



Carbon dioxide and water vapour exchange in a tropical dry forest as influenced by the North American Monsoon System (NAMS)

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ABSTRACT

To better understand the effects and relationship between precipitation, net ecosystem carbon dioxide (NEE) and water vapor exchange (ET), we report a study conducted in the tropical dry forest (TDF) in the northwest of Mexico. Ecosystem gas exchange was measured using the eddy correlation technique during the presence of North American Monsoon System (NAMS) in 2006. Patterns in NEE and ET were different in wet and dry periods. Three markedly defined periods were found during the six-month study period. A pre-monsoon period, where gas exchange was close to zero. A monsoon period, divided in two stages: 1) early monsoon: a strong increase in the respiratory rate marked by a peak of positive values, with a maximum of $22 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$, and, 2) late monsoon: an assimilation period occurred in the peak of the monsoon period, with sustained values around $-20 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$. The final was a post-monsoon period, where ecosystems returned to dormancy. NEE and ET trends in the TDF were similar to other seasonally dry ecosystems influenced by the NAMS. During the study period the TDF of Northwest Mexico acted as a sink capturing $374 \text{ g CO}_2 \text{ m}^2$ with an ecosystem water use efficiency ($-NEE/ET$) comparable to other ecosystems in the region. Mechanistic information about biological and environmental variables controlling gas exchange dynamics is still necessary to predict how seasonally dry ecosystems would respond to climate change.

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1. Introduction

The North American Monsoon System (NAMS) is a pronounced increase in rainfall from a dry period, mainly in May and June, to a rainy period, from July to September, over large areas in the southwest of the United States and the north-western Mexico (Adams and Comrie, 1997). This system confers seasonally dry and wet periods to most ecosystems in the region (Douglas et al., 1993; Gochis et al., 2006; Vivoni et al., 2007). In seasonally dry ecosystems, precipitation and soil moisture are the primary controls of biological activity (Huxman et al., 2004a; Kurc and Small, 2007). During the dry season, the biological activity in the ecosystem is almost null and the ecosystems remain dormant during this period, but with the onset of the NAMS, the input of precipitation into dry soil immediately stimulates gas exchange dynamics of the system in several ways. First, a marked CO_2 efflux from respiration and

physical displacement of CO_2 from organic and inorganic C sources is apparent (Emmerich, 2003; Huxman et al., 2004a,b). Then, a CO_2 assimilation period occurs along with the canopy development; however this activity is not significant in the ecosystem carbon accumulation until sometime later, when the full canopy development occurs (Huxman et al., 2004a; Yopez et al., 2007). Thus, in the NAMS regions we can distinguish these periods as the pre-monsoon or dry season, when vegetation is dormant and biological activity is low, but temperatures are optimal for growth and moisture starts to increase in the atmosphere. A monsoon period or growing season, that has two stages: 1) a rapid activation of biological processes as moisture becomes available 2) a stage of maximum activity at the peak of the monsoon. A post-monsoon period that is characterized by the sudden drop of leaves and the ecosystem returns to its dormancy as moisture becomes scarce and temperatures drop. There is evidence that this conceptual model applies well in arid and semi-arid pulse driven ecosystems under the influence of the NAMS but we want to test if this same model applies to the TDF in Sonora which represents the northern limit of

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these tropical ecosystems in America and is highly influenced by the NAMS.

The tropical dry forest (TDF) distribution covers large areas in the dry, markedly seasonal, tropical regions of the world (Murphy and Lugo, 1986; Becerra and Venable, 2008). In Mexico it is one of the four most extensive types of vegetation (Rzedowski, 1978). In its natural state, it is a dense community dominated by small to medium sized trees that lose their leaves and remain dormant during the dry season. This ecosystem extends from Central America, to the northern state of Sonora, Mexico and covers a great extension along the pacific coast (Martínez-Yrizar et al., 2000). In Sonora, the TDF appears, mainly, in the foothills of the Sierra Madre Occidental and occurs at elevations between 250 and 1200 m (Burquez and Martínez-Yrizar, 2004). The mean annual temperature is 24 °C and the mean annual precipitation 712 mm, with the rainfall being mainly seasonal and approximately 80% of the precipitation occurring during the NAMS (July to October) (Álvarez-Yépez et al., 2008).

In this paper, we report the results of a study conducted over the monsoon season in the TDF of north-western Mexico, to better understand the relationship and effects of the precipitation in the net ecosystem of carbon dioxide and water vapor exchange. We specifically address the flux variation that occurs during pre-, peak and post-monsoon periods during a single growing season.

2. Materials and methods

2.1. Site description

The study site was located in the south of Sonora, Mexico at Ejido La Estrella (27°50'40.7"N, 109°17'52"W), at 460 m of elevation, in the foothills of the Sierra Madre Occidental (Fig. 1). The location is 7.5 km east of the town of Rosario de Tesopaco and approximately 85 km from Ciudad Obregon. The climate of the zone is warm, semiarid according to Köppen's Classification (INEGI, 2007). The mean annual temperature is 22.1 °C and precipitation of 712 mm (Rosario Tesopaco Climatological Station No. 00026100, Comisión Nacional del Agua), with most of the rainfall (80%) falling during the monsoon from June to October. A second, highly variable, rainy season occurs between December and March. The soil in



Fig. 1. Localization of the micrometeorological tower in Sonora, Mexico. The county limits for Rosario de Tesopaco are shown.

this area is loamy-clay with 1.3 bulk density and very high rock content.

The main type of vegetation is tropical dry forest, dominated by leguminous trees. Some of the dominant species are *Lysiloma divaricatum*, *Ipomea arborecens*, *Acacia cochliacantha*, *Haematoxylum brasiletto*, *Celtis reticulata* and others (Sánchez-Mejía et al., 2007; Sánchez-Mejía et al., 2009). The forest canopy height is about 9–10 m. The vegetation cover is closed (MODIS LAI 1 km maximum estimated = 6.6) and most of the species lose their leaves in the dry season (From October to June). The vegetation cover rapidly increases with the presence of precipitation in late June or early July.

2.2. Meteorological measurements

A 13 m tower was installed in the TDF to make long-term meteorological and eddy covariance measurements above the canopy. The tower was positioned in the center of a homogeneous terrain ensuring the same coverage in at least 1 km in any direction. From the top of the tower, near-continuous measurements of water vapour, sensible heat and carbon dioxide fluxes, were made over the 2006 TDF growing season. Net radiation (NR) was measured with a four-component radiometer (CNR1, Kipp & Zonen, Delft, The Netherlands) attached to a horizontal boom extending 4 m from the tower. Air temperature (AT) and relative humidity (RH) were measured with a humidity and temperature probe (HMP45D, Vaisala, Helsinki, Finland). Wind direction and speed were measured with a wind vane/anemometer (Wind Monitor, R.M. Young, Traverse City, MI, USA). Four soil heat flux plates (HFT-1, Campbell Scientific, Logan, UT, USA) were used to measure soil heat flux (G). Soil moisture (SM) was measured with 3 time domain reflectometers all at 10 cm depth (CS615, Campbell Scientific, Logan, UT, USA), Soil Temperature data (ST) was obtained with a temperature probe (107-L, Campbell Scientific, Logan, UT, USA) and precipitation was measured with a tipping bucket rain gauge (TR-525USW, Texas Electronic, Dallas, TX, USA). Data were averaged over 30 min intervals, except for precipitation (half-hour sums), and were logged using a data logger (CR-23X, Campbell Scientific, Logan, UT, USA).

Net ecosystem water vapour and carbon dioxide gas exchange (ET and NEE, respectively), latent (LE) and sensible (H) heat and momentum fluxes were measured with the eddy correlation technique (Baldocchi et al., 2001; Baldocchi, 2003) in the 13 m tower. The eddy correlation system consisted of a 3-D Sonic Anemometer (CSAT3, Campbell Scientific, Logan, UTAH, EUA) and an open path gas analyzer (LI-7500, LI-COR, Lincoln, Nebraska, EUA) controlled by a data logger (CR5000, Campbell Scientific, Logan, UTAH, EUA). The eddy correlation system was approximately 3 m above the forest canopy. The measurements were made at 10 Hz, storing and averaging data every 30 min, using Reynolds averaging. The study period was from May 1st to October 31st 2006 (Day of Year – DOY-121 to 304).

Fluxes were later calculated off-line after performing coordinate rotations, accounting for density fluctuations following Webb et al. (1980), and applying a correction for using the sonic temperature instead of air temperature in the sensible heat flux calculations following Liu et al. (2001). System performance was assessed by examining the closure of the surface energy balance ($NR-G = LE + H$, where $y = 1.3337x - 1.5114$, $r^2 = 0.84$). The sum of half-hourly measurements of LE and H were regressed against the subtraction of G to NR. Previous to all the analysis, the nighttime fluxes were filtered using an initial rejection criteria of a friction velocity (u^*) value of 0.15 m s^{-1} , resulting in a rejection of about 75% of the nighttime data. Critical value of u^* was determined as the point where an increase in the u^* values had little effect on NEE estimates (Xu and Baldocchi, 2004). Missed values were replaced using the gap filling strategies described by Falge et al. (2001) and Reichstein

et al. (2005). Due to this constraint, carbon and water budget data should be treated with caution.

2.3. Ecosystem greenness

Ecosystem greenness was obtained from measurements of Normalized Difference Vegetation Index (NDVI) obtained from MODIS Terra (Salinas-Zavala et al., 2002; Barbosa et al., 2006). Values were from 16-day composite satellite images, which were interpolated to obtain daily values of NDVI. NDVI is the normalized ratio of the quantity of electromagnetic radiation reflected in the Near Infrared (NIR, 0.841–0.876 μm) and the Red (R, 0.620–0.670 μm), and is calculated as:

$$\text{NDVI} = \frac{\text{NIR} - \text{R}}{\text{NIR} + \text{R}} \quad (1)$$

NDVI takes values from -1 to 1 . Positive values ($\text{NIR} > \text{R}$) indicate green vegetation and surfaces with green vegetation cover. A higher NDVI value indicates an increase in green vegetation cover and vice versa. Several studies relate NDVI values to diverse biophysical variables like area and vegetation cover, primary productivity, chlorophyll density, as well as phenology (Salinas-Zavala et al., 2002; Weiss et al., 2004; Méndez-Barroso and Vivoni, 2010).

3. Results

3.1. Environmental conditions

Total precipitation measured at the tower in the experiment was 491 mm during the growing season. The rainy season started in June 20th, and concluded in early October. Twenty four days of the season had at least 5 mm of precipitation (13% of days). Monthly average values of air and soil temperature (Fig. 2a) varied in a range of about 10°C from DOY121 to DOY171, with values from 24 to 33°C of AT and from 32 to 43°C of ST, but after DOY172 values were similar until the end of the experiment, with a range of 24 – 31°C . The maximum values of AT (37°C) were found during June. A difference of 5°C was typically found in the daily trend of the AT from the maximum and minimum values. NR varied from approximately 15 W m^{-2} in cloudy days to more than 300 W m^{-2} (Fig. 2a). Maximum values of NR were found from D186 to D255, with a great fluctuation with cloudy and sunny days. The positive values of NR began approximately at 7:00 h, increasing rapidly until midday, when maximum values were found, NR then rapidly decreased. Daily behaviour of NR was similar during all months. Low average values of relative humidity (RH) were observed during the pre-monsoon period (Fig. 2b), but soon after the beginning of the monsoon period, the values increased to more than 40% in some cases. Similar to RH, soil moisture in the pre-monsoon period was very low with values less than $0.09 \text{ cm}^3 \text{ cm}^{-3}$ (Fig. 4b), but with the beginning of the precipitation, values increased rapidly, with maximum values at around $0.6 \text{ cm}^3 \text{ cm}^{-3}$ probably due to the high rocky content of this soil. SM decreased to minimum values of $0.15 \text{ cm}^3 \text{ cm}^{-3}$ in the post-monsoon. Vapor pressure deficit (VPD) daily behaviour was similar in all months, with minimum values early in the morning and a rapid increase between 7:00 and 15:00 h, followed by a decrease at dusk. The range of values was from 1.8 to 5 kPa in May, 1.5 to 4.8 kPa in June, 0.6 to 3.3 kPa in July, 0.3 to 2.3 kPa in August, 0.5 to 2.7 kPa in September and 0.7 to 3.2 kPa in October.

3.2. Seasonal trends of NEE and ET

During the pre-monsoon period, values of ET were close to zero (Fig. 3b) except for day of year (DOY) 156, when a small precipitation event occurred. With the onset of monsoonal rains, in mid

June, ET rapidly increased following precipitation. During the monsoon period, the ET ranged between 1.2 and 4.6 mm day^{-1} . Maximum values of ET occurred in days following precipitation events (Fig. 3b).

During the months of May and June, NEE showed values close to zero, similar to ET, coinciding with the driest period studied (Fig. 3a). Following the onset of rainfall, (on DOY171) we observed a rapid CO_2 release to the atmosphere that reached a maximum of $22 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ and gradually decreased towards DOY190 when the NEE values started to show a negative trend. Maximum CO_2 assimilation rates were found during the peak of the monsoon (between DOY213 and DOY265) when the ecosystem assimilated up to $20 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ but showed a marked fluctuation. After DOY265, with the end of the monsoon period, we can see a gradual decrease in the NEE values, showing fluctuations between assimilation and emission in the range of 5 to $-22 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$, until the end of the study period, when values were close to zero. In the same way, values of ET decrease with the post-monsoon, with a range of values between 0.5 and 2 mm day^{-1} .

Values of NEE and ET close to zero in the pre-monsoon period coincided with low values of NDVI (Fig. 3a). In the pre-monsoon period NDVI values were constant and close to 0.30, but rapidly increased with the presence of precipitation until values of 0.88 at the middle of the monsoon period were reached, approximately between DOY205 and DOY235. Peak NDVI coincided with the period with the highest gas exchange rate (Fig. 3a). Similarly, the post-monsoon NDVI values gradually decreased until a minimum of 0.55 was registered towards the end of the study period. Similar to the findings of Vivoni et al. (2008), from several monsoon-dominated ecosystems, the ET varied with time depending on vegetation greening since low (high) values of ET coincided with minimum (maximum) NDVI.

3.3. Differences in diurnal trends of NEE and ET

To illustrate the variation of the diurnal trends of NEE and ET, Fig. 4 shows the half-hour average values of NEE and ET in every month of the study. May shows the typical behaviour of the pre-monsoon. During this month values of ET and NEE were close to zero, with ET traces recorded during the hours close to midday. During the monsoon period, assimilation values of NEE in the day began approximately at 7:00 h, and sustained a rapid increase until 10:00 h, when the maximum values were found in all months. A rapid decrease in the assimilatory CO_2 trend (towards negative values) occurred at the onset of dark. In all cases and periods, nighttime values were positive. Diurnal behaviour of ET during the monsoon period follows the NR pattern. Water exchange typically started at 7:00 h, with a constant increase until midday (12:00 and 13:00) when maximum values of ET were observed. Following the peak, ET decreased until 19:00 h when the values of ET were close to zero.

In June, with the beginning of precipitation, values of ET during the day were between 0 and 3.2 mm, and we found only positive values of NEE, between 0.05 and $0.2 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. During July, August and September, daily gas exchange trends typically showed positive values of NEE during the nighttime and a range of negative values during the day. The range of values of ET and NEE were from 0 to 9.23 mm and from 0 to $-0.47 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in July, from 0 to 11.5 mm and 0 to $-1 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in August, and from 0 to 7.6 mm and 0 to $-0.55 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in September. In the post-monsoon period (October), ET and NEE dropped and there was a marked difference in the range of values compared to the monsoon period. The range of values during this period was between 0 and 4.9 mm of ET and 0 to $-0.15 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

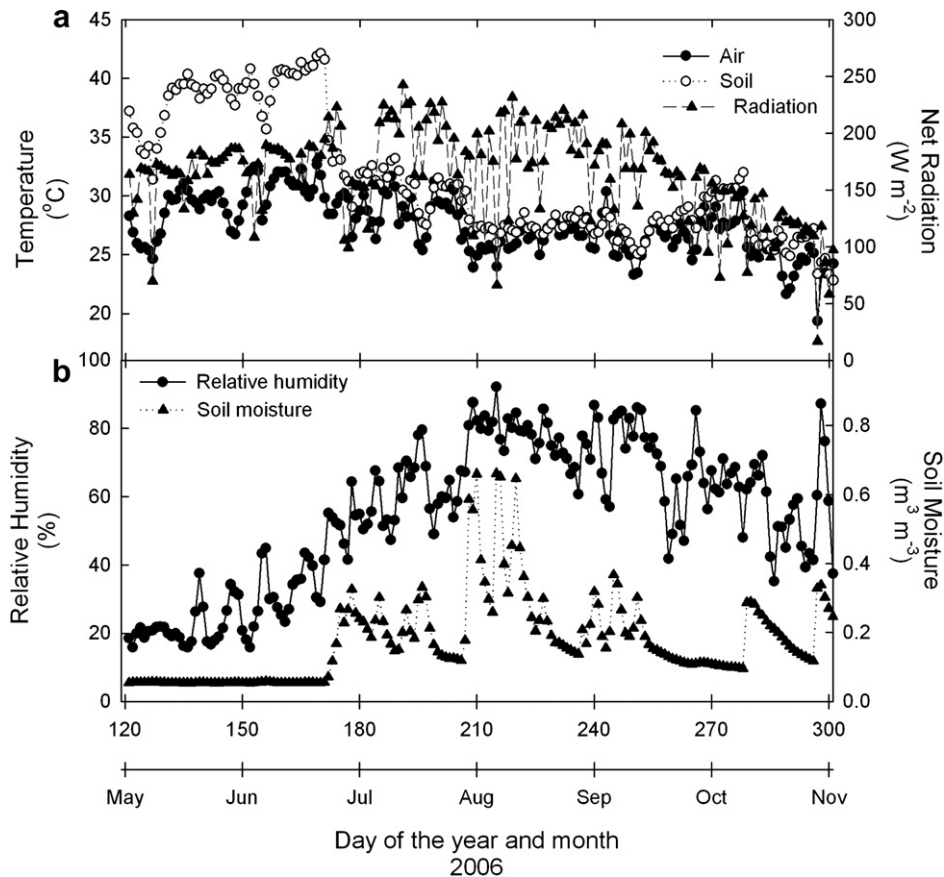


Fig. 2. Daily average values of several environmental variables during the study period a) Shows the values of air temperature, soil temperature and net radiation, b) shows values of relative humidity and soil moisture.

The relationship between and NEE and ET was generally weak but there were clear distinctions on each monsoonal period (Fig. 5). Notably, the late monsoon stage showed a stronger negative relationship.

3.4. Monthly carbon balance

Monthly carbon balance in the months of July, August and September indicated a sink of CO₂ and matched the maximum monthly values of ET, while in May, June and October, when the ecosystem was a source of carbon, we found the lowest monthly ET values. Maximum values of carbon assimilation were observed during the peak of the monsoon, when there was a significant amount of accumulated precipitation (Table 1). There was not an intraseasonal correspondence between the total monthly precipitation and the monthly carbon balance.

3.5. Ecosystem water use efficiency

We estimated the ecosystem water use efficiency (EWUE) using the formula used by Scott et al. (2006) and Emmerich (2007), which defines EWUE as:

$$EWUE = \frac{-\sum NEE}{\sum ET}$$

The EWUE is defined as the net carbon uptake per amount of water lost from the ecosystem and is a useful measure of the functionality of the seasonally dry ecosystems (Emmerich, 2007). Negative values of EWUE were observed during the pre- and post-monsoon periods

(Table 1). In May we found a EWUE of $-3.27 \text{ g CO}_2 \text{ mm H}_2\text{O}^{-1}$, in June $-6.84 \text{ g CO}_2 \text{ mm H}_2\text{O}^{-1}$ and in October $-2.01 \text{ g CO}_2 \text{ mm H}_2\text{O}^{-1}$. Suggesting that during these three rainless months, the ecosystem lost a total of 12.11 g of CO₂ per mm of evapotranspired water. During July, August and September EWUE values were 0.72, 3.55 and 3.08 g CO₂ mm H₂O⁻¹, respectively, giving a total of approximately 7.36 g of CO₂ acquired per every mm of evapotranspired water. Thus, the ecosystem became more efficient in its carbon acquisition during the rainy period.

4. Discussion

4.1. Factors controlling NEE during the wet and dry season

Patterns of net ecosystem CO₂ exchange and evapotranspiration were different during wet and dry periods. In seasonally dry ecosystems, precipitation and soil moisture are expected to be the primary control on the exchange of water and carbon between the land surface and atmosphere (Kurc and Small, 2007). In our case, during the pre-monsoon period, the carbon dioxide and water vapour exchange being close to zero indicated that the biological activity in the ecosystem was dormant and that the soil surface was too dry. The absence of leaves in trees and the absence of available moisture were likely the controlling factors. Isolated rains prior to the onset of the NAMS induced water vapour fluxes (up to 1 mm day⁻¹) which were most likely coming solely from soil evaporation since the canopy was still inactive. The arrival of the NAMS dramatically affected the trend of environmental conditions and the behaviour of the NEE and ET. With the first precipitation

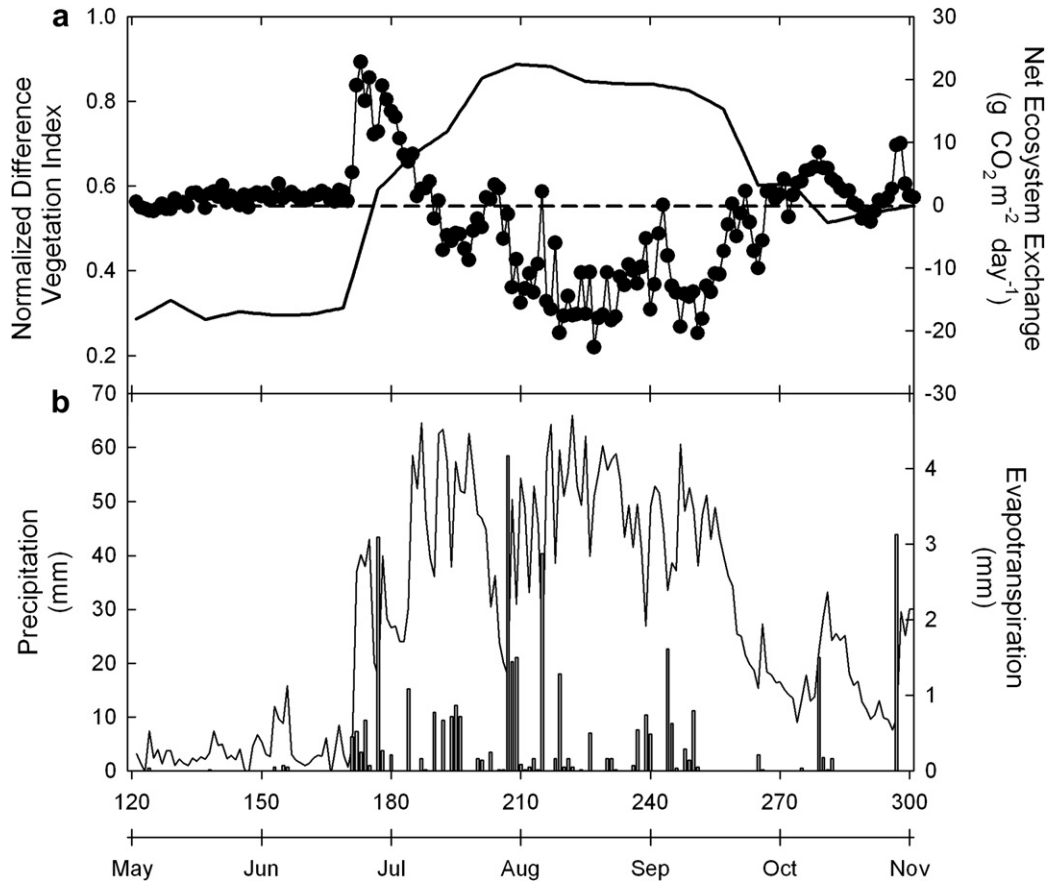


Fig. 3. Daily values showing the seasonal trends of NDVI, NEE (a) and, precipitation and ET (b) in a tropical dry forest in north-western Mexico during the summer monsoon season of 2006.

events, NEE rapidly responded and indicated a net CO₂ efflux from the ecosystem (positive values), suggesting a large respiration rate from the soil decomposing microbial activity (Jarvis et al., 2007). Soon after this respiratory period and along with the rapid canopy development, CO₂ exchange rates showed a marked assimilation trend as the monsoon activity peaked early in the season. This general pattern is consistent the conceptual model proposed by Huxman et al. (2004a) which suggests that the TDF shares common gas exchange features with other arid and semi-arid ecosystems.

As the ecosystem greened up (Fig. 3), negative NEE values indicated that photosynthetic assimilation started, and that gradually increased until the maximum leaf development was attained. However, the CO₂ exchange pattern during this assimilation period showed marked fluctuations with periods of high and low assimilation rates and occasional emission rates. The source of this variation might be explained by the accompanying fluctuation in solar radiation and precipitation, since periods of low assimilation and emission coincided with cloudy and rainy days (Fig. 2 and 3). This pattern is consistent with those observed in other arid and subtropical ecosystems (Scott et al., 2004; Méndez-Barroso and Vivoni, 2010).

Flux dynamics in the TDF illustrate the behaviour of seasonally dry ecosystems and the dependence of gas exchange with precipitation and moisture availability. During the pre-monsoon period, the TDF ecosystem lost a total of 347.62 g CO₂ m⁻² to the atmosphere, and during the rest of the monsoon period, the ecosystem gain a total of -722.38 g CO₂ m⁻², thus, though the duration of the study, the ecosystem was a net sink of CO₂ gaining -374.75 g CO₂ m⁻². Within the region of the NAMS influence, a Chihuahuan desert shrubland studied by Scott et al. (2006) was a total sink of

-77 g CO₂ m⁻² during July to October, values that are lower than the value found in TDF, and Yopez et al. (2007) found a total of -418 g CO₂ m⁻² during May to October in a semiarid riparian woodland, which suggests a sequestration potential of the TDF during years of average rainfall, similar to other seasonal dry ecosystems of the region.

Carbon dioxide efflux values found in the TDF presented in this study were also consistent with other seasonally dry ecosystems with a shape in the gas exchange trends responding to seasonal precipitation similar to that observed in woodlands, prairies (Xu and Baldocchi, 2004), shrublands (Scott et al., 2006), grasslands (Kurc and Small, 2007) and deserts (Hastings et al., 2005). Taking the pre-monsoon period in the TDF as representative of the dry season of other ecosystems, we get that NEE values close to zero are comparable among ecosystems. However, early in the wet period of 2006 our TDF reached maximum emission values of 22 g CO₂ m⁻² day⁻¹, a rate that was higher than the values found by Xu and Baldocchi (2004) in a mediterranean prairie and a Mojave desert ecosystem (Wohlfahrt et al., 2008) which showed values that were close to zero during their corresponding wet periods.

Positive NEE values during the early monsoon in the TDF were comparable to maximum efflux values of Chihuahuan shrublands that, depending on the location and environmental condition of a particular year, varied between 5 and 25 g CO₂ m⁻² day⁻¹ (Emmerich, 2003; Mielnick et al., 2005; Kurc and Small, 2007) and were somewhat higher to those reported for a semiarid riparian mesquite woodland (15.2 g CO₂ m⁻² day⁻¹; Scott et al., 2004).

In the case of assimilatory trends of NEE during the late monsoon of different ecosystems, we found that the maximum

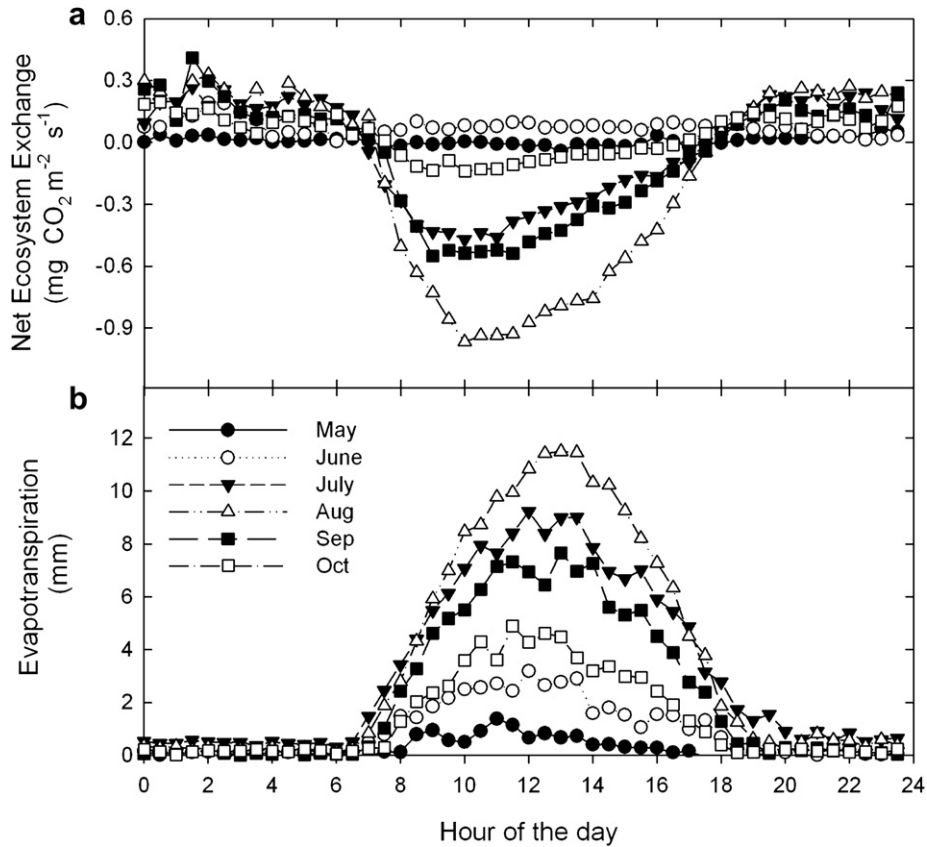


Fig. 4. Diurnal behaviour of NEE (a) and ET (b) in different months over the study period.

value obtained in the TDF was approximately $-22 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$, which is higher than the value of $-18 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ reported for a prairie (Xu and Baldocchi, 2004), a grassland and shrubland of -10 and $-20 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$, respectively (Emmerich, 2003), a mezquite woodland with values of $-9.5 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$, found by Scott et al. (2004), $-3.5 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ in the Mojave desert (Wohlfahrt et al., 2008) and -6 and $-7 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ found by Kurc and Small (2007) in a grassland and shrubland respectively.

With the information obtained we can see a marked influence of monsoonal precipitation in gas exchange characteristics of the TDF, expressed as a difference in the magnitude and patterns of the NEE. The TDF of north-western Mexico showed gas exchange patterns similar to other seasonally dry ecosystems. However, according to the data obtained and comparing with other studies, it seems that TDF has the capacity to fix a larger quantity of CO_2 . These results, however, need to be viewed with caution because in the present study we only report data from one growing season and highly filtered nighttime data. The patterns shown here underlie the necessity for larger temporal scale studies (more years) that determine the interseasonal, and interannual, variation in the gas exchange patterns of this ecosystem.

Monthly carbon balance (Table 1) in the TDF was higher than the values found in other seasonally dry ecosystems. Maximum carbon balance for emission in TDF was found in June, with a total of 199 g CO_2 , while the maximum value for assimilation was -396 g CO_2 , in August. In a semiarid riparian woodland, Yepez et al. (2007) found maximum values of 191 g CO_2 in July and -250 g CO_2 in October for emission and assimilation respectively, in a Chihuahuan Desert shrubland, Scott et al. (2006) found values of 128 g CO_2 in July and -95 g CO_2 in October. In both cases, values found in TDF were higher than the values of other seasonally dry ecosystems influenced by the NAMS. The absence of intraseasonal correspondence

of monthly precipitation and monthly carbon balance in the TDF (Table 1) can be explained by the fact that precipitation starts when the vegetation cover is still null and assimilation does not occur until a substantial canopy is developed (Huxman et al., 2004a). In

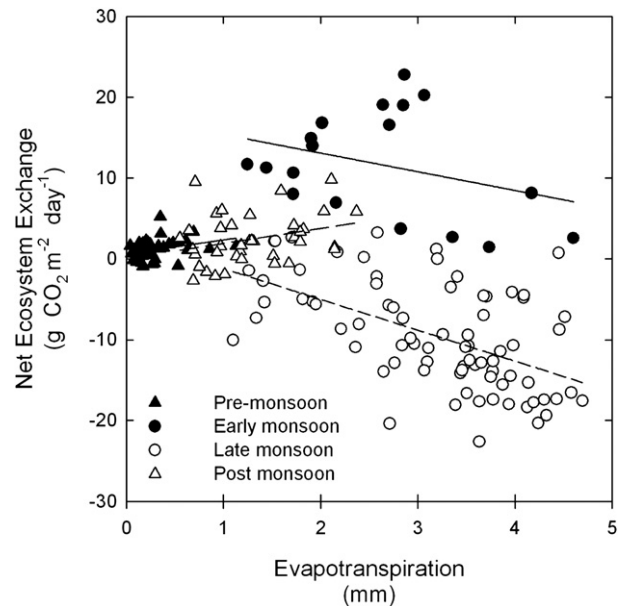


Fig. 5. Relationship between daily values of ET and daily values of NEE for the pre-monsoon period (DOY 121–171; $\text{NEE} = 1.72 \cdot \text{ET} + 0.64$, $r^2 = 0.1$), early monsoon stage (DOY 172–189; $\text{NEE} = -2.31 \cdot \text{ET} + 17.71$, $r^2 = 0.1$), late monsoon stage (DOY 190–266; $\text{NEE} = -3.81 \cdot \text{ET} + 2.61$, $r^2 = 0.3$) and post-monsoon period (DOY 267–304; $\text{NEE} = 1.87 \cdot \text{ET} + 0.04$, $r^2 = 0.09$).

Table 1

Monthly values of net ecosystem carbon exchange (NEE) in $\text{g CO}_2 \text{m}^{-2} \text{month}^{-1}$, evapotranspiration (ET) in $\text{mm H}_2\text{O month}^{-1}$, ecosystem water use efficiency (EWUE) in $\text{g CO}_2 \text{mm}^{-1} \text{H}_2\text{O}$ and precipitation (ppt) in mm month^{-1} .

Month	NEE	ET	EWUE	ppt
May	21.82	6.67	-3.27	0.76
Jun	199.73	29.22	-6.83	80.52
Jul	-69.92	97.10	0.72	181.11
Aug	-395.39	111.24	3.55	105.16
Sep	-212.76	68.98	3.08	53.35
Oct	82.50	41.09	2.00	70.61

our case, this lag lasted about a month as evidenced by the precipitation and NDVI trends (Fig. 3). Accordingly we observed that the higher values of precipitation appeared in July, while the maximum assimilation values occurred until August, when the vegetation cover was fully developed (Table 1).

5. Relationship between ET and NEE

Understanding the timing and magnitude of ET and NEE, provide mechanisms to link hydrological processes and ecosystem productivity (Yepez et al., 2007). Fig. 5 shows the relationship between daily values of ET and NEE during the study period. From this assessment, we see that the overall relationship between both fluxes is weak in all cases but that there are marked differences during the different periods. For example, during the late monsoon stage the relationship between ET and NEE was negative. This suggests that vegetation controls NEE through the regulation of water flux since this late monsoon stage coincides with the period when the vegetation is more abundant and more active. Reduced soil evaporation rates due to shaded ground by a closed canopy and high photosynthetic rates of transpiring plants might be mechanisms that strengthen this relationship. In contrast, the relationship during the pre- and post-monsoon periods, was positive coinciding with periods of null or low canopy activity.

Other factor showing the NEE in function of ET is the ecosystem water use efficiency (EWUE). In seasonally dry ecosystems, the EWUE shows the ability of the ecosystem to adjust their capacity of gas exchange to cope with environmental variables (Scott et al., 2006). The TDF ecosystem had higher values of EWUE during the monsoon period, this higher capacity of assimilating CO_2 with less water may be due to very active and dense vegetation activity resulting from the frequent occurrence of precipitation events.

The most efficient EWUE was found in the months of August and September (Table 1), however, the magnitude of the actual fluxes was contrasting. During August, we found the highest values of CO_2 assimilation and a higher ET, while in September there was a reduction in both processes but EWUE remained high. An explanation for this contrast might be related to the availability of water rather than the change in the biological capacity controlling gas exchange. The lowest (negative) value of EWUE was found in June, when the ecosystem released a high amount of CO_2 to the atmosphere prior to the monsoon (Table 1).

The EWUE of the TDF during the peak of the monsoon ($3.55 \text{ g CO}_2 \text{ mm}^{-1} \text{ H}_2\text{O}$) was similar to the EWUE reported by Scott et al. (2006) during the same season in a shrubland of the Chihuahuan desert in Arizona, where EWUE was close $3 \text{ g CO}_2 \text{ mm}^{-1} \text{ H}_2\text{O}$, and the value obtained by Emmerich (2007) in another shrubland with an EWUE of $4.68 \text{ g CO}_2 \text{ mm}^{-1} \text{ H}_2\text{O}$. The main differences were that their positive values of EWUE were found in the months of August, September and October; while in the TDF the positive values were found in July, August and September, indicating that the shrubland became more efficient later in the monsoon period, while our TDF

showed its higher efficiency earlier in the monsoon period. Contrary, Emmerich (2007) found a high EWUE in grassland, with a maximum value of $7.35 \text{ g CO}_2 \text{ mm}^{-1} \text{ H}_2\text{O}$. These comparisons indicate that the TDF has a EWUE comparable with other seasonally dry ecosystems influenced by the NAMS.

6. Conclusions

The climate in the study region is characterized by summer monsoon precipitation which produces gas exchange patterns distinctive of seasonally dry ecosystems. Measurements of net ecosystem carbon dioxide and water vapour exchange obtained in the TDF during the monsoon period were highly influenced by the presence of precipitation. The ecosystems showed three different periods, characterized by the magnitude and response of the gas exchange to precipitation and canopy development:

- The first period occurred prior to active precipitation (pre-monsoon), when gas exchange was close to zero due the absence of leaves and moisture.
- The second period occurred during the monsoon, divided in two stages. The first stage was characterized by a large positive CO_2 efflux probably due to the high respiratory flux as a response to the increase of biological activity with the onset of precipitation. The second stage came after full canopy development, when a strong assimilation of CO_2 was observed.
- The gradual decrease in gas exchange rates to minimal values, when plants began to lose their leaves, characterized the third (post-monsoon) period.

The tropical dry forest of north-western Mexico has the typical behaviour of the seasonally dry ecosystems, however, during the summer growing season of 2006, sustained rates of CO_2 gain amounted $-374 \text{ g CO}_2 \text{ m}^{-2}$ which is on the upper limit for seasonally dry ecosystems, under the influence of the NAMS. In contrast, the TDF had comparable ecosystem water use efficiency.

Despite of the clear influence of the vegetation in the patterns of gas exchange between the ecosystems and the atmosphere in the TDF, mechanistic information about biological and environmental variables controlling gas exchange dynamics is still necessary in this ecosystem. Understanding these factors is fundamental to predict how seasonally dry ecosystems would respond to an imminent change in precipitation regimes and general climatic patterns due to global change.

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