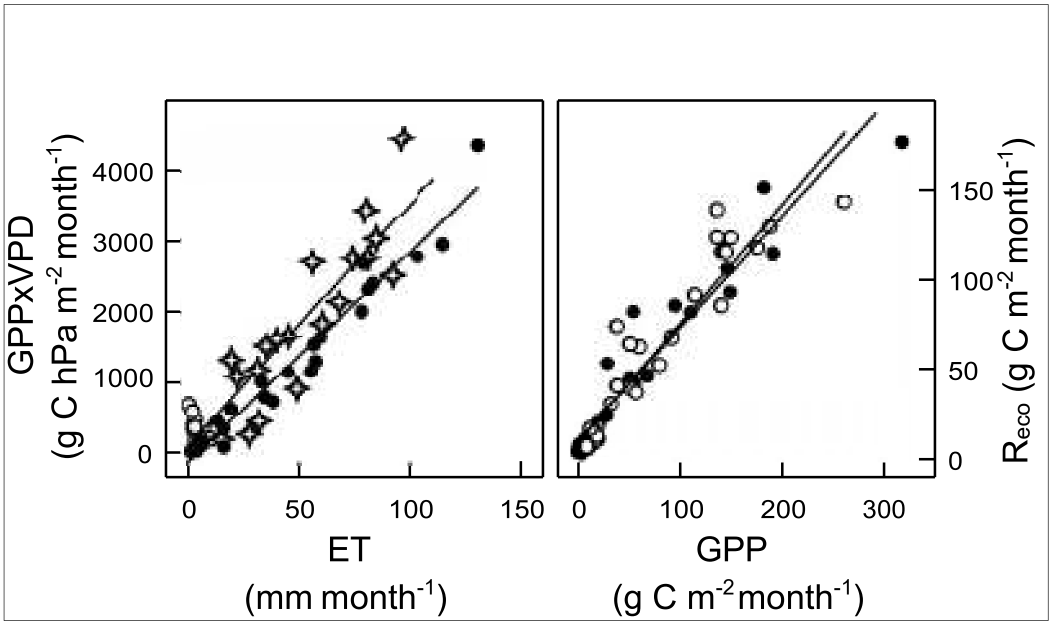

Figure 5: a) Peak summer leaf area index response to seasonal precipitation y b) the effect of leaf area index on net ecosystem production. Black symbols are for the shrubland and gray symbols for the buffelgrass savanna.

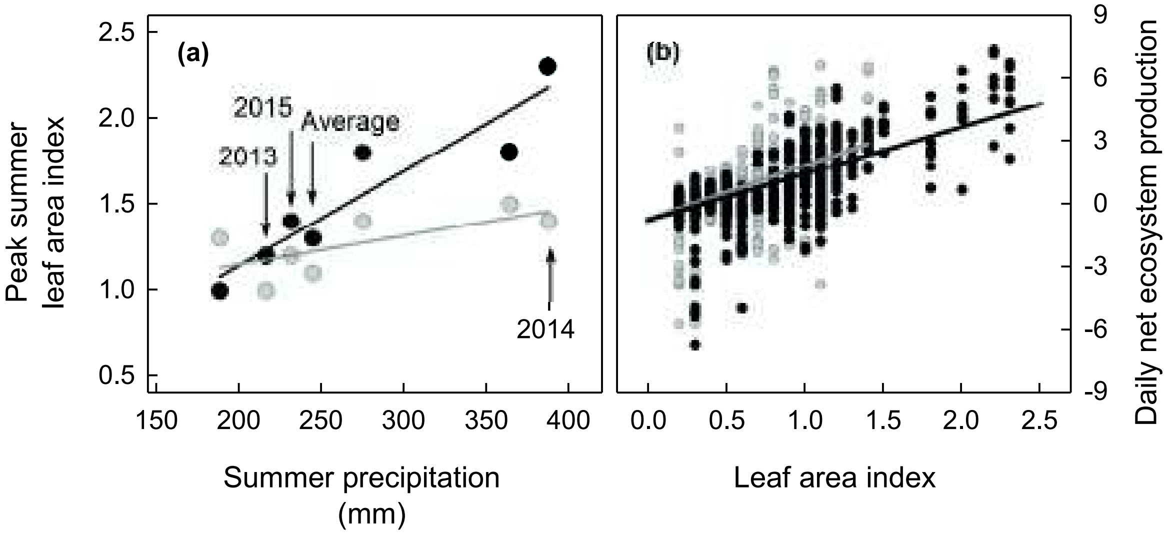

Figure 6: Between-site difference in evapotranspiration as a driver of the difference in net ecosystem production for shrubland buffelgrass savanna sites. Closed circles are values for summer months, and open circles are for months from the other seasons.

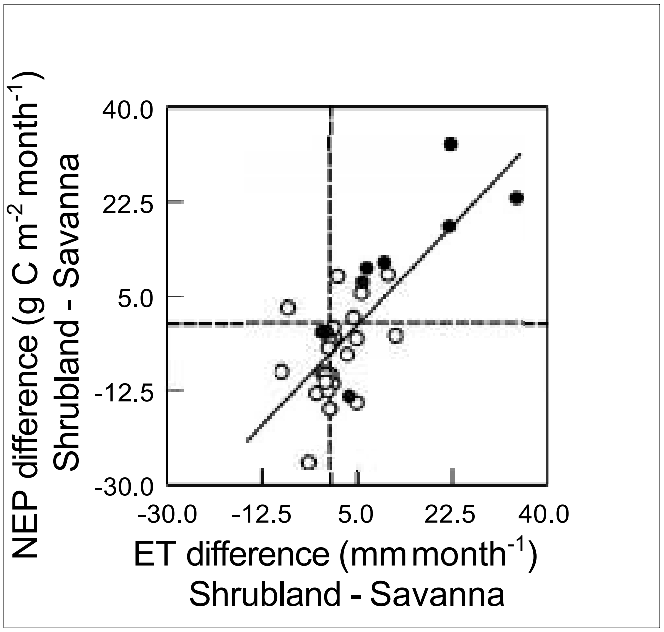

Figure 7: Proposed links between ecosystem structural changes, with changes in water and CO_2 fluxes caused by land cover and use change from shrubland to exotic buffelgrass savanna. C_3: cover of plants with C_3 photosynthetic pathway, C_4: cover of plants with C_4 photosynthetic pathway, WUE_i: inherent water-use efficiency, GPP: gross primary production, R_{eco}: ecosystem respiration, NEP: net ecosystem production, ET: evapotranspiration, ET/P: evapotranspiration to precipitation ratio. Elements with ^{1,2} are supported by Castellanos et al. (2016) and Celaya et al (2015).

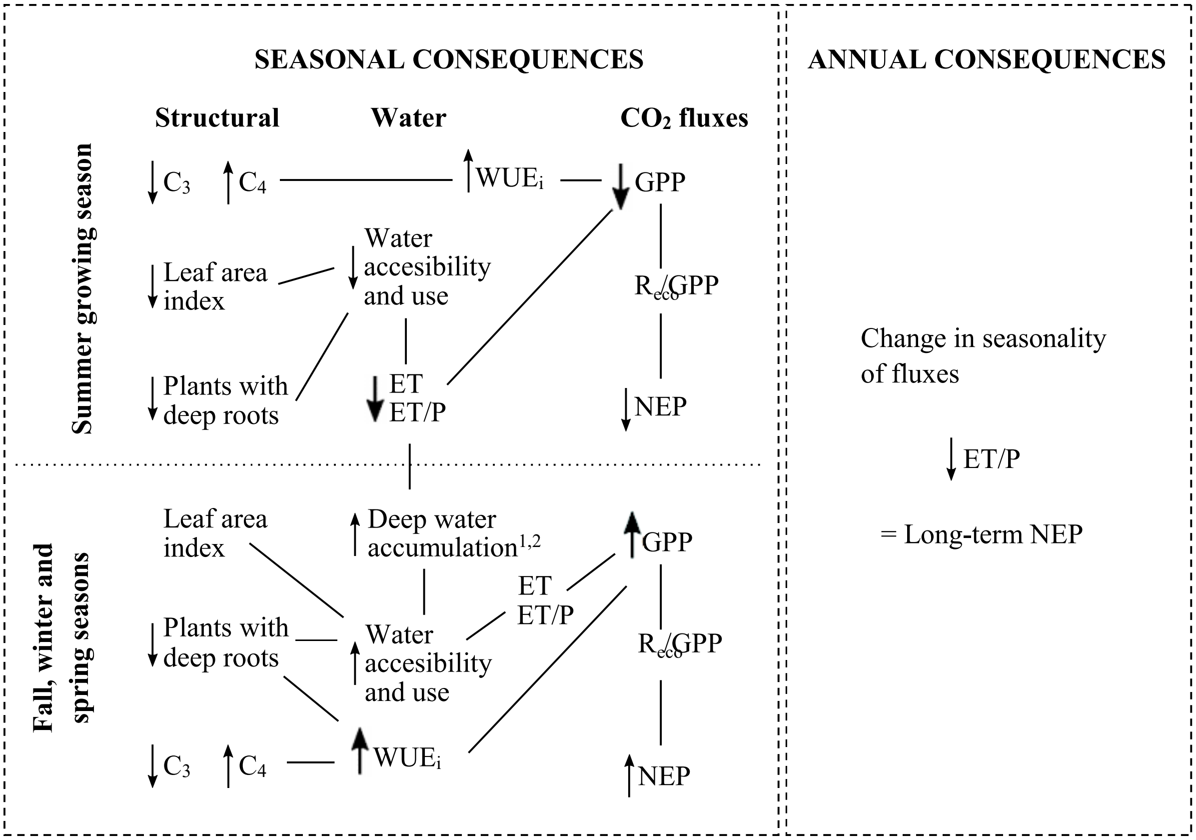

Table 1: Results of the statistical comparison of monthly WUE, WUE$_i$, and the relationship of R$_{eco}$/GPP the shurbland and the buffelgrass savanna site.

	R^2	Intercept	Independent variable effect	Site (savanna) effect	Independent variable x Site (savanna) effect
WUE (GPP vs ET)	0.90	-5.91	1.95****	7.28*	0.02
WUEi (GPP*VPD vs ET)	0.90	25.86	31.42****	189.17****	2.43*
Reco vs GPP	0.91	9.60****	0.65****	0.41	0.02

* $p < 0.1$ (marginally significant), ** $p < 0.05$, *** $p < 0.01$, **** $p < 0.001$
When no significant interaction effect is found, the independent variable effect correspond to the overall slope.
When interaction effect is statistically significant, the independent variable effect correspond to that of shrubland site and the independent variable x 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 change on 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.

	Annual sums			Summer sums			Summer contribution		
	2013*	2014	2015	2013	2014	2015	2013	2014	2015
Net ecosystem production (g C m^{-2})									
Shrubland	16.38	183.31	192.77	36.38	192.56	138.76	222.19	105.05	71.99
Savanna	74.72	140.45	199.24	43.9	124.83	112.04	58.75	88.88	56.23
P	0.0293	0.3178	0.8431	0.7715	0.0685	0.2148			28.01
Ecosystem respiration (g C m^{-2})									
Shrubland	326.4	561.05	673.95	261.23	448.11	336.79	80.03	79.87	49.97
Savanna	402.49	556.94	763.08	282.8	405.69	368.45	70.26	72.84	48.28
P	0.0171	0.9377	0.0262	0.0847	0.0045	0.0117			
Gross primary production (g C m^{-2})									
Shrubland	342.78	744.36	866.73	297.62	640.67	475.57	86.83	86.07	54.87
Savanna	477.21	697.39	962.33	326.69	530.52	480.49	68.46	76.07	49.93
P	0.0051	0.5785	0.1269	0.3826	0.0168	0.8699			
Evapotranspiration (mm)									
Shrubland	236.06	400.07	581.9	194.39	323.54	268.03	82.35	80.87	46.06
Savanna	245.65	320.99	518.62	184.95	256.51	240.44	75.29	79.91	46.36
P	0.722	0.0441	0.0468	0.5546	0.0001	0.0945			
Evapotranspiration / Precipitation									
Shrubland	0.94	0.97	1.15	0.9	0.84	1.15			
Savanna	0.97	0.78	1.03	0.85	0.66	1.03			

IV. DISCUSIÓN

El objetivo del presente estudio fue determinar la importancia de algunos factores bióticos en los procesos de la productividad neta de ecosistemas áridos, mediante el estudio de características fisiológicas a nivel de hoja y la dinámica temporal de flujos de CO_2 y agua a nivel ecosistema. Esto nos permitiría tener un mejor entendimiento de las consecuencias de modificar la vegetación en la productividad y el potencial de secuestro de carbono de los ecosistemas. A nivel de hoja, detectamos altos valores en los parámetros bioquímicos de la fotosíntesis (V_{cmax} y J_{max}) y una alta inversión de nitrógeno en Rubisco, las cuales favorecieron la tasa de fotosíntesis de las especies ante un amplio rango de condiciones. A nivel ecosistema, encontramos que sitios con cobertura vegetal contrastante (matorral y sabana de zacate buffel inducida) pero expuestos a similares condiciones ambientales (debido a que ambos sitios eran adyacentes) pueden ser un sumidero de carbono comparable a largo plazo, pero el cambio en cobertura modifico la estacionalidad de los procesos. Estos hallazgos reportados en las tres publicaciones que componen este documento, sugieren maneras en las que algunos factores bióticos influencian la magnitud y temporalidad de los flujos de carbono y agua.

En nuestro estudio, diferentes características biológicas afectaron de diferente manera la dinámica temporal de los flujos. En primer lugar, encontramos que los valores de V_{cmax}, J_{max} e inversión de nitrógeno en estas características en las especies C_3 dominantes de los sitios causaron un incremento en la tasa de fotosíntesis de 7 a 13 μmol m^{-2} s^{-1} por encima de la obtenida con valores de V_{cmax} y J_{max} comúnmente utilizados para parametrizar especies de arbustos a nivel global (Figura 3 del primer artículo, Kattge *et al.*, 2009). Estas características deben ser especialmente importantes para permitir tasas relativamente altas de GPP durante periodos favorables y mantener captura de C durante periodos de estrés moderado, en especial en el sitio de matorral que está dominado por especies C_3. Aún desconocemos cómo son los parámetros bioquímicos de la fotosíntesis en especies C_4, y como estos pudieran impactar los flujos en nuestros sitios de estudio.

A nivel ecosistema encontramos un efecto aparente sobre la productividad neta del ecosistema por el aumento en dominancia de la vía C_4 con el establecimiento del zacate buffel, aunque otros factores bióticos pudieron ser más importantes. En particular, se esperaría un aumento en la captura bruta y neta de C por unidad de ET cuando el zacate buffel estuviera activo, debido a la alta eficiencia de uso de agua típica de esta vía fotosintética (Ehleringer & Monson, 1993). En nuestro estudio, se detectó un incremento en GPP por unidad de ET causado por la transformación. Sin embargo, los flujos durante el verano sugieren que la productividad neta en la sabana está limitada biológicamente por su uso de agua (Figura 2, 4 y 5 del tercer artículo). Esta limitación concuerda con lo que se esperaría de un ecosistema donde la diversidad de plantas ha sido simplificada, donde la perdida de complementariedad de las especies tendería a causar una disminución en el uso de recursos limitantes (Cardinale *et al.*, 2007). En nuestros sitios, esto ocurrió porque el patrón heterogéneo de sistemas radiculares del matorral (Canon, 1911) se transformaron a uno mayormente superficial en la sabana (Mnif y Chaleb, 2009). Por otro lado, encontramos que el valor máximo de índice de área foliar en la sabana es similar durante veranos lluviosos y secos, mientras que el matorral presentó valores muy variables según la cantidad de precipitación estacional (Figura 5 del tercer articulo). Esto corresponde a una limitación morfológica en la productividad neta en la sabana, y que concuerda con respuestas similares reportadas para otros pastizales (Knapp *et al.*, 2008). Así, la los cambios en diversidad de plantas y las características y respuestas del dosel fueron claves para explicar los cambios en los flujos durante el verano.

El análisis de los datos de flujos durante las estaciones menos lluviosas del año (periodo de octubre a junio) sugiere que la limitación en uso de agua en la sabana durante el verano pudo haber resultado en acumulación de agua en el suelo a 1.5-2 m. Esta agua acumulada no puede ser utilizada por el buffel debido a su sistema radicular superficial y que solo posee hojas verdes durante las épocas cálidas y lluviosas del año. Sin embargo, esta agua pudiera ser usada por las especies nativas de la sabana, que aunque tienen una cobertura baja

(< 10%), presentan raíces profundas y hojas durante la mayor parte del año. La acumulación de agua en la sabana fue confirmada por mediciones de campo durante periodos con lluvia por encima del promedio (Castellanos et al., 2016; Celaya et al., 2015), y existe evidencia de su uso mediante mediciones de humedad del suelo (Castellanos et al., 2016) y de intercambio gaseoso a nivel ecosistema y hoja (Figura 3 y 4 del segundo artículo, Anexo). Casos similares de acumulación de agua han sido reportados en otros ecosistemas dominados por pastos (Kurc y Small, 2007). Así, la presencia de especies con fenología y sistemas radiculares contrastantes con los del zacate buffel (buffel principalmente activo durante el verano y, capaces de usar esa agua acumulada le permitió a la sabana extender su periodo con captura neta de C durante el 85% de los días del año, la cual es una proporción alta para un ecosistemas dominados por zacates (Wagle *et al*., 2015). Las limitaciones en la productividad del verano en la sabana y sus flujos durante las épocas más secas resultaron en un amortiguamiento de la variación interanual de la productividad neta, en especial durante los años secos (Tabla 2 del artículo tercero).

Los parámetros bioquímicos (V_{cmax} y J_{max}) de las especies, características y respuestas del dosel, la diversidad y complementariedad de especies, y su fenología, fueron factores bióticos clave en nuestro sistema de estudio, los cuales influenciaron la magnitud, estacionalidad y la variación interanual de la productividad neta. Sin embargo, entender a fondo la contribución de los factores bioticos en la productividad neta de ecosistemas áridos presenta varios retos. En primer lugar, las condiciones meteorológicas estresantes típicas de los ecosistemas áridos hacen que la caracterización de respuestas ecofisiológicas en campo sea una tarea muy difícil. Por ejemplo, las curvas de respuesta obtenidas durante varias fechas en que las plantas se encontraban en estrés severo resultaron de poca calidad y utilidad (observación personal), y el descartarlas redujo el número de muestra utilizados en nuestros análisis. En segundo lugar, los factores bióticos no solo contribuyen al modificar la respuesta del ecosistema a los factores abióticos como ha sido asumido en algunos estudios recientes (p ej. Hui *et al*., 2013; Shao *et al*., 2014 y 2015), sino que cambios bióticos pueden influir indirectamente sobre factores abióticos como la disponibilidad de agua o nutrientes, e influenciar así la dinámica temporal de los procesos del ecosistema, como fue evidente en este estudio. Son estas influencias indirectas las que son menos entendidas, más complicadas de estudiar, y menos tomadas en cuenta en modelaciones de los procesos a gran escala (Chapin *et al.*, 2000; 2003; Field *et al.*, 2007). En tercer lugar, la frecuencia y fuerza de las interacciones ecológicas, en especial las positivas, harían que los efectos bióticos sean mayores, aunque tal vez más difíciles de separar experimentalmente. Aun así, conforme se incremente el número de observaciones de características fisiológicas de las especies, los de diseños experimentales y arreglos de sitios con condiciones ecológicas contratantes, y los estudios que combinen datos con modelos, se mejorara el entendimiento de la contribución de los factores bióticos al funcionamiento de ecosistemas áridos.

V. CONCLUSIONES

En los ecosistemas áridos del mundo, factores abióticos (p ej. clima) y bióticos (p ej. composición, estructura, características fisiológicas) están cambiando drásticamente por causas naturales y antropogenicas (Hassan *et al.,* 2005). Sin embargo, desconocemos (en la mayoría de los casos) como modificar la biota impacta el funcionamiento de estos ecosistemas y los servicios que de ellos se derivan, como el secuestro de CO_2. Mediante el estudio de la fisiología de las especies y el intercambio gaseoso a nivel ecosistema en sitios con cobertura vegetal contrastante, fuimos capaces de caracterizar la dinámica de los flujos de carbono y agua a diferentes escalas temporales y de identificar maneras en las que los factores abióticos y bióticos que controlan esta dinámica.

Encontramos valores altos en parámetros bioquímicos (V_{cmax} y J_{max}) de la fotosíntesis C_3 en todas las especies de estudio, los cuales son una característica fisiológica importante que favorece la tasa de fotosíntesis en las especies y en los ecosistemas. Nuestros datos en conjunto con las pocas mediciones de estos parámetros que existen para especies de ecosistemas áridos del mundo, indican que estos rangos de valores pudieran ser comunes en estos ecosistemas. Además, encontramos que la precipitación y la disponibilidad de agua (medida como evapotranspiración) determinan una alta proporción de la productividad neta y los flujos de carbono que la componen. Sin embargo, encontramos que la diversidad y complementariedad, las características del dosel de índice de área foliar y respuesta del índice de área foliar a la precipitación y la fenología de las especies, ya sea directa o indirectamente, modificaron la estacionalidad y variabilidad interanual de los flujos, pero no productividad neta a largo plazo, cuando un matorral es transformado a sabana de zacate buffel.

Durante el periodo de estudio, ambos sitios, matorral y sabana de zacate buffel fueron sumideros de carbono comparables. Sin embargo, es posible que si las condiciones climáticas se tornan más áridas pudiéramos esperar que la sabana representara un mayor sumidero mientras pueda seguir teniendo agua acumulada a profundidad, como fue observado durante el año comparativo más seco (2013). Ademas, es posible esperar que si las condiciones de mayor aridez persisten por varios años consecutivos y el agua acumulada se agota, la ventaja de la sabana se disminuya con el tiempo y ambos sitios sean un sumidero comparable. Por otro lado, el manejo de los ecosistemas también puede influir en su potencial de secuestro de carbono. Dado que el índice de área foliar fue un fuerte determinante de la magnitud de la productividad neta diaria, es de esperar que mayor presión de pastoreo durante años secos se traduzca en una disminución de la productividad neta y con ello del potencial de secuestro de carbono. Este efecto sería más evidente en la sabana donde la gran mayoría de la cobertura vegetal es palatable, y no tanto en el matorral donde árboles y arbustos grandes pueden no ser accesibles al ganado. Es importante resaltar que el aumento en la dominancia del zacate buffel en sitios donde no es nativo se asocia con un aumento en el riesgo de fuego, lo cual comprometería el secuestro a largo plazo en estos ecosistemas. En contraparte, condiciones meteorológicas y acciones de manejo que aumenten la disponibilidad de agua en los ecosistemas muy probablemente se traduzcan en una mayor productividad neta y captura de carbono tanto en matorrales naturales como en ecosistemas dominados por zacate buffel.

VI. RECOMENDACIONES

Uno de los hallazgos de este estudio es que los altos valores en los parámetros V_{cmax} y J_{max} parecen ser una característica común en especies perennes C_3 de zonas áridas, aunque los datos existentes aún son limitados. Se deben realizar más estudios que caractericen estos parámetros y atributos relacionados (contenido de nitrógeno y fósforo, área foliar específica, conductancia del mesófilo, etc.) para un mayor número de especies y para otras zonas áridas cálidas del mundo. Esta información permitiría tener una mejor representación de la variación de estos parámetros entre especies y entre los tipos funcionales típicos de las zonas áridas, los atributos que pueden dar información de ellos, así como parametrizaciones de modelos más cercanas a la realidad y estimaciones de los flujos a mayores escalas más precisas.

En este estudio fue evidente diferentes componentes del balance hídrico (p ej. precipitación, evapotranspiración y almacenamiento de agua) pueden tener diferente efecto en la dinámica temporal de los flujos de carbono. Al mismo tiempo, los factores bióticos pueden tener una retroalimentación sobre estos componentes del balance hídrico, modificando su magnitud. Estudios que ayuden a comprender mejor el papel de los diferentes componentes del balance, estas retroalimentaciones y bajo qué circunstancias son importantes pudieran ser muy informativos en el entendimiento del funcionamiento de estos ecosistemas

Los hallazgos de este estudio y de otros (Atkinson *et al.,* 2016; Scott *et al.,* 2014) sugieren que las ventajas en el proceso de fotosíntesis y eficiencia de uso de agua a nivel de hoja de la vía fotosintética C_4 sobre la C_3 pueden no traducirse en las mismas ventajas a mayores niveles ecológicos (planta, ecosistema). Se requieren estudios que ayuden a entender cómo otras características asociadas a la vía fotosintética C_4, como mayor asignación de biomasa y actividad en raíces (Atkinson *et al.,* 2016), o una posible retroalimentación en el contenido de agua del suelo o sobre los procesos microbianos puede contrarrestar o modificar estas ventajas.

Entender las diferentes maneras en las que los factores bióticos influencian los flujos de carbono y agua en los ecosistemas áridos es una tarea que difícilmente puede ser respondido solo con observaciones y experimentos. Se deben realizar estudios que combinen datos con modelos que permitan explorar el efecto directo de modificar un solo factor o combinaciones de factores y su efecto indirecto sobre factores abióticos limitantes. Además, debido a que normalmente los ecosistemas áridos son dominados por especies con atributos contrastantes, es deseable que los modelos permitan la incorporación de las diferencias en las características de las especies dominantes, no un solo valor fijos para describir a todo el ecosistema.

Por último, el conocimiento que se ha generado sobre los factores que controlan la magnitud de los procesos en ecosistemas áridos y los encontrados en este estudio, puede permitir realizar estimaciones del impacto del cambio de cobertura en los flujos de carbono y agua a mayores escalas espaciales, en especial sobre la transformación de matorrales a sabanas de zacate buffel. Este tipo de escalamiento requeriría juntar datos existentes sobre los procesos, modelos que describan cómo los diferentes factores controlan los procesos, e información de campo y de percepción remota. Estudios de este tipo serían muy valiosos para entender las consecuencias ecológicas del cambio de cobertura, y proveer información que ayudara a desarrollar un manejo de los ecosistemas áridos a nivel regional no solo orientado a la ganadería sino a la provisión de servicios ecosistémicos como el secuestro de carbono y regulación climática.

VII. LITERATURA CITADA

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