Variations of net ecosystem production due to seasonal precipitation differences in a tropical dry forest of northwest Mexico

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Abstract Due to their large extent and high primary productivity, tropical dry forests (TDF) are important contributors to atmospheric carbon exchanges in subtropical and tropical regions. In northwest Mexico, a bimodal precipitation regime that includes winter precipitation derived from Pacific storms and summer precipitation from the North American monsoon (NAM) couples water availability with ecosystem processes. We investigated the net ecosystem production of a TDF ecosystem using a 4.5 year record of water and carbon fluxes obtained from the eddy covariance method complemented with remotely sensed data. We identified a large CO2 efflux at the start of the summer season that is strongly related to the preceding winter precipitation and greenness. Since this CO2 efflux occurs prior to vegetation green-up, we infer that respiration is mainly due to decomposition of soil organic matter accumulated from the prior growing season. Overall, ecosystem respiration has an important effect on the net ecosystem production but can be overwhelmed by the strength of the primary productivity during the NAM. Precipitation characteristics during NAM have significant controls on sustaining carbon fixation in the TDF into the fall season. We identified that a threshold of ~350 to 400 mm of monsoon precipitation leads to a switch in the annual carbon balance in the TDF ecosystem from a net source (+102 g C/m²/yr) to a net sink (−249 g C/m²/yr). This monsoonal precipitation threshold is typically exceeded one out of every 2 years. The close coupling of winter and summer periods with respect to carbon fluxes suggests that the annual carbon balance is dependent on precipitation amounts in both seasons in TDF ecosystems.

1. Introduction

Ecosystem respiration is one of the largest components of net ecosystem production (NEP) in forested ecosystems and represents a dynamic source of CO2 from the surface to the atmosphere that can determine the carbon sequestration potential of an ecosystem [Schlesinger and Andrews, 2000]. Tropical dry forests (TDF) are important ecosystems in Mexico due to their large extent (~180,000 km²) and high primary productivity, tropical dry forests (TDF) are distinguished by a strong seasonality largely controlled by the availability of rain from the North American monsoon (NAM) during the summer [Vivoni et al., 2008; Lizárraga-Celaya et al., 2010], followed by a weaker winter precipitation regime and a springtime drought [Sánchez-Azofeifa et al., 2005]. In the northwestern limit of TDFs, the summer monsoon represents the most important water source in the region and determines biological activity and ecosystem fluxes [Campos et al., 1998; Pérez-Ruiz et al., 2010; Forzieri et al., 2014]. Moreover, this region is susceptible to El Niño–Southern Oscillation that impacts winter precipitation which has been linked to the subsequent summer monsoon [Zhu et al., 2007; Mahmood and Vivoni, 2014; Dannenberg et al., 2015].

In seasonally dry ecosystems such as the TDF, carbon exchanges are highly dependent on the annual and seasonal variations of precipitation due the tight relation between water inputs and processes such as net primary production (NPP) [Sala et al., 1988; Méndez-Barroso et al., 2009], litter decomposition, and concomitant respiratory fluxes [Fierer and Schimel, 2003; Anaya et al., 2007] and transpiration [Scott et al., 2009; Reyes-Garcia et al., 2012; Peng et al., 2013], among other physiological and hydrological processes.
Leuzinger and Korner, 2010; Cherwin and Knapp, 2012. Variations in precipitation during the summer season, for example, a delayed start of the monsoon, are recognized to affect the annual carbon balance through alterations of productivity and respiration [Hutyra et al., 2007]. Ecosystem respiration ($R_{eco}$), comprising heterotrophic (i.e., decomposers) and autotrophic (i.e., plants, roots) components, substantially affects the net carbon balance in tropical dry forests [Goulden et al., 1998; Valentini et al., 2000]. For example, in seasonally dry ecosystems, CO$_2$ release from respiration during the first summer rains can be more than 45% of the carbon fixed by plants during the growing season [Yépez et al., 2007]. This large loss of CO$_2$ to the atmosphere has been observed following rewetting periods due to precipitation and at the ecosystem level from eddy covariance and soil respiration measurements in several seasonally dry ecosystems [Jenerette et al., 2008; Unger et al., 2010]. As a result, changes in precipitation distribution (i.e., timing, duration and magnitude), including seasonal and long-term droughts, are capable of altering respiration and impacting the overall carbon balance in TDF ecosystems [Rohr et al., 2013; Cable et al., 2013; Reichstein et al., 2013].

Ecosystem carbon fluxes are also affected by time lag effects induced by antecedent wetness conditions, leading to nonlinear responses to precipitation events during the growing season [Reynolds et al., 2004; Cable et al., 2013; Lupascu et al., 2014]. Reichmann et al. [2013] showed that positive legacies (i.e., higher primary production than expected) occur in periods with wet preceding conditions, while negative legacies (i.e., less production than expected) result from dry antecedent periods. In the case of ecosystem respiration, antecedent soil moisture is known to have marked effects in its response to precipitation events [Cable et al., 2013; Lupascu et al., 2014]. Similarly, a longer preceding dry period favors carbon accumulation, thus enhancing decomposition rates, mineralization, and microbial activity that amplify respiration after early season rainfall events [Jarvis et al., 2007; Yépez et al., 2007; Cable et al., 2008; Yan et al., 2014]. Since biological activity in TDFs occurs primarily during the monsoon [Forzieri et al., 2011], we hypothesize that variations in antecedent precipitation will control summer carbon fluxes through effects on substrate availability for decomposition [Austin and Vitousek, 2000; Vasconcelos et al., 2007]. Limited decomposition during the dry spring period should favor accumulation of labile soil organic matter [Wieder and Wright, 1995; Vourlitis et al., 2001].
Consequently, the first summer rains with favorable soil moisture and temperature conditions should stimulate microbial activity leading to a rapid heterotrophic respiration response [Unger et al., 2010; Carbone et al., 2011; Thiessen et al., 2013]. An opposite trend is expected for low productivity in the previous growing season and below average winter precipitation leading to a reduced heterotrophic respiration from microbial activity and thus lower ecosystem respiration at the start of the rainy season.

In this study, we investigate the ecosystem carbon balance in a tropical dry forest ecosystem through the measurement of carbon and water fluxes using a nearly continuous, 4.5-year record of net ecosystem exchange (NEE), gross primary productivity (GPP), and respiration ($R_{eco}$) obtained from the eddy covariance (EC) technique. The study site is located in a secondary tropical dry forest in northwestern Mexico, under the influence of the North American monsoon [Pérez-Ruiz et al., 2010]. The EC measurements over the multiple years (second half of 2004 to 2008) provide the opportunity to compare winter and summer periods with varying seasonal precipitation patterns and their subsequent effects on ecosystem carbon fluxes. We focus attention on comparing the relative magnitude of periods when ecosystem respiration predominates (after the first summer rains) and when autotrophic activity controls carbon exchanges (after full leaf out), as characterized through remote-sensing data on vegetation greenness. The analysis of carbon and water fluxes from the EC technique along with a remotely sensed vegetation index helps us to understand the switch in respiration and productivity controls on the ecosystem carbon balance. As mentioned above, we test the hypothesis that the amount of winter precipitation has a direct control on the heterotrophic respiration response to the first summer rains, leading to differences in carbon losses which affect the overall carbon balance during the summer season. When considered over the annual scale, we also hypothesize that the autotrophic activity stimulated by the amount of precipitation during the North American monsoon will dictate whether the TDF ecosystem is a net carbon source or sink.

2. Materials and Methods

2.1. Site Description

The study area is located in southern Sonora, ~86 km northeast of Ciudad Obregón, Sonora, Mexico, in the Ejido La Estrella (27°50′N, 109°17′W, with an elevation of 460 m, Figure 1). The eddy covariance tower is located 7.5 km east of the town Rosario de Tesopaco near the slopes of the Sierra Madre Occidental on privately owned land. Pérez-Ruiz et al. [2010] first reported on the site characteristics and the eddy covariance measurements. The climate is hot and semi-arid (BSH) according to the Köppen classification [Instituto Nacional de Estadística y Geografía, 2009], while the tropical dry forest (or “bosque tropical caducifolio” in Spanish, Rzedowski [1978]) is dominated by leguminous trees (Figure 2). Some of the dominant species are Lysiloma diversicaturn (Mauto), Ipomea arborescens (Tree morning glory), Acacia cochlacantha (Huinolo), Haematoxylum brasiletto (Brazilwood), and Celtis reticulata (Netleaf hackberry), among others [Sánchez-Mejía et al., 2007a]. The mean basal area at the study site is 14.83 ± 3.3 m$^2$ ha$^{-1}$, and the aboveground biomass is estimated to be 43.20 ± 9.5 Mg ha$^{-1}$ [Sánchez-Mejía et al., 2007b]. These values and the high counts of Acacia cochlacantha indicate that the area is part of a secondary forest with significant management activities in the past [Van Devender et al., 2000]. The secondary forest can be classified as being in a stage of natural regeneration about 5 to 50 years after a land cover disturbance, following the conceptual model of Alvarez-Yépez et al. [2008] for tropical dry forests of western Mexico. Soils at the site are silty clay in texture with a bulk density of 1.3 kg/m$^3$ and a high rock content. The long-term average annual precipitation is 647 mm/yr (1966–1987 and 2003–2013), obtained from the Comisión Nacional de Agua (CNA) station 00026100, with around 80% of the annual total precipitation occurring during the North American monsoon (July–September). The average temperature at the site is 24.3°C.

2.2. Site Measurements

Ecosystem flux measurements were performed using the EC technique [Baldocchi, 2003, 2008]. A 13 m tower was positioned in the center of a flat landscape with homogeneous vegetation conditions in the surrounding 1 km radius. Measurements were conducted with a three-dimensional sonic anemometer (CSAT-3, Campbell Scientific Inc.) and an open path infrared gas analyzer (LI7500, LI-COR Inc.) installed 3 m above the tree canopy and oriented with the prevailing wind direction from the west. High-frequency (10 Hz) water vapor and CO$_2$ concentrations and air temperature measurements were used with the turbulent wind velocities to obtain latent heat flux (LE) or evapotranspiration (ET), sensible heat flux (H), and net ecosystem exchange.
(NEE) averaged every half hour. By convention, positive and negative NEE values represent carbon release (respiration) and fixation (production) by the ecosystem, respectively. A four component radiometer (CNR1, Kipp & Zonen) was used to measure net radiation ($R_{net}$), while wind speed and direction were measured with an anemometer (Wind Monitor, R.M. Young). A humidity and temperature sensor (HMP45D, Vaisala) was used to measure vapor pressure and air temperature (TA) at two heights (2.5 and 6.8 m). Vapor pressure deficit (VPD) was calculated as the difference of the saturated vapor pressure, estimated according to Murray [1967], and the actual vapor pressure. Volumetric soil water contents at a 10 cm depth were measured by five water content reflectometers (CS615, Campbell Sci.) located at representative sites around the EC tower. To calculate the relative soil water content (SWC), we averaged the five measurements and normalized this quantity by the maximum volumetric soil water content reported during the study period. In addition, soil heat flux (G) was measured with four plates (HFT-1, Campbell Sci.), soil temperature was obtained with a temperature probe (107-L, Campbell Sci.) at a single site, and precipitation was measured with a tipping-bucket rain gauge (TR-525USW, Texas Electronics Inc.). While the soil moisture and temperature sampling did not cover the entire EC footprint, as performed by Vivoni et al. [2010] in a subtropical scrubland in Sonora, the observations are considered representative for the ecosystem. Measurements were conducted from July 2004 to December 2008, and data were averaged at 30 min intervals, as commonly performed in surface energy, water, and carbon studies [e.g., Xu and Baldocchi, 2004; Scott et al., 2009; Templeton et al., 2014]. To compute averages of meteorological and flux variables, we defined seasons spanning different days of year (DOY) as winter (DOY 335 to 59 or early December to late February) and summer season (DOY 101 to 270) comprising of a premonsoon (DOY 101 to 171 or mid-April to mid-June) and a monsoon (DOY 172 to 270 or mid-June to late September) period for each year. For the purposes of this study, we do not conduct detailed analysis for the fall (DOY 271 to 334) and spring (DOY 60 to 100) seasons at the site. Additional details on the eddy covariance measurements were reported in Pérez-Ruiz et al. [2010].

2.3. Data Quality Control, Flux Partitioning, and Gap Filling

Eddy covariance flux measurements were corrected for density fluctuations [Webb et al., 1980] and the correction of Liu et al. [2002] to account for using sonic temperature to calculate sensible heat flux. Data below a threshold of a critical friction velocity, $u^* = 0.15$ m/s, were removed [Aubinet et al., 2000; Xu and Baldocchi, 2004]. Data gaps due to unfavorable conditions or instrument failure were filled using the Max Planck online tool (http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/) based on the standardized methods of Reichstein et al. [2005], consisting of 49.3%, 51.5%, 38.9%, 46.1%, and 36.2% of missing data for 2004, 2005, 2006, 2007, and 2008, respectively.
Table 1. Energy Balance Closure Using Net Radiation (R\textsubscript{net}), Ground (G), Latent (LE), and Sensible (H) Heat Fluxes\textsuperscript{a}

<table>
<thead>
<tr>
<th>Period</th>
<th>Sample Size</th>
<th>Slope (m)</th>
<th>Intercept (b)</th>
<th>$R^2$</th>
<th>$\Sigma(LE+H)/\Sigma(R_{net}-G)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>All years</td>
<td>75066</td>
<td>0.63</td>
<td>28.27</td>
<td>0.86</td>
<td>0.90</td>
</tr>
<tr>
<td>2004</td>
<td>8400</td>
<td>0.65</td>
<td>42.02</td>
<td>0.91</td>
<td>1.03</td>
</tr>
<tr>
<td>2005</td>
<td>15141</td>
<td>0.54</td>
<td>39.94</td>
<td>0.88</td>
<td>0.97</td>
</tr>
<tr>
<td>2006</td>
<td>17519</td>
<td>0.60</td>
<td>28.47</td>
<td>0.91</td>
<td>0.83</td>
</tr>
<tr>
<td>2007</td>
<td>16486</td>
<td>0.65</td>
<td>25.78</td>
<td>0.87</td>
<td>0.94</td>
</tr>
<tr>
<td>2008</td>
<td>17520</td>
<td>0.75</td>
<td>8.20</td>
<td>0.84</td>
<td>0.82</td>
</tr>
</tbody>
</table>

\textsuperscript{a}The slope (m) and intercept (b) represent parameters in the relation \(LE + H = m(R_{net} - G) + b\), with the coefficient of determination \(R^2\) and the ratio of \(\Sigma(LE+H)/\Sigma(R_{net}-G)\) indicated for each year and all years. Only the second half of 2004 is included.

The approach is an enhancement of the rectangular hyperbolic light response function described by Falge et al. [2001]. The same tool was used for partitioning NEE into gross primary production (GPP) and ecosystem respiration \((R_{ec})\) for the data fulfilling the appropriate turbulent conditions. In this method, ecosystem respiration was computed as a function of air temperature [Lloyd and Taylor, 1994; Reichstein et al., 2005] as

$$R_{eco}(T) = R_{eco,ref}e^{-\left(\frac{T_{ref} - T}{T_{ref} - T_{o}}\right)} \times \sqrt{b^2 - 4ac}$$

where \(R_{eco,ref}\) is the respiration rate at a reference temperature \((T_{ref} = 283.15 K)\), \(E_o\) is the temperature sensitive parameter related to activation energy fitted according to the temperature response of \(R_{eco}\), \(T_o\) is a constant temperature of 227.13 K, and \(T\) is the absolute air temperature (°K). GPP was obtained as \(GPP = |NEE| - R_{eco}\) [Flanagan et al., 2002]. The partitioning method employed has been previously described [Migliavacca et al., 2011; Goulden et al., 2011; Babst et al., 2014] and has shown interannual variability comparable with other methods [Desai et al., 2008]. The surface energy balance \((R_{net} - G = LE + H)\) was inspected (Table 1) using the half-hourly measurements as a measure of data quality [McMillen, 1988]. Our results showed a similar energy balance closure with respect to an analysis of 50 site years at FLUXNET sites [Wilson et al., 2002] and other studies [Scott, 2010; Schreiner-McGraw et al., 2015]. Over the study years, turbulent energy fluxes are underestimated by ~12% relative to available energy, as observed at other sites [Twine et al., 2000]. Similarly, the ratio of the sum in turbulent fluxes over the sum of available energy, \(\Sigma(LE+H)/\Sigma(R_{net}-G)\), was between 0.83 and 1.03, with the largest value likely due to an underestimation of \(R_{net}\). Although closure errors have implications on the surface energy balance, their impact of CO\(_2\) fluxes are less certain and susceptible to the mechanisms creating the imbalance, such as a bias of \(R_{net}\), neglected energy sinks and sources, or erroneous measurements of the turbulent [Wilson et al., 2002; Baldocchi, 2003]. Additional details on the data processing are available in Pérez-Ruiz et al. [2010].

2.4. Ecosystem Greenness

We quantified ecosystem greenness using the normalized difference vegetation index (NDVI) derived as the ratio of the reflectances in the near infrared (NIR) (0.841–0.876 mm) to the red (R, 0.620–0.670 mm) bands as:

$$NDVI = \frac{NIR - R}{NIR + R}.$$  \hspace{1cm} (2)

obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on board the EOS Terra satellite. We utilized the 16 day composite during 2004–2008 of a single pixel with resolution of 250 m centered on the EC tower which is of a sufficient scale to capture the typical time-variable source area or measurement footprint of the EC technique [e.g., Kormann and Meixner, 2001; Detto et al., 2006; Vivoni et al., 2014]. Analysis of NDVI for a broader area around the EC tower (1 km by 1 km) demonstrated no appreciable differences, indicating spatial homogeneity of the signal around the measurement location. Previous studies have used MODIS observations as a reliable measure of ecosystem phenological patterns [Roerink et al., 2003; Zhou et al., 2003], including prior efforts at the site [Vivoni et al., 2008; Pérez-Ruiz et al., 2010].

3. Results

3.1. Seasonal and Interannual Variations in Meteorological and Soil Conditions

Annual precipitation measured at the TDF site from 2005 to 2008 was 498, 509, 557, and 793 mm, respectively, such that all years, with the exception of 2008, had below average amounts. Table 2 presents the
seasonal and interannual variations in the meteorological and soil water conditions during the study years. The highest antecedent winter precipitation was received during 2005 and 2008 (24% and 12% of annual precipitation) and resulted in high values of the relative soil water content (SWC) during each winter (0.56 and 0.38, respectively) as compared to other years (2006 and 2007 with 1% and 8% of annual precipitation). The wet winter periods (2005 and 2008) were also accompanied by higher daily winter ET (1.30 and 1.05 mm/d) and lower VPD (1.00 and 1.25 mb). The premonsoons (DOY 101-171) were fairly similar in terms of meteorological and soil conditions across all years, with the exception of slightly higher ET for 2005 and 2008. Spring and fall seasons were omitted from the table.

Based on this analysis, we divided the study years into two categories, antecedent wet winter (2005 and 2008) and antecedent dry winter (2006 and 2007), and conducted monthly analyses of measured meteorological and soil conditions, as presented in Figure 3. Given the similar net radiation ($R_{net}$) and air temperature among all winters, the striking differences between years are in the wintertime SWC and ET, both of which can persist into the premonsoon period (Figure 3 and Table 2). These differences provide the opportunity to inspect the potential role of antecedent winter conditions controlling the net ecosystem production occurring during the wet summer (monsoon) in the TDF ecosystem through the process of ecosystem respiration.

The North American monsoon and its significant precipitation events lead to dramatic changes in the meteorological and soil conditions relative to premonsoon periods. These include small increases in $R_{net}$, large reductions in VPD, and significant increases in ET and SWC (Table 2 and Figure 3). Monsoon precipitation (DOY 172-270) during the study years varied from ~350 mm to 730 mm, with the largest accumulation in 2008 and the smallest amount in 2005. Seasonal precipitation corresponds well with the seasonal average of daily ET as the wetter monsoon in 2008 had a substantially larger value (3.33 mm/d) than the drier monsoon in 2005 (1.78 mm/d). Seasonal ET during the 2008 wet monsoon also exhibited an earlier onset, a higher peak amount, and a delayed demise, as compared to 2005, and extended into the fall season (Figure 3). The two monsoon periods with antecedent dry winters exhibited precipitation, daily ET, and SWC that were between the dry and wet extremes represented by 2005 and 2008, respectively. This reveals that there does not seem to be a correlation between antecedent winter wetness and the strength of the North American monsoon in this TDF ecosystem. This is confirmed by an analysis of the long-term record (1966–2013) at the CNA station 00026100 that exhibited a weak correlation ($R^2 = -0.03$) between winter and monsoon precipitation amounts.

**3.2. Seasonal and Interannual Variations of Net Ecosystem Exchange and Greenness**

Based upon the classification of antecedent winter conditions, we inspected the seasonal evolution of net ecosystem exchange and compared these to vegetation index values depicting the ecosystem greening process in Figure 4. For all years, the premonsoon season (DOY 101–171) was characterized by high air temperatures (TA) and relatively low soil water content. The two monsoon periods with antecedent wet winters (2005 and 2008) Table 2. Seasonal Values of Precipitation (PPT), Air Temperature (TA), Vapor Pressure Deficit (VPD), Evapotranspiration (ET), Relative Soil Water Content (SWC), Water Use Efficiency (GPP/ET), Respiration-Evapotranspiration Ratio ($R_{eco}/ET$), the Ratio of $R_{eco}$ to GPP and the Net Ecosystem Production (NEP) for Each Season and Year.

<table>
<thead>
<tr>
<th>Season and DOY</th>
<th>Year</th>
<th>PPT (mm)</th>
<th>TA (°C)</th>
<th>VPD (mb)</th>
<th>ET (mm/d)</th>
<th>SWC (–)</th>
<th>GPP/ET (g C/kg H2O)</th>
<th>$R_{eco}/ET$ (g C/kg H2O)</th>
<th>$R_{eco}$/GPP (–)</th>
<th>NEP (g C/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>2005</td>
<td>119.12</td>
<td>17.33</td>
<td>1.00</td>
<td>1.30</td>
<td>0.56</td>
<td>1.26</td>
<td>1.30</td>
<td>1.03</td>
<td>7.15</td>
</tr>
<tr>
<td></td>
<td>2006</td>
<td>4.06</td>
<td>20.48</td>
<td>0.95</td>
<td>0.20</td>
<td>0.12</td>
<td>1.81</td>
<td>2.78</td>
<td>1.54</td>
<td>16.33</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>44.96</td>
<td>17.48</td>
<td>1.43</td>
<td>0.59</td>
<td>0.30</td>
<td>1.03</td>
<td>1.21</td>
<td>1.18</td>
<td>8.48</td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>98.30</td>
<td>17.29</td>
<td>1.25</td>
<td>1.05</td>
<td>0.38</td>
<td>1.60</td>
<td>0.82</td>
<td>0.51</td>
<td>~86.75</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>78.40</td>
<td>18.84</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Premonsoon</td>
<td>2005</td>
<td>0.00</td>
<td>26.46</td>
<td>2.60</td>
<td>0.77</td>
<td>0.15</td>
<td>0.55</td>
<td>1.90</td>
<td>3.48</td>
<td>73.57</td>
</tr>
<tr>
<td></td>
<td>2006</td>
<td>9.65</td>
<td>28.53</td>
<td>3.19</td>
<td>0.24</td>
<td>0.09</td>
<td>2.22</td>
<td>3.19</td>
<td>1.44</td>
<td>16.63</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>0.00</td>
<td>26.78</td>
<td>2.76</td>
<td>0.33</td>
<td>0.12</td>
<td>1.64</td>
<td>1.98</td>
<td>1.21</td>
<td>7.97</td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>0.25</td>
<td>27.47</td>
<td>2.92</td>
<td>0.51</td>
<td>0.08</td>
<td>1.44</td>
<td>2.99</td>
<td>2.09</td>
<td>56.42</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>29.20</td>
<td>24.90</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monsoon</td>
<td>2005</td>
<td>349.50</td>
<td>28.48</td>
<td>1.75</td>
<td>1.78</td>
<td>0.39</td>
<td>3.04</td>
<td>3.06</td>
<td>1.01</td>
<td>3.73</td>
</tr>
<tr>
<td></td>
<td>2006</td>
<td>411.24</td>
<td>27.25</td>
<td>1.45</td>
<td>3.08</td>
<td>0.46</td>
<td>2.05</td>
<td>1.59</td>
<td>0.77</td>
<td>~140.67</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>398.03</td>
<td>26.95</td>
<td>1.17</td>
<td>2.98</td>
<td>0.51</td>
<td>1.82</td>
<td>1.56</td>
<td>0.86</td>
<td>~74.72</td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>729.47</td>
<td>26.52</td>
<td>1.21</td>
<td>3.33</td>
<td>0.48</td>
<td>2.16</td>
<td>1.74</td>
<td>0.80</td>
<td>~141.50</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>474.10</td>
<td>28.95</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Long-term averages (1966–2013) of seasonal precipitation and air temperature are presented for comparison. Only complete yearly data sets were considered.*
and 2008) exhibited increasingly positive NEE (respiration-dominated) beginning near DOY 80, in response to rising air temperatures (Table 3). In contrast, the years with antecedent dry winters (2006 and 2007) had a delay in the increment of $R_{eco}$ by about 1 month (DOY 110) with a much shorter duration of the respiration-dominated period. NEE during the premonsoon period was highly sensitive to SWC with substantial increases in NEE (more respiration) immediately after a soil wetting event. The premonsoon period was also characterized by low NDVI (~0.25) across all years, with a fairly similar greening onset despite differences in the antecedent winter conditions (Figure 4). This indicates that changes in NEE in response to increasing TA and SWC during the premonsoon are decoupled from primary productivity and mainly linked to heterotrophic (microbial) respiration in the TDF ecosystem. As a result, the ratio of $R_{eco}$/GPP is substantially larger during the premonsoon period as compared to winter and monsoon periods and higher for the years with antecedent wet winters (Table 2).

![Figure 3. Monthly meteorological and soil conditions for years with (left) antecedent wet winters and (right) antecedent dry winters, including net radiation ($R_{net}$), vapor pressure deficit (VPD), evapotranspiration (ET), relative soil water content (SWC), and precipitation. Only the second half of 2004 is included.](image1)

![Figure 4. Seasonal evolution of carbon exchanges and ecosystem greenness for years with (left) antecedent wet winters and (right) antecedent dry winters, including daily net ecosystem exchange (NEE) and NDVI as well as meteorological and soil water conditions. Values represent 5 day averages. Only complete yearly data sets were considered.](image2)
Net ecosystem exchange abruptly decreases toward negative values (fixation-dominated) after the onset of greenness due to the North American monsoon. Despite the variations in the greening onset date across the years, there is a clear correlation between the increase in NDVI ($R^2$ values up to $\sim0.8$) and a net gain of CO$_2$ in NEE during the monsoon season (DOY 172–270). Furthermore, monsoon seasons with higher NDVI sustained over longer periods also exhibit a prolonged period of negative daily NEE values, indicating larger carbon assimilation. Ecosystem greenness and net carbon uptake during the monsoon are highly dependent on within-season precipitation and not linked to the antecedent winter conditions (Table 2). The monsoon period with the highest precipitation (2008) was distinguished from other years by having the longest fixation-dominated period and the most negative NEE. High precipitation during 2008 did not augment the intensity of greening or carbon fixation rates, but instead allowed the assimilatory period to be sustained for a longer period, leading to a low $R_{eco}$/$GPP = 0.80$ (Table 2). In contrast, a short summer drought observed in 2007 resulted in a low SWC and a reduction in NDVI, which lead to a NEE near zero during late August (DOY 240, Figure 4). Both cases demonstrate that the precipitation distribution (i.e., timing, duration and magnitude) during the monsoon period has an important control on sustaining carbon fixation in the TDF ecosystem.

### 3.3. Antecedent Wetness Controls on the Partitioning of Net Ecosystem Exchange

The overall effects of the summer periods on net ecosystem exchange can be summarized by the ratio of the amount of carbon respired during the dominant CO$_2$ efflux period early in the growing season ($R_{DR}$) to the amount of carbon fixed over the growing season after ecosystem greening out ($F_{DR}$). Table 3 shows that years with antecedent wet winters have $R_{DR}/F_{DR}$ of $\sim0.5$ or greater, while those with antecedent dry winters have $R_{DR}/F_{DR} < 0.4$. Year-to-year differences in the respiration and fixation-dominant responses are depicted in Figure 5. As observed in other seasonally dry ecosystems (Yépez et al., 2007; Sponseller, 2007; Scott et al., 2009), respiration is the primary flux at the onset of the North American monsoon and up to the period when productivity increases substantially, typically 25 days after the start of the rainy season.

Note that $R_{eco}$ remains high throughout the summer (i.e., monsoons average from 4.7 to 5.8 g C/m$^2$/d) and diminishes in the subsequent winter. Respiration after ecosystem greening is composed of both autotrophic and heterotrophic fluxes, while ecosystem respiration following rain events prior to leaf out can be attributed mainly to the rapid activity of heterotrophs, as observed in tropical forests [Saleska et al., 2003; Baker et al., 2008; Goulden et al., 2004; Rowland et al., 2014]. Antecedent wet winters (2005 and 2008) lead to an elongation of the duration of the respiration-dominant conditions, as compared to preceding dry winters (2006 and 2007), from $\sim$60 days to over 110 days. In addition, the amount of CO$_2$ released during the respiration-dominant period nearly doubles in response to a wet preceding winter (Table 3). Thus, the winter and summer periods are closely linked with respect to carbon fluxes, even if the two periods are not associated in terms of precipitation, as suggested at other sites [Zhu et al., 2007].

Monsoon periods had higher amounts of fixation (more negative NEE) for higher amounts of precipitation (Figure 6), as shown in other studies [Sala et al., 1988; Scott et al., 2010]. GPP was highest during 2008 (1099 g C/m$^2$) when monsoon precipitation was $\sim$50% above the long-term average and lowest in 2006 (831 g C/m$^2$) when precipitation was $\sim$15% less than the seasonal average at the site. Nevertheless, both years exhibited similar water use efficiencies ($GPP/ET$) and $R_{eco}$/$GPP$ ratios (Table 2), indicating that the TDF ecosystem adjusts its monsoon season productivity, respiration, and water use to the available precipitation. Thus, the main reason for the variation in GPP among the monsoon periods is the difference in the length of the fixation-dominant period ($F_{DR}$), with higher precipitation leading to elongations into the fall.

---

**Table 3. Relation Between Winter Precipitation (P and Percentage of Annual Total) and Carbon Fluxes During the Study Period**

<table>
<thead>
<tr>
<th>Year</th>
<th>Winter P (mm)</th>
<th>Winter %</th>
<th>Start Date</th>
<th>Duration (days)</th>
<th>NEE (g C/m$^2$)</th>
<th>Start Date</th>
<th>Duration (days)</th>
<th>NEE (g C/m$^2$)</th>
<th>% (g C/m$^2$)</th>
<th>$R_{DR}/F_{DR}$</th>
<th>NEP</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>119.12</td>
<td>24</td>
<td>4 April</td>
<td>115</td>
<td>163.8</td>
<td>July 28</td>
<td>56</td>
<td>$-110.8$</td>
<td>148</td>
<td>80.1</td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>4.06</td>
<td>1</td>
<td>7 May</td>
<td>63</td>
<td>74.1</td>
<td>July 9</td>
<td>69</td>
<td>$-204.3$</td>
<td>36</td>
<td>-125.2</td>
<td></td>
</tr>
<tr>
<td>2007</td>
<td>44.96</td>
<td>9</td>
<td>17 May</td>
<td>61</td>
<td>82.8</td>
<td>July 17</td>
<td>97</td>
<td>$-214.1$</td>
<td>39</td>
<td>-124.7</td>
<td></td>
</tr>
<tr>
<td>2008</td>
<td>98.30</td>
<td>12</td>
<td>10 April</td>
<td>89</td>
<td>138.5</td>
<td>July 8</td>
<td>131</td>
<td>$-282.5$</td>
<td>49</td>
<td>-153.1</td>
<td></td>
</tr>
</tbody>
</table>

*Respiration-dominated and fixation-dominated periods are characterized by the start date, duration, and NEE. $R_{DR}/F_{DR}$ periods. Only complete yearly data sets were considered.*
season (56 days for 2005 and 131 days for 2008). Long fixation periods during the monsoon and extending into the fall affect whether the TDF ecosystem is a net source or sink of carbon. We found that three of the four monsoons in the study period acted as a net carbon sink (2006 to 2008, with $\Delta C = 75$ to $142 \text{ g C/m}^2$) due to longer duration of the monsoon precipitation (Tables 2 and 3), while one summer (2005) was a net carbon source ($+4 \text{ g C/m}^2$). The predominantly heterotrophic ecosystem respiration pulse during the respiration-dominant period accounted for 36% (2006) to 148% (2005) of the total carbon uptake during the monsoon in the TDF ecosystem.

3.4. Role of Antecedent Conditions on Carbon and Water Fluxes

Interannual and seasonal variations in ecosystem carbon fluxes reflect the influence of the antecedent winter conditions and the role of monsoon precipitation. Figure 6 summarizes ecosystem carbon fluxes at the TDF ecosystem in terms of the summer season respiration and fixation-dominant periods (Figure 6a) and for annual totals (Figure 6b). Within the summer season consisting of premonsoon and monsoon periods, higher seasonal precipitation leads to a change in the sign of net ecosystem productivity (NEP). This change in sign appears to occur for a monsoon precipitation between 350 and 400 mm. Negative NEP results from higher seasonal precipitation, primarily due to sustained carbon uptake during the fixation-dominant period (Figure 6a). The carbon sink strength is strongly controlled by the distribution and magnitude of precipitation during the North American monsoon, whereas the strength of the carbon source controlled by the
respiratory flux is dependent on the antecedent winter precipitation. This is supported by strong linear relations between the respiration-dominant carbon fluxes (i.e., \( R_{\text{DR}} \)) and the antecedent winter precipitation and winter NDVI (Table 4). Given the strong coefficients of determination \( (R^2 > 0.9) \) found, it seems plausible that increased accumulation of litter from the antecedent growing season, combined with a soil moisture legacy from winter precipitation, controls the respiratory pulse at the start of the summer growing season. Overall, these results hold at the annual time scale (Figure 6b), with wetter years experiencing negative NEP (i.e., GPP > \( R_{\text{eco}} \)) attributed to the monsoon fixation period and high values of \( R_{\text{eco}} \) experienced due to antecedent productivity and wet winters.

4. Discussion and Conclusions

Eddy covariance flux measurements over a 4.5 year period showed that changes in seasonal precipitation can notably influence carbon flux dynamics at a tropical dry forest ecosystem. Wet winter conditions are positively correlated with increases in NDVI values, suggesting an extended period of active vegetation during late winter and spring. Antecedent wet winters during the study period (2005 and 2008) increased the respiratory efflux during the premonsoon period, as has been observed in other seasonally dry ecosystems [Yépez et al., 2007; Scott et al., 2010]. This increased respiration flux prior to vegetation green-up suggests winter soil moisture, and an increase of labile soil organic matter was the carbon source for heterotrophic respiration. Studies in other forests, particularly those subject to cold temperatures that limit microbial activity [e.g., Vogel et al., 2005; Schindlbacher et al., 2007], have also identified higher ecosystem respiration when higher temperatures induce snowmelt [Liptzin et al., 2009]. In the case of TDF ecosystems, the presence of water from the first summer rains during a period of optimal temperature is considered responsible for the high CO2 efflux (carbon loss) measured by the eddy covariance technique.

While this work did not include direct observations of soil CO2 efflux at the site, relevant mechanisms of heterotrophic respiration have been suggested in prior studies. Increased rates of microbial activity have been identified after rewetting of dry soils [Jarvis et al., 2007] driven by the breakdown of soil aggregates [Birch, 1958; Appel, 1998; Xiang et al., 2008], an increase of microbial populations [Griffiths and Birch, 1961], and turnover of osmoregulants [Fierer and Schimel, 2003]. These mechanisms trigger microbially driven decomposition, mineralization, and pulses of CO2 emissions [Anaya et al., 2012; Austin et al., 2004; Carbone et al., 2011]. As a result, prior studies suggest that carbon fluxes are regulated by substrate availability that is ready to be decomposed under the optimal temperature and soil moisture present in the early part of the growing season. A similar link between antecedent wetness, soil organic matter availability, and the subsequent decomposition was identified in a seasonally dry forests of Brazil [Sanches et al., 2008], suggesting that the identified mechanisms might be common to other regions. Despite these similarities, longer-term studies (>10 years) in seasonally dry ecosystems are required to identify how interannual variability in seasonal precipitation affects the annual carbon balance.

Whether TDF ecosystems are a net sink or source of carbon on an annual time scale depends primarily on the length of the monsoon period when the ecosystem greens and its precipitation distribution (i.e., timing, duration and magnitude). Contributions from mainly heterotrophic respiration (carbon source) in the premonsoon period are overwhelmed by the strength of primary productivity (carbon sink) during the NAM. At this site, when monsoon precipitation exceeds 350 to 400 mm, sufficient soil moisture promotes the growth of shallow and deep-rooted plants [Huxman et al., 2004; Méndez-Barroso et al., 2009] that can lead to net carbon uptake. Under these conditions, the duration of the fixation-dominant period is extended well into the fall season (more than doubles from 56 to 131 days) that progressively assimilates carbon, resulting in a switch from a net source (+102 g C/m²/yr) to a net sink (−249 g C/m²/yr) in the TDF ecosystem. Based on long-term records, the monsoon precipitation threshold amount identified as the switch from net carbon source to sink is exceeded approximately one out of every 2 years (56% of the time) and represents 77 to 86% of the mean annual precipitation at the site. We expect that a similar set of carbon dynamics occurs in other tropical dry forests that
experience a bimodal precipitation regime, in particular, for those occupying vast amounts of land in Mexico (Figure 1). However, it is yet to be determined if the monsoon threshold on the annual carbon balance holds for other TDF ecosystems that experience different precipitation amounts [Forzieri et al., 2011]. In addition, it is expected that other seasonally dry ecosystems [Bullock et al., 1995] subject to a bimodal precipitation regime might also experience similar carbon flux dynamics. For example, Scott et al. [2009] and Hamerlynck et al. [2013] discuss drought effects on subsequent carbon fluxes in a semiarid savanna and a semiarid grassland, respectively, both subject to the North American monsoon. Nevertheless, additional efforts would be required to characterize the strength of the carbon release (respiration) and fixation (production) for these sites given their differing amounts of total biomass and vegetation response to the North American monsoon.

The sensitivity of carbon exchanges to the variation in seasonal precipitation in the TDF ecosystem suggests that changes to either winter or summer meteorological conditions are important. For example, drier winter conditions and a more intense summer monsoon under climate change, as suggested by Robles-Morua et al. [2015] for Sonora, might promote a stronger carbon sink in TDF ecosystems. In such a case, the drier antecedent winter conditions would suppress ecosystem respiration, primarily from microbial decomposition, in the early part of the growing season, while the wetter summer would promote a longer carbon fixation period. These projections, however, would need to also account for the physiological adaptations of TDF ecosystems to higher atmospheric CO$_2$ concentrations and its impact on vegetation water use efficiency. For instance, Forzieri et al. [2014] showed a long-term increase in rain use efficiency of the tropical dry forests in the NAM region and suggested that CO$_2$ fertilization might explain the trends observed from precipitation data and remotely sensed vegetation indices. Furthermore, seasonal changes in carbon exchanges mediated by microbial and plant communities also impact water fluxes, in particular, with respect to the return of soil water to the atmosphere. Evaporation and transpiration exchanges in TDF ecosystems play an important role on the delivery of water vapor to the atmosphere that can potentially serve as a source of subsequent rainfall, a process known as precipitation recycling [Domínguez et al., 2008; Méndez-Barroso and Vivoni, 2010]. Thus, the strong coupling between carbon and water fluxes in TDF ecosystems extends beyond the ecological and hydrological processes occurring at the land surface to include an important atmospheric component. Additional attention is warranted on how seasonal variations of carbon and water fluxes in TDF ecosystems are linked to historical atmospheric conditions and those projected by climate change scenarios that also account for the response of tropical dry forests.

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