Articles

Understory contribution to water vapor and CO$_2$ fluxes from a subtropical shrubland in northwestern Mexico

Contribución del estrato arbustivo a los flujos de agua y CO$_2$ de un matorral subtropical en el Noroeste de México

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Abstract

The net ecosystem production and evapotranspiration (ET) of arid and subtropical ecosystems is poorly understood by the lack of measurements of CO_2 and water vapor fluxes. Moreover, the contributions related to the fluxes in the different strata (*i.e.* understory) have been poorly studied. The present investigation estimates ET and CO_2 fluxes of a shrubby understory with the presence of *Mimosa distachya* from a subtropical shrubland in relation to the net estimates of ecosystem ET and net CO_2 fluxes determined with the eddy covariance technique. Instantaneous ET and CO_2 exchange measurements were carried in four plots for different time periods during the day (9, 11, 14 and 18 hours) using a static chamber (16.4 m^3) coupled with a fast response infrared gas analyzer. The variation of the fluxes during diurnal cycles was used to integrate the magnitude of the flux during the daylight hours. There was great variation in the understory fluxes, during July and September where there was more CO_2 gain from the atmosphere towards the ecosystem with a net CO_2 exchange of -1.35 ± 1.93 g C m^{-2} d^{-1} and -1.15 ± 0.74 g C m^{-2} d^{-1}, respectively, indicating that photosynthesis was higher than respiration in this stratum. In a dry period during August the CO_2 flux was -0.85 ± 0.73 g C m^{-2} d^{-1}. During these periods, ET was 3.63 ± 0.15 mm d-1 in July; 2.71 ± 0.08 mm d^{-1} in August, and 1.59 ± 0.5 mm d^{-1} in September. Comparing these results with the total ecosystem ET and the net CO_2 exchange, it was found that the understory contributes with 17 and 21% to CO_2 fluxes and from 25 to 39% in water vapor fluxes during the North American Monsoon.

Keywords: Biogeosciences, ecohydrology, understory, evapotranspiration, net CO_2 exchange, *Mimosa distachya*.

Resumen

La productividad neta del ecosistema y evapotranspiración (ET) de los ecosistemas áridos y subtropicales es poco entendida por la escasez de mediciones de flujos de CO_2 y vapor de agua. Todavía las contribuciones relativas a los flujos en los diferentes estratos (p. ej., sotobosque) han sido pobremente analizadas. Este estudio estima ET y los flujos de CO_2 en un estrato arbustivo con presencia de *Mimosa distachya* de un matorral subtropical, en relación con estimaciones netas de la ET y el flujo de CO_2 del ecosistema, determinado con la técnica de covarianza de vórtices. Se tomaron lecturas instantáneas de ET y del intercambio de CO_2 en cuatro parcelas durante distintos periodos durante el día (9, 11, 14 y 18 horas), usando una cámara estática (16.4 m^3), equipada con un analizador de gases infrarrojo de rápida respuesta. La variación de flujos durante los periodos de medición se usó para integrar la magnitud del flujo durante el día. Se presentó gran variación en los flujos durante julio y septiembre, donde hubo más ganancia de CO_2 de la atmósfera hacia el ecosistema, con un intercambio neto de CO_2 de -1.35 ± 1.93 g C m^{-2} d^{-1} y -1.15 ± 0.74 g C m^{-2} d^{-1}, para cada mes, respectivamente, lo cual indica que la fotosíntesis fue más alta que la respiración en este estrato. En un periodo seco durante agosto, el flujo de CO_2 fue de -0.85 ± 0.73 g C m^{-2} d^{-1}. Durante estos periodos, el ET fue de 3.63 ± 0.15 mm d^{-1} en julio; 2.71 ± 0.08 mm d^{-1} en agosto, y 1.59 ± 0.5 mm d^{-1} en septiembre. Comparando estos resultados con los flujos netos de vapor de agua y CO_2 del ecosistema, se encontró que el estrato arbustivo aporta entre 17 y 21%

a los flujos de CO_2 y de 25 a 39% en los flujos de vapor de agua durante el monzón de Norteamérica.

Introduction

Arid and semi-arid ecosystems cover about 40% of the earth's surface (Shaw, Huxman, & Lund, 2005). These ecosystems have taken an important interest in the study of the global carbon cycle (C) due to the complexity in the dynamic functional processes that define their productivity; representing up to 30% of net primary productivity, store about 15% of the organic C content in the soil and control the global CO_2 sink potential in terrestrial ecosystems (Schlesinger & Bernhardt, 2013; Poulter *et al*., 2014; Ahlström *et al*., 2015), generally are limited by water availability, where precipitation is the main factor that regulates their productivity (Biederman *et al.,* 2017). Rainfall regimes in these ecosystems are seasonal, precipitation events occur as "intermittent

pulses" (Ehleringer, 2001; Huxman *et al*., 2004), making their biogeochemical processes highly sensitive to intensity and frequency of precipitation (Austin *et al*., 2004; Verduzco *et al*., 2015), which makes the eco-physiological activity from the vegetation and soil organisms very dynamic and difficult to predict (Vargas *et al*., 2013; Biederman *et al*., 2016).

The balance of C and H_2O in terrestrial ecosystems is delimited by the exchange of elements and energy, which occurs through the CO_2 assimilation during photosynthesis (GPP, gross primary productivity) and the CO_2 release into the atmosphere through ecosystem respiration (R_{eco}). This CO_2 exchange between the atmosphere and the ecosystem is the net balance of GPP and R_{eco} being known as net ecosystem exchange (NEE), which is a robust approximation of net ecosystem productivity (PNE = -NEE) (Chapin, Matson, & Vitousek, 2011; Grace, Mitchard, & Gloor, 2014).

The exchange of elements and energy between the ecosystem and the atmosphere has been measured by different techniques, but at ecosystem level the most widely used is the eddy covariance technique (EC; Baldocchi, 2008). However, this technique has limitations to represent fluxes from different strata of the ecosystem, since, it assumes a relatively large and homogeneous area of land, it does not distinguish between the different strata of the ecosystem (*i.e*., understory and soil microbiota). Therefore, the relative contributions to ecosystem fluxes from canopy and understory elements are not widely known (Scott *et al*., 2003). It has been found that due to the understory conditions such as low wind speed, high heterogeneity and intermittent turbulence, EC

measurements are inconsistent. Static chambers are a suitable technique to study the gas exchange dynamic at small scales with a wide spatial variability (Angell, Svejcar, Bates, Saliendra, & Johnson, 2001; Yépez *et al.*, 2005) and present an acceptable correlation with the eddy covariance technique (Angell & Svejcar, 1999; Czóbel *et al.*, 2005; Wohlfahrt, Fenstermaker, & Arnone III, 2008).

Due to the structure of the understory, which consists in a mosaic of heterogeneous patterns, very common in arid and semi-arid areas (Loik, Breshears, Lauenroth, & Belnap, 2004), the use of static chambers is recommended to detect the effects of vegetation and land use change in CO_2 and water vapor fluxes (Delgado-Balbuena *et al.*, 2013). Few researches have quantified evapotranspiration and CO_2 fluxes at intermediate scales or in specific compartments from ecosystems (Scott *et al.*, 2003). However, it has been observed that in arid and semi-arid ecosystems the understory or lower strata of the ecosystem can contribute with 44% of the net C fluxes (Misson *et al.*, 2007) and 62% of the ET in a mesquite forest (Yépez *et al.*, 2007).

Because it is possible with the use of static gas exchange chambers to quantify these ecosystem fluxes (Arnone & Obrist, 2003; Jasoni, Smith, & Arnone, 2005; Delgado-Balbuena *et al.*, 2013), in this study CO_2 and water vapor fluxes were measured in an understory with the presence of *Mimosa distachya* in a subtropical shrubland from Northwest Mexico, to estimate the relative contribution to the net ecosystem fluxes. We hypothesize that understory contributes with a significant proportion of the total CO_2 and water vapor fluxes of the ecosystem, besides that, their

relative contribution varies in the soil water availability during the rainy season.

Materials and methods

Study site

The study site is a subtropical shrubland located in the municipality of Rayón in the central part of the State of Sonora (29.74 ° N, -110.54 ° W) at an altitude of ~632 m.s.n.m (Vivoni *et al*., 2010). The climate of the area is semi-warm arid -BSoh (x') - according to the classification of García (1998). This area has a strong seasonality influenced by the North American Monsoon System that allows an active rainy season during the summer, representing ~70% of the annual rainfall (Villarreal *et al.*, 2016). Historical records report a mean annual temperature of 21.4 ° C with a mean precipitation of 502 mm year^{-1} during the period 1974-2016 (CICESE, 2018). The site is equipped with an eddy covariance system (Baldocchi *et al*., 2001; Baldocchi, 2008), which continuously measures the CO_2 and water vapor flux from the shrubland (Watts *et al*., 2007). Soils are shallow (~1 m) and are classified as regosol-yermosol with

sandy loam texture (from 0 to 30 cm) and sandy clay (from 30 to 100 cm) (Verduzco *et al*., 2018).

The vegetation at the site is characterized mainly by microphyll species, with the presence of thorns and the loss of leaves during the dry season (Rzedowski, 2006). It has a two-strata defined by: (1) a tree layer, dominated by *Prosopis velutina*, *Acacia cochliacantha*), *Parkinsonia praecox* and *Fouquieria macdougalii consortia* with *Jatropha cordata*; and (2) a shrub layer formed by *Ambrosia cordifolia*, *Encelia farinosa*, *Lycium berlandieri* and a notable presence of *Mimosa distachya* (Tarin *et al*., 2014).

Net CO_2 exchange (NCE) and evapotranspiration of the shrub layer (ET_{arb})

For convenient purposes in the present study we use the terms of net CO_2 exchange (NCE) and evapotranspiration of the shrub layer (ET_{arb}) to refer to the CO_2 exchange and the measured water vapor flux with the static chamber. Meanwhile, net ecosystem exchange (NEE) and evapotranspiration of the ecosystem (ET) are referred to the exchange of CO_2 and water vapor flux from the eddy covariance technique (EC).

Gas exchange measurements were made during the summer of 2012, on the days of the year 199, 220-221 and 258-259 during the North American monsoon season. The CO_2 and water vapor fluxes were

quantified using a static gas exchange static chamber, a method developed and explained in detail in Arnone and Obrist (2003). The chamber is a modified version of the 4.2-meter diameter dome manufactured by Shelter Systems Inc. (Menlo Park, CA, USA). The chamber has a height of 2.0 m, a weight of 30 kg, volume of 16.4 m^3 and covers an area of 12.25 m^2. Its structure is formed by a moderate semi-transparent and translucent polyethylene (PE) cover that allows passing 90% of the light into the chamber (Arnone & Obrist, 2003). The version used by Arnone and Obrist (2003) was modified by constructing a lower base for greater support and sealing (Figure 1).
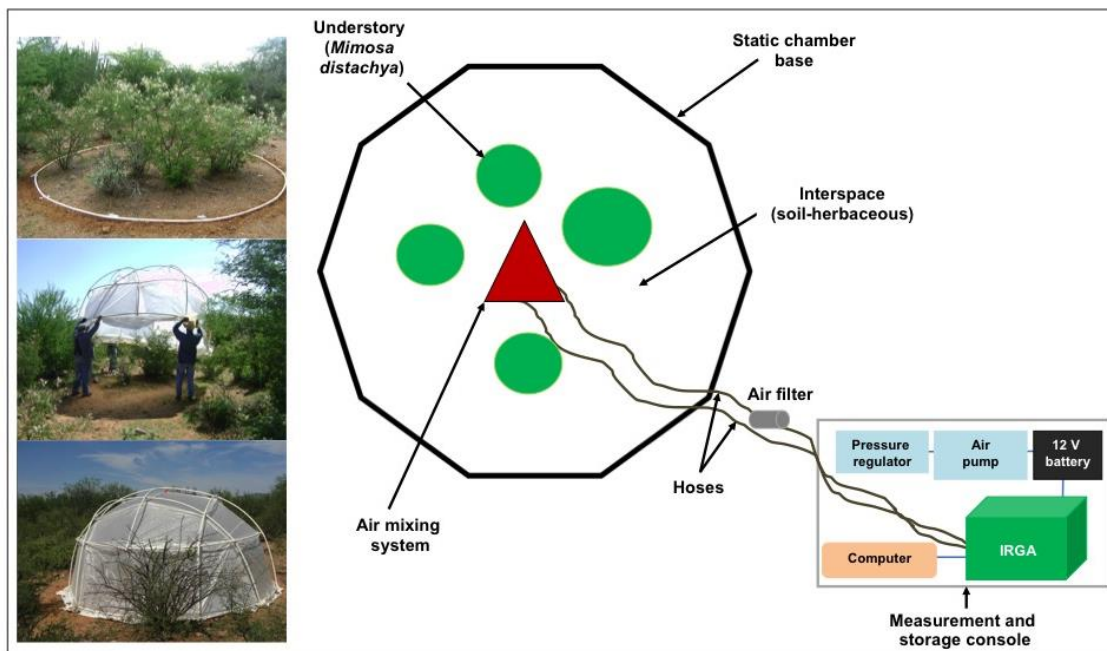
Figure 1. Experimental design for gas exchange measurements with a static chamber and a diagram of the measurement, control and storage system.

Four experimental plots with presence of *M. distachya* and a similar leaf area were selected, which was determined with a ceptometer (Sun Scan SS1, Delta T Devices Ltd., Cambridge, UK) (Table 1). The measurements length were performed to 120 from 140 seconds the chamber was placed on each experimental plot, after each measurement, the chamber was removed and aerated for several minutes before the next measurement in another plot (Hamerlynck *et al*., 2011). Instantaneous measurements of NCE and ET_{arb} were taken in the experimental plots in four periods of the day (9, 11, 14 and 18 hours).

Table 1. Leaf area index for experimental plots in the understory of the subtropical shrubland.

Plot	Mean	Standard deviation	Standard error
1	0.6	0.30	0.12
2	0.6	0.32	0.11
3	0.8	0.46	0.16
4	0.9	0.77	0.27

Before each measurement, an air mixing system consisting of six 12 cm diameter fans was placed at the center of each plot, four fans were oriented horizontally and two oriented vertically to homogenize the air inside the chamber. The air inside the static chamber was circulated to an infrared gas analyzer (IRGA, LI-840, LI-COR Biosciences, Lincoln, NE, USA) to determine the CO_2 and water vapor concentrations (change). For this, a pneumatic pump (GAST, Benton Harbor, MI, USA) was used to circulate the air into IRGA, a flow regulator (Dwyer Instruments, Inc., Michigan City, IN, USA) to control the air at 1 liter per minute and a filter (Balston DFU, Haverhill, MA, USA) to prevent impurities towards the IRGA. Data was collected by the IRGA and was stored in a laptop using the data acquisition software from the LI-840 (Figure 1).

Flux calculation with static chambers

The NCE and ET_{arb} calculation in each experimental plot was obtained through the flux equation for static chambers from Jasoni *et al*. (2005):

$$F = \frac{m \cdot V \cdot P}{A \cdot R \cdot T} \qquad (1)$$

where *F* is the instantaneous net flux of CO_2 (µmol m^2 s^{-1}) or H_2O (mmol m^2 s^{-1}), *m* is the change ratio of CO_2 and H_2O concentration with respect

to time (*i.e.* Figure 2), V is the total volume of the static chamber (m^3), P is the atmospheric pressure (kPa), R is the ideal gases constant (8.3144 m^3 Pa mol^{-1} K^{-1}), T is the mean air temperature during the measurement (K) and A is the area of the static chamber (m^2).
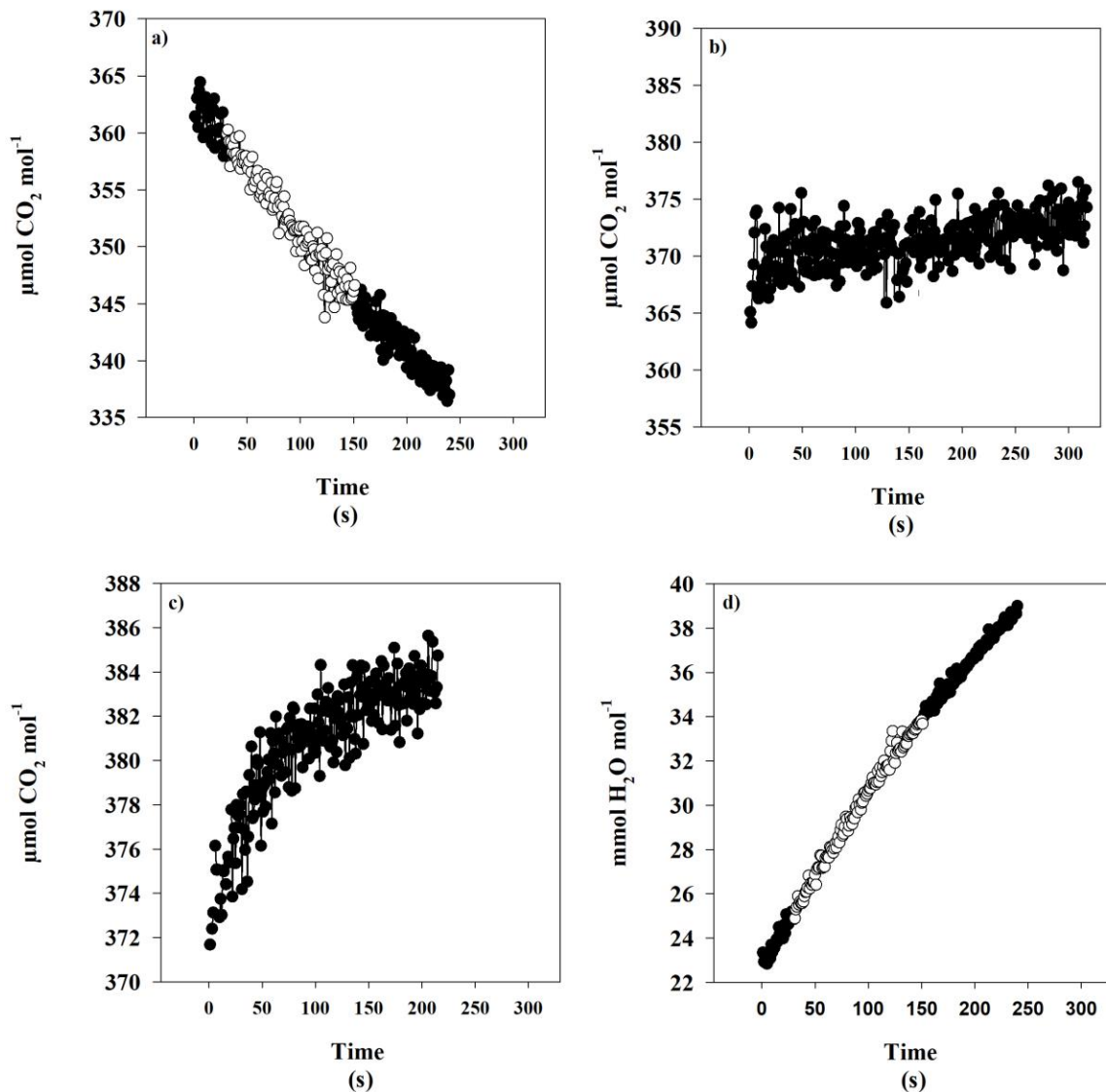

Figure 2. Examples of instantaneous changes in CO_2 and water vapor concentrations inside the chamber along a measurement period in an

experimental plot with the presence of *M. distachya*. Panel a) represents CO_2 assimilation; b) compensation between assimilation and emission; c) CO_2 emission and d) water loss. The white portion is the 120 seconds considered for NCE and ET_{arb} calculation.

During each measurement P was obtained from the IRGA and T with a thermocouple. To obtain the slope (m) of each measurement, the data of gas concentration increments were recorded 30 s after the measurements starting, in order to allow stabilization conditions inside the chamber. In each measurement, instantaneous increases in CO_2 and H_2O were plotted to determine m, negative slopes represent CO_2 assimilation from the ecosystem, while positive slopes are CO_2 and water vapor emissions into the atmosphere (Figure 2).

To integrate the CO_2 and water vapor fluxes during daytime, the procedure of Potts *et al*. (2006) was followed, where the instantaneous NCE and ET_{arb} values of each plot were calculated using an adjustment curve and the integration trapezoidal function (SigmaPlot v.12, Systat Software, Inc., Chicago, IL, USA).

Net ecosystem exchange (NEE) and evapotranspiration (ET)

The eddy covariance technique (EC) employs high frequency measurements (10 Hz) of gas concentrations (i.e. H_2O, CO_2 or CH_4), the wind direction in three dimensions allows to estimate the vertical exchange of energy and gases between the ecosystem and the atmosphere based on the turbulence that occurs in the atmosphere (Baldocchi, 2014; Aubinet, Vesala, & Papale, 2012). The flux is defined as the covariance of the vertical fluctuations of the wind speed and the concentration of CO_2 and water multiplied by the mean air density in a period of time (Delgado-Balbuena et al., 2019).

The eddy covariance system at the study site consisted of a three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Logan, Utah, USA) and an open-path infrared gas analyzer (LI-7500, LI-COR Biosicences, Lincoln, Nebraska, USA) that perform the measurements at 20 Hz and were located at a height of 6 m above the vegetation. Additionally, meteorological variables measurements were made including; relative humidity and temperature (HMP45D, Vaisala, Helsinki, Finland), precipitation (TR-525USW, Texas Electronics, Dallas, TX, USA) and soil moisture (CS616, Campbell Scientific, Logan, UT, USA). Data derived from the EC system and the meteorological sensors were stored in a datalogger (CR5000, Campbell Scientific, Logan, Utah, USA). Subsequently, data were processed and averaged in half hours to obtain NEE and ET (Verduzco et al., 2018). Previous studies describe in more detail the EC system instrumentation and the meteorological sensors at study site, as well as, the processing and quality control of NEE and ET data (Watts et al., 2007; Vivoni et al., 2010; Méndez-Barroso et al., 2014; Tarin et al., 2014).

To represent the daytime fluxes and to compare with the NCE and ET_{arb} measurements, a mean of seven days of NEE and ET observations were made, that included three days previous to measurements with the static chamber, the day of measurement and three days after.

Results

Environmental conditions

Figure 3 shows the variations of the environmental conditions during the CO_2 and water vapor fluxes measurements period in the subtropical shrubland of Rayón, Sonora, Mexico. Temperature (T) varied between 24.48 and 34.79 ° C, while relative humidity (RH) showed an inverse behavior to temperature with values between 77.90 and 21.52%. During the rainy season at the study site 39 precipitation events were recorded, of which 62% were greater than 3 mm and the remaining (39%) were less than 3 mm, with dry periods (intervals between the of precipitation events less than or equal to four days). Similar to RH, soil moisture (SM) responded to precipitation patterns. Soil moisture increased with the presence of rain and decreased when the precipitation pulses ended, the

highest value observed of SM was 0.20 m^3 m^{-3} after a precipitation event greater than 70 mm and the lowest was 0.01 m^3 m^{-3}.
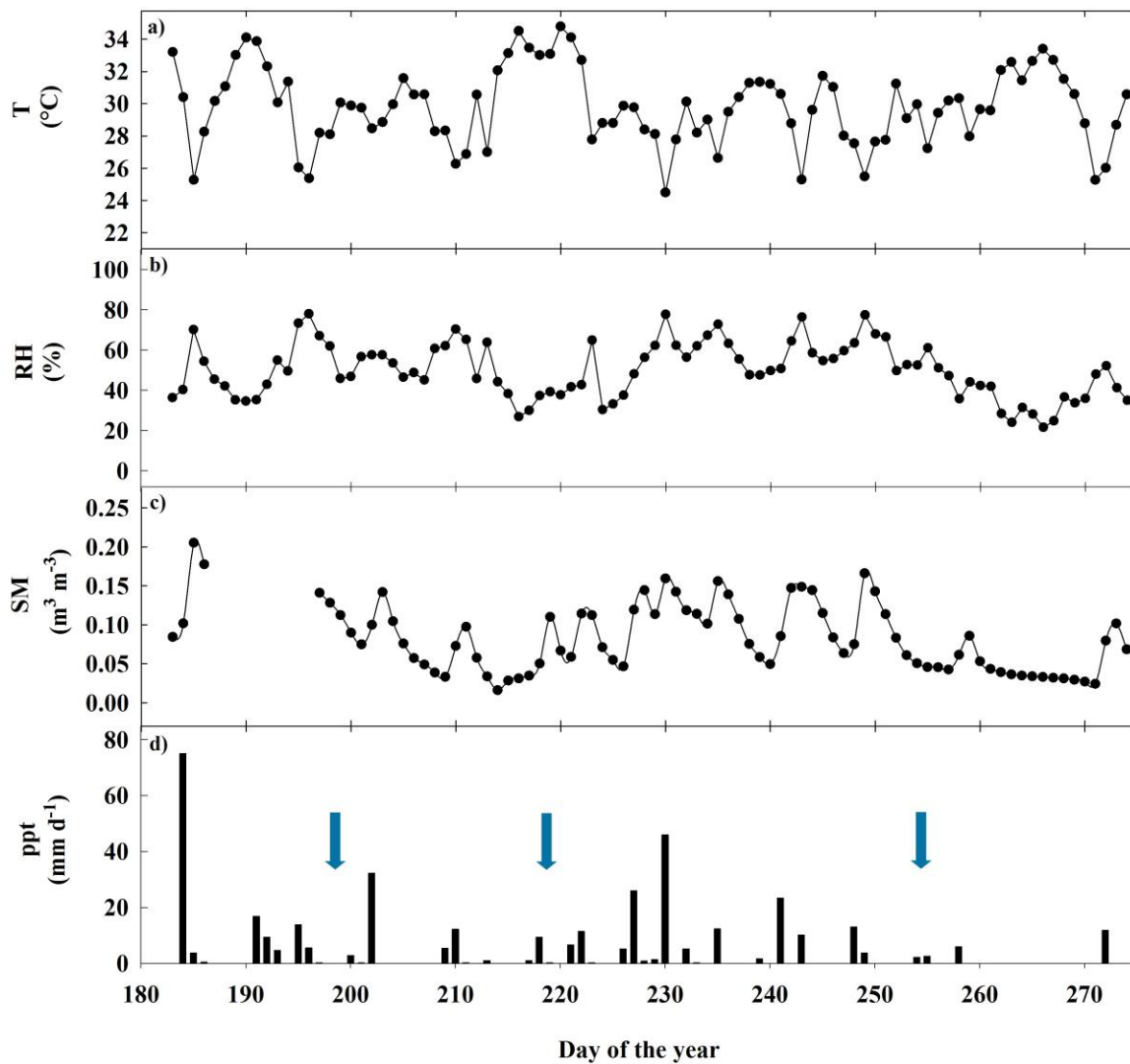

Figure 3. Mean daytime micrometeorology for the period July-September 2012: a) temperature (T), b) relative humidity (RH), c) soil moisture (SM) and d) precipitation (ppt). The arrows indicate the days

of the year (199, 220-221 and 258-259) when the NCE and ET_{arb} measurements were made with the static chamber.

On the other hand, the mean value of ET_{arb} at 09:00 hours, during July was 2.40 ± 0.09 mm d^{-1}, while in August showed a value of 1.54 ± 0.10 mm d^{-1} and September of 0.84 ± 0.10 mm d^{-1}. Maximum ET values were observed between 11:00 and 14:00 hours with values of 2.59 ± 0.16, 1.73 ± 0.09, 2.54 ± 0.07 mm d^{-1} for July, August and September, respectively, showing minimum values at 18:30 hours (in the range of 0.07 to 0.72 mm d^{-1}).

NCE and water vapor flux at the shrub layer

Figure 4 illustrates the magnitude and variations of NCE and ET_{arb} during a diurnal cycle in summer of 2012. Maximum mean (n = 4) in NCE fluxes were detected at 11:00 hours with values of -2.46 ± 0.54 and -5.08 ± 0.96 µmol m^{-2} s^{-1} for August and September, respectively, except for July which showed the highest NCE value at 9:00 with -6.83 ± 1.32 µmol m^{-2} s^{-1}. During the afternoon, the mean fluxes decreased to -0.35 ± 1.72, -1.02 ± 0.10 and -0.21 ± 0.27 µmol m^{-2} s^{-1}. Notably, the same variations of NCE with respect to NEE are observed during the daytime periods, coinciding with its maximum CO_2
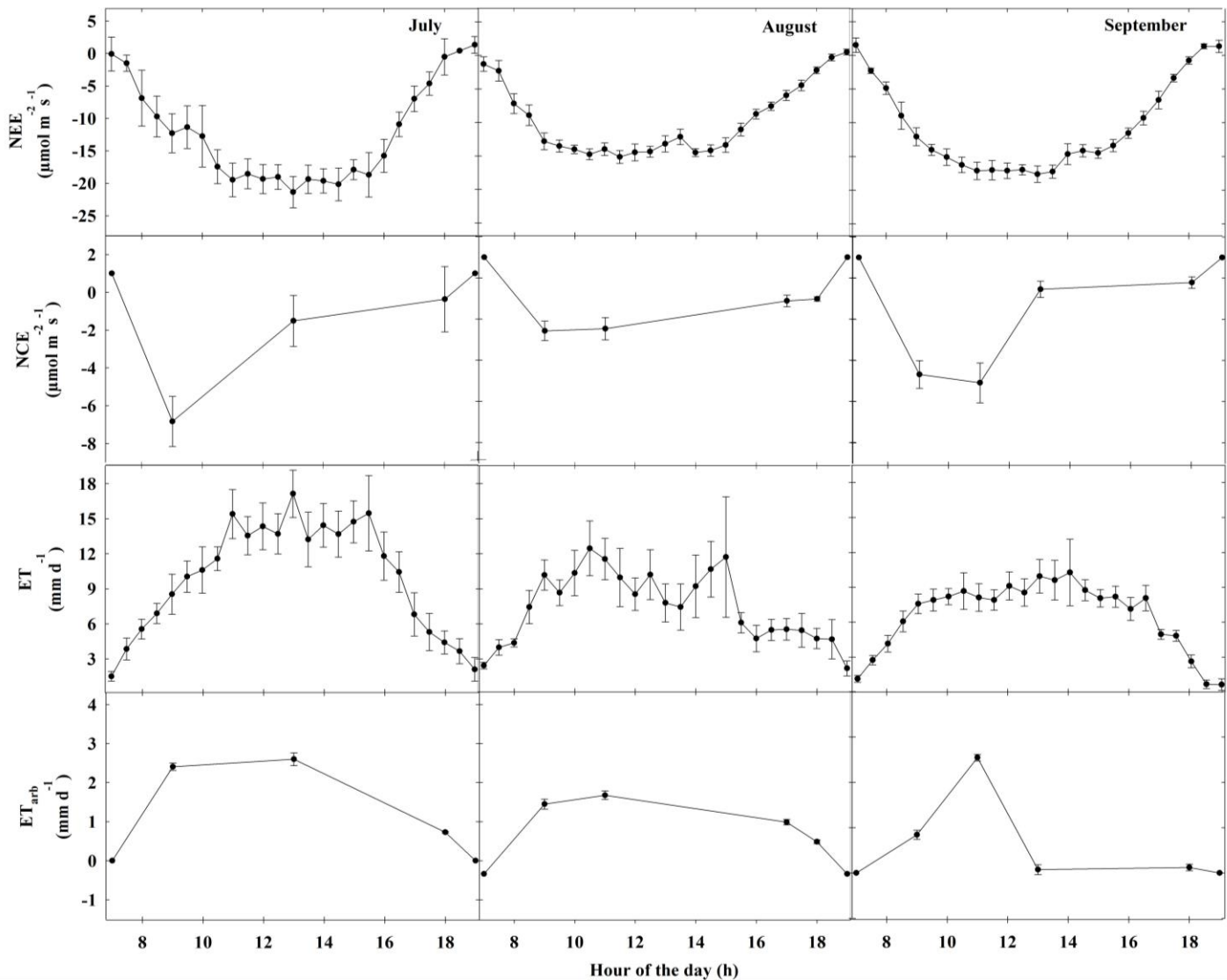
assimilation values at the same times of the day.

Figure 4. Diurnal variations of the net CO_2 exchange (NCE) and evapotranspiration (ET_{arb}) in the understory with the presence of *M. distachya* and the total net ecosystem exchange (NEE) and evapotranspiration (ET) from the ecosystem determined by the eddy covariance technique during the study period.

Evapotranspiration and net ecosystem exchange

The ecosystem ET and the CO_2 fluxes obtained with the EC technique are shown in Figure 4. Negative values of NEE began approximately at 7:00 hours during July and August with ranges between -1.28 and -0.08 µmol m^{-2} s^{-1}, while in September the ecosystem begin to show a net CO_2 gain at 7:30 with -2.23 µmol m^{-2} s^{-1}. These values starting to show a continuous and quick increasing until approximately 11:00 hours for the three months, with maximum values of CO_2 assimilation of -18.54, -15.14 and -17.12 µmol m^{-2} s^{-1}, for July, August and September respectively. During the afternoon, the ecosystem responds to the diminution in solar radiation and negative CO_2 decreased to minimum values of -0.51, -0.29 and -3.37 µmol m^{-2} s^{-1}.

Water vapor exchange at the ecosystem level begin at 6:30 hours with solar radiation availability and the increase in temperature. During July mean values were between 1.10 and 17.14 mm d^{-1}; August showed ET ranges between 1.50 and 12.43 mm d^{-1}. The results measured by EC technique indicate that September differs from the previous measured months, the beginning of the water vapor flux dynamic in the ecosystem occurred at 07:00 hours and concluded with the day light cycle at 17:30 hours, showing a range of values between 1.13 and 10.27 mm d^{-1}.

Evapotranspiration values did not start near or equal zero, because the measurements were made only with the solar radiation availability.

Dynamics of integrated fluxes of the shrub layer and the ecosystem

The understory with the presence of the legume *M. distachya* has an important contribution to the CO_2 and water vapor fluxes dynamic during daylight hours in the subtropical shrubland. It presented great variability in the total daytime fluxes, where July and September were the months with the highest C gains, with values of -1.3 ± 1.93 g C m^{-2} d^{-1} and -1.15.85 ± 0.74 g C m^{-2} d^{-1}, respectively, suggesting that in this understory during these periods photosynthesis was stronger than respiration. In August, when a dry period occurred, NCE was -0.85 ± 0.73 g C m^{-2} d^{-1}, lower than the other two months. The ET_{arb} in July was 3.63 ± 0.15mm d^{-1}, while August was 2.71 ± 0.08 mm d^{-1} and September with 1.59 ± 0.05 mm d^{-1}. Notably, evapotranspiration variations followed the pattern of water availability with the lowest fluxes in September (Figure 5).
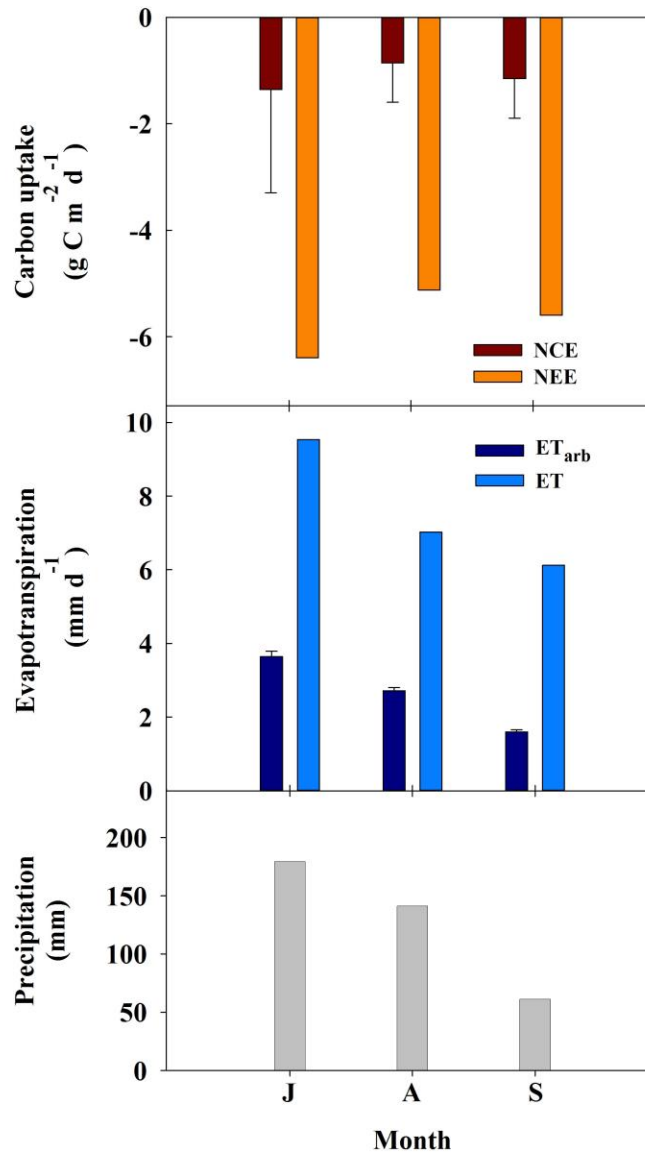
Figure 5. Comparison of NCE and ET$_{arb}$ fluxes and total fluxes from the ecosystem (NEE and ET) during the study period, where J = July, A = August, S = September.

The contribution to the CO_2 and water fluxes from the understory was considerable. Its relative contribution to net CO_2 ecosystem flux during the studied period was 20% and 35% to water flux. Maximum CO_2 gain values were observed during the month of July, both measured by the static chamber and the EC system. On the other hand, NCE and NEE varied according to the availability of moisture. Notably, the variation in ET_{arb} and ET followed the pattern of water availability in the soil, showing the lowest fluxes in September.

Discussion

Dynamics of CO_2 and H_2O fluxes are more active during the rainy season. The relative contribution of the understory or lower strata of the ecosystem is still unknown. In our study site, there is dominance of the leguminous *M. distachya* in the understory, thus our hypothesis suggested that this shrub has an important contribution to water and CO_2 fluxes magnitude and dynamics in this ecosystem.

There are methodologies that allow the measurement of CO_2 and water fluxes and separate these fluxes at ecosystem and understory level, such as static chambers, which are useful tools for measuring CO_2 and water vapor fluxes in different strata in ecosystems and experimental plots (Arnone & Obrist, 2003; Yépez *et al*., 2005).

The area covered by static chambers includes all representative components of the ecosystem, thus eliminating the need to separate flux measurements in shrub spaces (soil vs. grasslands) and the shrub layer, a necessary procedure for small chambers used by Angell and Svejcar (1999) and Angell *et al*. (2001), in addition to allow replication which facilitates statistical rigor (Yépez *et al*., 2005).

Moreover, it has been demonstrated that static chamber methods have a consistent relation with fluxes estimated with the EC technique (Oechel *et al*., 1998; Angell *et al.*, 2001; Wohlfahrt *et al*., 2008), without losing the representativeness of the ecosystem.

Our results show a dynamic and variable patterns of CO_2 and water vapor fluxes over the daytime periods, prevailing a considerable CO_2 assimilation values (Figure 4), which represents a relative contribution between 17% and 21% of the net CO_2 ecosystem flux (i.e. NEE), while ET of the understory represented between 25% and 39% of the total ET flux in the ecosystem. This response suggests that there was enough moisture in the soil during the monsoon season for *M. distachya* to remain physiologically active, since photosynthesis during daylight hours was always dominant, despite presenting a major decrease starting at noon, which probably limited its contribution to net CO_2 ecosystem flux (Figure 4).

The soil microorganisms activity was probably also influenced by the availability of water in the soil to contribute to gas exchange dynamics.

In our experimental plots, there is an important presence of biological soil crusts, which could contribute to the net CO_2 exchange. In

the Mojave Desert, Jasoni *et al.* (2005) attribute that high assimilation rates may have been due to the photosynthesis of the autotrophic soil communities such as biological crusts, where under optimal conditions of water availability and temperature are able to carry out their biological activity and significantly contribute to the biogeochemistry of the ecosystem (Delgado-Baquerizo, Maestre, & Gallardo, 2013).

Most precipitation events in arid and semi-arid ecosystems are rain pulses less than 3 mm (Loik *et al.*, 2004), small rain pulses cause a response from most plants, but large enough to stimulate a response from biological crusts, which are usually from 1 to 2 mm from the soil surface and between the vegetation cover (Austin *et al.*, 2004). Therefore, it would be plausible to consider an important contribution from the biological soil crusts to the C fluxes in the understory. For example, at our site in average presented 3-day intervals between each precipitation event and 58% was greater than 3 mm (Figure 2). Considering that, there was an optimal presence of moisture in the plots of the understory with the presence of *M. distachya*, an ideal microenvironment was suitable for a high physiological activity of this legume and the biological soil crusts.

We are not aware about studies that provide data from daytime NCE and ET patterns in lower ecosystem strata such as the understory in semi-arid ecosystems. However, the relative contribution of the understory with the presence of *M. distachya* is similar to previous studies reported in several semi-arid areas (Misson *et al.*, 2007; Yépez, Scott, Cable, & Williams, 2007). Likewise, it is possible to compare our NCE estimates (Figure 4) measured with the static chamber during the rainy season with other shrubland ecosystems. For example, Jasoni *et al.* (2005) reports

daytime assimilation values of -1.5 µmol m^{-2} s^{-1} in the Mojave Desert; while Obrist, DeLucia, and Arnone, (2003), and also Prater Obrist, Arnone III, and DeLucia (2006) report values of -3 µmol m^{-2} s^{-1} and ranges from 0.2 to 4.3 µmol m^{-2} s^{-1}, respectively while Angell *et al*. (2001) shows values between -7 and -10 µmol m^{-2} s^{-1} in the Great Basin Desert. In the context of daytime C gains in grasslands and managed crops, it can be mentioned that our estimates are within the ranges of -0.1 and -6 g C m^{-2} d^{-1} reported by Delgado-Balbuena *et al*. (2013).

The net CO_2 exchange of the subtropical shrubland studied during the monsoon season show similar values with other seasonally dry ecosystem from Mexico (Delgado-Balbuena *et al*., 2019) and particularly those that belong to the North America monsoon region (Hinojo-Hinojo *et al*., 2019). In general, C gain values are consistent with other arid and semi-arid ecosystems, since the observed gain of -6.39 g C m^{-2} d^{-1} is in the values range reported for the Mojave desert of -1.7 g C m^{-2} d^{-1} (Wohlfahrt *et al*., 2008) and for semi-arid meadows with values between -6 g C m^{-2} d^{-1} (Zhao *et al*., 2006) and -3.9 g C m^{-2} d^{-1} (Kato *et al*., 2004).

Conclusion

The variability CO_2 and water vapor fluxes in the ecosystem were influenced by the presence of rainfall during the summer monsoon

season. The use of static chambers (with an area of 12.25 m^2 and a volume of 16.4 m^3) is a useful tool to measure ecosystem gas exchange and allows studying the relative contribution and variability at small scales with wide spatial heterogeneity, without losing the representativeness of the ecosystem. It is important to make distinctions between the different strata present in arid and semi-arid ecosystems, since each one contributes differently to variations in gas exchange with the atmosphere. Comparing our results with EC technique estimates, we found that the understory with the presence of *M. distachya,* represents an important and significant contribution to the CO_2 and water exchange in the ecosystem, since it can contribute up to 20 and 35%, respectively.

The study of the relative contributions of the understory and their dynamics towards CO_2 and water vapor allow us to understand the functional dynamics of arid and semi-arid ecosystems.

It is important to understand the influence of precipitation in and CO_2 and water vapor fluxes because it is expected that climate change will affect precipitation patterns and therefore, create a response in ecosystem flux dynamics.

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