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# Eddy covariance carbon flux in a scrub in the Mexican highland

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**Abstract**

Vegetation fixes C in its biomass through photosynthesis or might release it into the atmosphere through respiration. Measurements of these fluxes would help us understand ecosystem functioning. The eddy covariance technique (EC) is widely used to measure the net ecosystem exchange of C (NEE) which is the balance between gross primary production (GPP) and ecosystem respiration ($R_{eco}$). Orbital satellites such as MODIS can also provide estimates of GPP. In this study, we measured NEE with the EC in a scrub at Bernal in Mexico, and then partitioned into gross primary production (GPP-EC) and $R_{eco}$ using the recent R package Reddyproc. Measurements of GPP-EC were related to the estimates from the MODIS satellite provided in product MOD17A2H, which contains data of the gross primary productivity (GPP-MODIS). The Bernal site was a carbon sink despite it was an overgrazed site, the average NEE during fifteen months of 2017 and 2018 was -0.78 g C $m^{-2}$ $d^{-1}$ and the flux was negative in all measured months. The GPP-MODIS underestimated the ground data when representing the relation with a Theil-Sen regression: GPP-EC = 1.866 + 1.861 GPP-MODIS; an ordinary less squares regression had similar coefficients and the $R^2$ was 0.6. Although cacti (CAM), legume shrubs ($C_3$) and herbs ($C_3$) had a similar vegetation index, the nighttime flux was characterized by positive NEE suggesting that the photosynthetic dark-cycle flux of cacti was lower than $R_{eco}$. The discrepancy among the GPP flux estimates stresses the need to understand the limitations of EC and remote sensors, while incorporating complementary monitoring and modelling schemes of nighttime $R_{eco}$, particularly in the presence of species with different photosynthetic cycles.

## 1 Introduction

Xerophytic shrubland or "scrub" occupies more than 60% of the almost 2 million $km^2$ of Mexican territory; in North America and other regions of the world, they are an important ecosystem due to their potential to sequester large amounts of carbon (Biederman et al., 2017). Compared to tropical and temperate forests, scrub is a type of vegetation that has had less attention in C flux measurements with the eddy covariance technique (Vargas et al., 2013); which is implemented in the MexFlux network to generate scientific knowledge and understand the dynamics of Mexican ecosystems in the context of global climate

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change (Delgado-Balbuena et al., 2018a). Improving knowledge about this type of vegetation is important because they dynamically perform as sources or sinks of C, depending on available precipitation (Biederman et al., 2017).

The micro-meteorological eddy covariance technique (EC), measures at the plant community level the net ecosystem exchange of $CO_2$ (NEE), $H_2O$ or $CH_4$, in a non-destructively way, and continuously over time (Baldocchi, 2014). The EC has advantages compared to other techniques that need to scale measurements from the leaf, plant or soil levels up to the ecosystems scale, especially when the vegetation is heterogeneous (Yepez et al., 2003). However, EC is an expensive technique, data analysis and processing are complicated, and specific assumptions must be meet regarding the terrain, vegetation and micro-meteorological conditions, among other aspects (Richardson et al., 2019). Decomposition of NEE into gross primary productivity (GPP) and ecosystem respiration ($R_{eco}$) provides a better understanding of carbon fluxes from the biosphere into the atmosphere and the other way around.

Productivity and carbon sequestration is estimated with remote sensors from the MODIS (Moderate-Resolution Imaging Spectroradiometer) satellite, that provide input data for the MOD17A3H product containing information on the annual net primary productivity (NPP); derived by adding band values of net photosynthesis (PSN) included in the MOD17A2H product (Running et al., 1999). The MOD17A2H contains composite values of gross primary productivity (GPP) and PSN for periods of eight consecutive days in a homogeneous spatial grid and with a historical record of almost twenty years. MOD17 products are important in theoretical and practical applications, such as carbon sequestration inventories or carrying capacity assessment (De Leeuw et al., 2019; Neumann et al., 2015; Running et al., 1999). However, the validation of the GPP and PSN provided in MOD17A2H is a continuous effort, as the algorithm is improved in successive versions.

In this paper we present $CO_2$ flux data obtained with the EC technique in a scrub with continuous grazing management. The objective was to obtain monthly and eight-day estimates of NEE and GPP during the measurement campaign of 2017 and 2018. We explored an empirical relation between GPP from the EC tower and the GPP values provided by MOD17A2H v6 product looking for a better understanding of the carbon flux in an arid environment and contribute to the validation efforts of the MODIS product with ground data.

## 2 Materials & Methods

### 2.1 Site

The study site (N 20,717, W 99,941) is part of the database of carbon flux in Mexico (Delgado-Balbuena et al., 2018a). It is located in the municipality of Ezequiel Montes in Querétaro at 2 050 m a.s.l., with a BS climate with summer rains (García, 1964), mean annual rainfall is 476 mm and mean annual temperature of 17.1 °C (CICESE, 2015). The terrain is flat, where soils are Vertisols with abundant sub rounded basaltic stones, without rocky outcrops, soil depth is greater than 0.6 m. The soil has a clay loam texture. The vegetation is less than 2 m in height with an overgrazed herbaceous stratum. The vegetation corresponds to secondary scrub with the dominant genera *Acacia* and *Prosopis*. The property is private, with grazing dairy cattle receiving additional concentrated foodstuffs under stall-feeding. The dairy buildings and cattle yards are outside the EC instrumentation measurement footprint. Grazing is continuous, water for livestock is only available in the feeding and milking area; there are no pasture divisions and the perimeter fence is made of stone. These characteristics of the animal production model and the state of vegetation are representative of land management practices and the scrub vegetation in this region.

### 2.2 Data of Eddy Covariance System

We only report the continuous measurements of the exchange of $CO_2$ for the period of April 2017 to August 2018 using the EC technique. Due to equipment malfunction and incomplete datasets some periods of time were eliminated. The fluxes were measured at a height of 6 m with the following instruments: A Biomet system (Licor Biosciences, USA) to measure $H_2O$ and $CO_2$ fluxes using an IRGASON-EC-150 open circuit analyzer, and a CSAT3 sonic anemometer, KH20 krypton hygrometer, these were connected to a CR3000 datalogger (Campbell Scientific Inc., Logan UT, USA). All data were collected at 10 Mhz in the datalogger and reported as μmol $CO_2$ $m^{-2}$ $s^{-1}$. Data was processed with the Eddypro package (Licor Biosciences, Lincoln, NE, USA) to convert them into average fluxes of 30-minute intervals. The negative $CO_2$ fluxes corresponded to NEE, which is equivalent to NEP (net ecosystem production) but with opposite sign.

The relative humidity and air temperature were measured with an HMP155A probe (Vaisala Corporation, Helsinki, Finland); net radiation was measured with a NR-Lite2 radiometer (Kipp & Zonen BV Delft, The Netherlands); and the photosynthetic active radiation (PAR) was measured with a quantum sensor SKP215 (Skye Instruments, Llandrindod Wells, UK). Measurements of the soils heat flux was implemented with four self-calibrating HFP01SC plates at 80 mm depth and in four representative positions of the landscape (Hukseflux Thermal Sensors BV, Delft, The Netherlands). Three time domain reflectometry probes (TDR) CS616 measured volumetric water content in the ground (θ) installed vertically, and two sets of TCAV thermocouples measured the temperature at 60 and 40 mm depths and above the HFP01SC plates (Campbell Scientific Inc., Logan, UT, USA). The TE525 (Texas Electronics, Dallas, TX, USA) tipping bucket rain gauge was installed at 1.2 m high and three meters away from the tower. All these meteorological variables were measured every 5 seconds and average values were stored every 30 minutes; rainfall was accumulated for the same time interval. Sensible (H) and latent (LE) heat fluxes were calculated using the EddyPro package. Details of the energy balance closure and its adjustment are not presented here, since this is not directly relevant for $CO_2$ flux (Wilson et al., 2002).

Only quality flagged records were used to account the $CO_2$ flux (qc_co2_flux = 0) according to the Mauder and Folken (2004) policy in the Eddypro program (Licor, 2019). However, this quality-checking is not sufficient especially in the case of $CO_2$; therefore, data was post processed using the Reddyproc package of R (R Development Core Team, 2009), to estimate the friction speed thresholds ($u$*), gap-fill data, and partition the NEE flux into its GPP and $R_{eco}$ components(Wutzler et al., 2018). The filled-in estimates of NEE (NEE_uStar_f), GPP (GPP_uStar_f), and $R_{eco}$ (Reco_uStar) were used from the $u$* annual base scenario because the difference between the base $u$* scenario and the 95% $u$* uncertainty threshold was 0.033 m $s^{-1}$; only 8.5% of half hour records had a $u$* outside the 95% $u$* threshold. Only data with a flag equal to 0 was used for the variable NEE_uStar_fqc, as defined by Reddyproc. Carbon dioxide flux data were time integrated and converted to g C $m^{-2}$ $d^{-1}$ using the molar ratio of C.

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### 2.3 Primary productivity comparison

Data from product MOD17A2H v 006 of the MODIS satellite of the National Aeronautics and Space Administration (NASA) was used for the study site. The images necessary for the period were downloaded from the Land Processes Distributed Active Archive Center (LP DAAC) portal, and a polygon of 1 km² was cropped, the central coordinate being the location of the EC instrumentation tower. The four pixels of the polygon were valued in their utility, according to the quality layer (QC) of the MOD17A2H product. The study site was classified as "grassland" according to the land use and vegetation classification layer provided by the University of Maryland (UMD), by product MCD11Q1 for 2018. The average GPP of the useful pixels of the polygon was considered as the observed value for each date, in this case, every eight days of the years 2017 and 2018. The GPP values reported by the product MOD17A2H (GPP-MODIS, g C $m^{-2}$ $d^{-1}$) were considered a GPP estimate of the EC data processed with recent R package Reddyproc (GPP-EC). Theil-Sen regression was used to characterize the relationship between GPP-EC as a response variable, and GPP-MODIS as an explanatory variable. The relationship was also represented with least squares regression (OLS).

Unlike the OLS regression, Theil-Sen regression has few assumptions on the distribution of residuals, is robust to outliers, and is a non-parametric test (Fernandes and Leblanc, 2005). In the OLS, it is assumed that the explanatory variable is measured without any error, but in the present case, both GPP-EC and GPP-MODIS have measurement error. The procedure was carried out with the summary.mblm function of the mblm package of R (Komsta, 2005).

### 2.4 Vegetation characterization

Thirty points were randomly selected for sampling within a 1-km² quadrant, using the Google Earth interface. The center point of the quadrant was the location of EC tower. The sampling was carried out in 13 points considering limitations of accessibility and representativeness of the vegetation. Each sampling point consisted of circular plot of 30 meters in diameter. The floristic list indicated the community structure and assembly (Krebs, 1989). For the scrub and tree species, the importance value index (IVI) was determined at each sampling point. The IVI is the sum of relative dominance, relative density and relative frequency of the species present. For each plant, two stem diameters, the number of individuals (abundance) and identity of each species were measured (Keel et al., 1993), as well as the coverage, which is the horizontal projection of the aerial parts of the individuals on the ground, expressed as a percentage of the total area (Wilson, 2011). The leaf area index (LAI) was measured in four individuals of the species with the highest IVI using a LI-2000 analyzer (Licor Inc.); The LAI corresponds to the leaf area (m²) per unit of surface area (m²) and is dimensionless. Measurements were made during twilight time at days 160 to 170 of the year 2017, following the protocol recommended by the manufacturer.

In order to determine an independent midday value of C assimilation, the flux of C (μmol $CO_2$ $m^{-2}$ $s^{-1}$) was measured with a portable photosynthesis system analyzer LI-6400XT (Licor Inc.) in plants with high IVI or known to be of ecological importance for the scrub vegetation in the region. Three plants of each genus were selected, and measurements were made on three leaves of each plant. The measurements were made on day 231 of 2017 at approximately 13:00 hours. Other variables

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measured were $H_2O$ flux and stomatal conductance (mol m$^{-2}$ s$^{-1}$). Statistical differences between species for the measured variables were established with ANOVA and the Tukey test using a significance of 0.05. Statistical procedures were performed with the SAS / GLM 14.1 program (SAS Institute Incorporated, Cary, NC, USA).

## 3 Results and discussion

### 3.1 Water and Carbon Exchanges

Twenty-four species of cacti and shrub were identified; on average, each sampling plot had 10.3 species. The IVI was similar between all cacti (0.36±0.04), shrub legumes (0.38±0.04) and other shrubs (0.23±0.06) sampled. *Cylindropuntia imbricata* presented the largest IVI, followed by *Acacia farnesiana*, *Acacia schaffneri and Prosopis laevigata* (Table 1). The greatest IVI in these species was explained by the dispersion caused by cattle, either by ingesting or transporting seeds or plant parts (Belayneh and Tessema, 2017). The IVI of the herbaceous stratum represented by grasses was not characterized, due to the state of overgrazing and the absence of reproductive structures in plants, which difficult measuring of their abundances, frequencies and dominances. The grass genera present were *Melinis*, *Chloris*, *Cynodon* and *Cenchrus*, corresponding all to invasive tropical grasses.

Scrub species of higher IVI had a similar LAI (1.2), although the magnitude of the LAI of *P. laevigata* stood out (Table 1). There was a difference in the $CO_2$ flux between the scrub genera examined, with *Prosopis* and *Mimosa* having the highest averages, although the photosynthetic efficiency for water use was worse for the *Mimosa* genera (Table 2). The average $CO_2$ flux for P*rosopis* was in the same order of magnitude already reported for *P. glandulosa* (Carmona-Hernández et al., 2007), and higher than values reported for *P. velutina* in a riparian environment in Arizona by Yepez et al. (2007), who registered a $CO_2$ gain per unit of transpired $H_2O$ of 1.06 to 1.22 μmol mol$^{-1}$.

Carbon dioxide absorptions had a diurnal behavior beginning at dawn and ending before sunset (Figure 1). During night the flux was positive, indicating respiration even when at the site, the cacti had a high IVI. The average flux of $CO_2$ measured in leaves of the bushes was 9.3 μmol m$^{-2}$ s$^{-1}$ (n = 18), while the NEE during the study period was –3.5 to –16.1 μmol m$^{-2}$ s$^{-1}$ from 12:00 to 13:00 with the EC technique. The two techniques provided estimates in the same order of magnitude of the instantaneous $CO_2$ flux, although different respiration components and absorption rates are confounded in the EC measurements, particularly regarding cacti.

Although summer rains are characteristic of the sites climate, a negative NEE flux occurred at all measured months (Figure 1). The lowest $CO_2$ flux was recorded in January and February 2017 and in May 2018 (Table 3), this behavior results from the phenology of the vegetation, since most of species lost their leaves in the dry season, and the effects of low temperature and / or low precipitation. Within the rainy season, the flux of $CO_2$ increased, compared to the months of January to June. The correlation between NEE and precipitation was -0.45. When the sum of the precipitation of the current month and that of the previous month was considered, the correlation with NEE was -0.7, suggesting that continuous availability of soil moisture is important for the absorption of $CO_2$ in this environment. This result is consistent with other studies in which the relationship

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between the net productivity of the ecosystem (NEP) and precipitation is initially positive, but is leveled from 1000 to 1500 mm annually (Xu et al., 2014).

Although the carbon balance in ecosystems is influenced by different factors such as soil type and amount of nutrients, it has been found that the relationship with soil temperature and humidity is particularly strong (Anderson-Teixeira et al., 2011; Hastings et al., 2005). It is possible that the canopy of the bushes intercepted the rainfall in some months completely, because the scrub can intercept up to 20% of the precipitation and its canopy storage capacity is 0.97 mm (Mastachi-Loza et al., 2010). Considering only the daily rain events greater than 5 mm, the correlation between precipitation and NEE rose to -0.72. In the present study, the interception of rain by vegetation was not calculated, but the results suggest that it would be important to explore the relationship between net precipitation and NEE, possibly through an independent soil water balance.

The average NEE at a global level is -156 ± 284 g C $m^{-2}$ $y^{-1}$ (Baldocchi, 2014). The highest frequency among sites that measured NEE with EC occurs from 200 to 300 g C $m^{-2}$ $y^{-1}$, but in sites with biometric measurements, the peak occurs at 100 g C $m^{-2}$ $y^{-1}$ (Xu et al., 2014). Using the daily averages of Table 3, the average NEE during the measurement period was -0.78 g C $m^{-2}$ $d^{-1}$ and annually would be -283.5 g C $m^{-2}$ $y^{-1}$. This result was higher than the annual values of the induced grassland and scrubland vegetation characterizing the Sonora desert plains (138 and 130 g C $m^{-2}$ $y^{-1}$, Hinojo-Hinojo et al., 2019). In New Mexico, NEE values measured with EC are between 35-50 g C $m^{-2}$ $y^{-1}$ in desert grassland and 344-355 g C $m^{-2}$ $y^{-1}$ in mixed coniferous forest (Anderson-Teixeira et al., 2011). In this sense, in the sarcocaulescent scrubland of Baja California, the NEE was -39 and -52 g C $m^{-2}$ $y^{-1}$ in 2002 and 2003, respectively (Hastings et al., 2005). Although the measurements of the present study had gaps and were compared with annual studies, we considered that the reported value of C was representative of the main season of growth of this type of scrub.

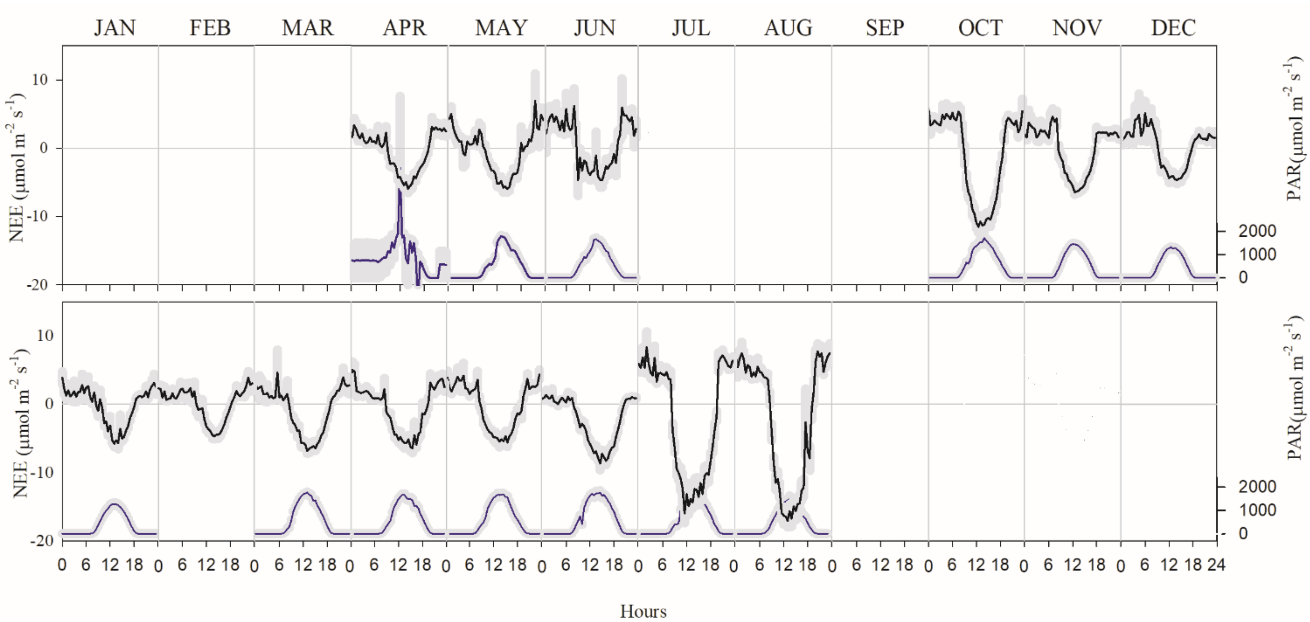


**Figure 1. Net ecosystem exchange (NEE) and photosynthetic active radiation (PAR) in 2017 and 2018 at Bernal site. Negative values in the $CO_2$ flux indicate photosynthesis.**

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Values of GPP MODIS underestimated the measured GPP EC (Figure 2). The OLS regression had an adjusted $R^2 = 0.6$ but the assumptions of constant variance and independence were not met. Thus, the Theil-Sen regression was considered more representative of the relationship between the two estimates, although it also underestimated the EC values. In the Theil-Sen equation: y = 1.866 + 1.861 x, the intercept was different from 0 ($p < 0.05$) and the slope was far from 1. Ideally, the relationship between the two sensors should have a slope equal to 1. In other studies, results have been similar. The GPP of MOD17A2H did not relate well (EC = 0.11 + 0.17 MODIS, $R^2 = 0.67$) with estimates of GPP in semi-desert vegetation of the Sahel (Tagesson et al., 2017). With data from different types of vegetation in the Heihe basin in China, MODIS17A2H overestimated the GPP from EC (EC = 1.15 + 0.24 MODIS, $R^2 = 0.68$, Cui et al., 2016). For scrub sites in Mexico, the relation between GPP calculated from EC and MOD17A2H was not good (MODIS = 383.82 + 0.467 EC, $R^2 = 0.6$, Delgado-Balbuena et al., 2018b). In arid and semi-arid ecosystems in China, optimizing parameters of the MODIS GPP model with site-specific data, improved the estimate to explain 91% of the variation in the GPP of the data observed by EC (Wang et al., 2019). These same authors propose improving the land use classification used by the MOD17A2H algorithm and recalibrating light use efficiency parameters, among others, to solve the GPP estimation problem.

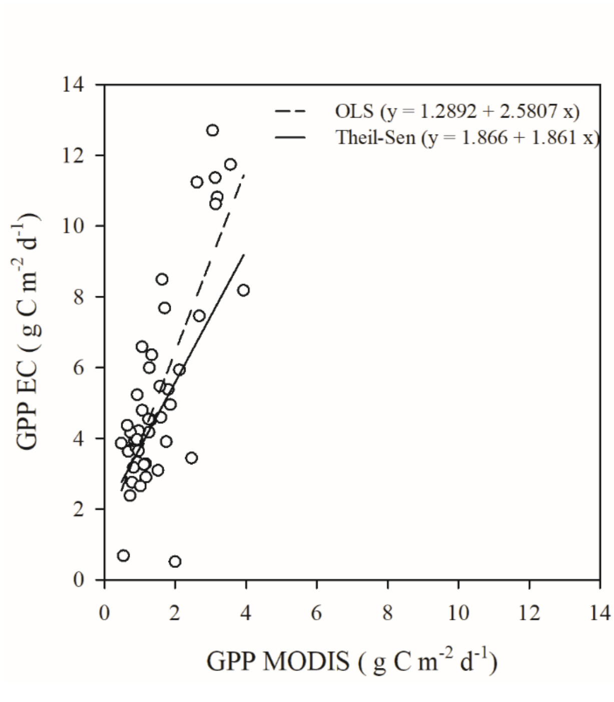


**Figure 2. Relationship between the gross primary productivity obtained by the eddy covariance technique (GPP EC) and the GPP values of MODIS (GPP MODIS) for the Bernal site. The lines represent the non-parametric model Theil Sen and the OLS model.**

The relationship between the GPP MODIS and the GPP EC presented in Figure 2 is an approximation, because the uncertainty in the respiration component must be considered. The empirical relationship between nocturnal NEE and soil temperature has

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been used to represent ecosystem respiration ($R_{eco}$) in order to separate the processes that contribute to daytime NEE (Richardson and Hollinger, 2005; Wofsy et al., 1993). Nighttime NEE should be equal to the rates of autotrophic and heterotrophic respiration, while during daytime, NEE should be equal to the combined rates of carboxylation and oxidation of RUBISCO, autotrophic respiration and heterotrophic respiration. Then the GPP can be calculated as the difference between daytime NEE and $R_{eco}$, estimated through its relationship with temperature (Goulden et al., 1996). In the present study, $R_{eco}$ was calculated based on the procedure of Reichstein et al. (2005) implemented in Reddyproc (Wutzler et al., 2018). Although it is possible to measure or model the partition of respiration (Running et al., 2004; Wang et al., 2018), the presence of cacti complicates, assuming that all nighttime flux represents ecosystem respiration (Owen et al., 2016; Richardson and Hollinger, 2005). On the other hand, the instrumentation at the study site did not include measurements of plant or soil respiration partition to validate the $R_{eco}$ estimates.

A problem regarding data comparison from remote orbital sensors and terrestrial observations is that different quantities are fundamentally measured. MODIS measures the radiation reflected by the earth's surface in two spectral bands at 250 m spatial resolution per pixel, five bands at 500 m and 29 bands at 1 000 m. The EC technique has a footprint to measure $CO_2$ that varies dynamically in shape and size, but is generally considered to be 1 $km^2$. To solve the scaling, MODIS products related to the carbon cycle have been validated with the EC technique and biometric measurements on several spatial scales using process-based ecosystem models and characterizing areas up to 47 $km^2$ around the EC measuring tower (Cohen et al., 2003). In our site, the variation in the NEE signal remained in the same order of magnitude during the study period (Figure 1), but in the corresponding MODIS data, the variation of the signal increased by an order of magnitude ($s > 0.1$) when the vegetation was most active (Figure 3). This behavior was interpreted as greater heterogeneity in vegetation activity in the four pixels used (4 $km^2$). In the area of 1 $km^2$ in which the vegetation was characterized, we found that the variation in the botanical composition was in the same order of magnitude for the species found and the LAI variation for the species with the highest IVI was also similar.

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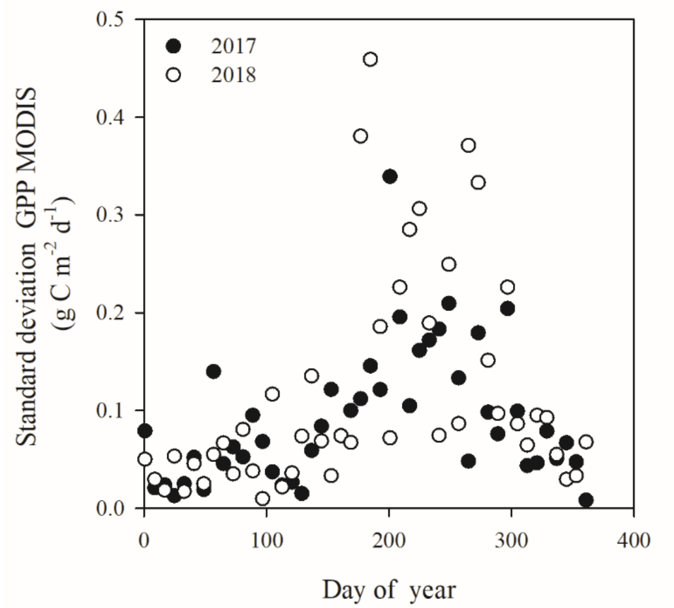


**Figure 3. Time series of the standard deviation of the gross primary productivity of the MODIS MOD17A2H product (GPP MODIS) for the Bernal site during 2017 and 2018.**

## 4 Conclusion

225 The Bernal site was a carbon sink notwithstanding its overgrazed condition. This is due to the contribution to the carbon flux of the remaining shrub species in this area. Ground and remote sensed estimates of GPP were comparable by means of a regression equation; MODIS estimates of GPP for this vegetation type cannot be taken at face value; the MODIS land cover type product misclassified the Bernal site and was most likely affecting the GPP estimate. Although the importance value index of cacti was high in the study area, their metabolic activity did not outweigh the respiration component of the $CO_2$ flux during nighttime; therefore, is necessary to measure autotrophic and heterotrophic respiration components of the ecosystem. Precipitation was related to NEE but the soil water balance must be studied because the growing season of this vegetation type expands well beyond the predominant summer monsoon.

## 5 Data availability

Database and programming code are available at https://doi.org/10.5281/zenodo.3598595

## 6 Author contribution

Guevara-Escobar contributed to conceptualization, formal analysis, investigation, methodology, software, supervision, validation, visualization, writing – original draft and review & editing.

E. González-Sosa was in charge of funding acquisition, project administration, resources, supervision and writing – review.

M. Cervantes-Jimenez contributed to investigation, methodology, validation, visualization, writing – original draft and review & editing.

M. E. Queijeiro-Bolaños helped with investigation, validation, writing – review.

H. Suzán-Azpiri contributed with conceptualization and writing – review.

I. Carrillo- Ángeles helped with investigation and writing – review.

V. H. Cambrón-Sandoval contributed with writing – review and funding acquisition.

## 7 Competing interest

The authors declare that they have no conflict of interest.

## 5 Acknowledgments

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**Table 1. Importance value index (IVI) and leaf area index (LAI) of the main species present at the Bernal, Querétaro study site.**

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| Species | Plant type | IVI | SEM[1] | LAI | SEM |
|---|---|---|---|---|---|
| *Coryphantha cornifera* | Cactus | 0.07 | 0.27 | | |
| *Bouvardia ternifolia* | Herb | 0.07 | 0.27 | | |
| *Karwinskia humboldtiana* | Shrub | 0.07 | 0.27 | | |
| *Forestiera phillyreoides* | Shrub | 0.09 | 0.27 | | |
| *Ferocactus latispinus* | Cactus | 0.09 | 0.27 | | |
| *Cylindropuntia leptocaulis* | Cactus | 0.09 | 0.27 | | |
| *Asphodelus fistulosus* | Shrub | 0.09 | 0.19 | | |
| *Brickellia veronicifolia* | Shrub | 0.10 | 0.27 | | |
| *Dalea lutea* | Shrub | 0.11 | 0.15 | | |
| *Eysenhardtia polystachya* | Legume | 0.13 | 0.15 | | |
| *Myrtillocactus geometrizans* | Cactus | 0.14 | 0.27 | | |
| *Schinus molle* | Shrub | 0.14 | 0.19 | | |
| *Jatropha dioica* | Herb | 0.15 | 0.19 | | |
| *Mammillaria uncinata* | Cactus | 0.16 | 0.12 | | |
| *Opuntia tomentosa* | Cactus | 0.17 | 0.11 | | |
| *Opuntia robusta* | Cactus | 0.23 | 0.07 | | |
| *Opuntia hyptiacantha* | Cactus | 0.26 | 0.07 | | |
| *Mimosa monancistra* | Legume | 0.28 | 0.12 | | |
| *Mimosa depauperata* | Legume | 0.31 | 0.12 | | |
| *Zaluzania augusta* | Shrub | 0.33 | 0.10 | | |
| *Viguiera linearis* | Herb | 0.36 | 0.11 | | |
| *Acacia schaffneri* | Legume | 0.41 | 0.07 | 1.13 | 0.15 |
| *Prosopis laevigata* | Legume | 0.41 | 0.07 | 1.48 | 0.12 |
| *Acacia farnesiana* | Legume | 0.56 | 0.09 | 1.12 | 0.37 |
| *Cylindropuntia imbricata* | Cactus | 0.74 | 0.07 | 1.13 | 0.11 |

[1] SEM: standard error of the mean.

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**Table 2. Characteristics of the gas flux determined in leaves of some shrub species using an LI6400XT portable photosynthesis system analyzer. The determination was made at approximately 1:00 p.m. on August 19, 2017 (day 231).**

| Genus | $CO_2$ flux µmol $m^{-2}s^{-1}$ | | Stomatal conductance mmol $m^{-2}s^{-1}$ | | $H_2O$ flux mmol $m^{-2}s^{-1}$ | | Water use efficiency µmol/mmol |
|---|---|---|---|---|---|---|---|
| *Karwinskia* | 4.52 | a[2] | 0.08 | a | 1.65 | a | 2.74 |
| *Acacia* | 6.85 | ab | 0.14 | ab | 2.97 | ab | 2.30 |
| *Celtis* | 5.81 | a | 0.18 | abc | 3.46 | abc | 1.68 |
| *Montanoa* | 10.00 | abc | 0.24 | abc | 4.12 | bc | 2.43 |
| *Prosopis* | 14.62 | c | 0.29 | bc | 5.75 | c | 2.54 |
| *Mimosa* | 13.94 | bc | 0.76 | c | 12.21 | c | 1.14 |
| SEM[1] | 1.80 | | 0.04 | | 0.55 | | |

[1] SEM: standard error of the mean. [2] Within the same column, means with the same letter were similar ($p< 0.05$).

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**Table 3. Average values of the net ecosystem exchange (NEE), gross primary productivity (GPP), ecosystem respiration ($R_{eco}$), accumulated rainfall (P) and average monthly temperature (Ta) in a scrub at Bernal site. Negative values of NEE indicate photosynthetic absorption.**

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| | | NEE | GPP | $R_{eco}$ | Ta | P |
|---|---|---|---|---|---|---|
| | | | μmol m-2 s-1 | | °C | mm |
| **2017** | JAN | | | | | 0 |
| | FEB | | | | | 0 |
| | MAR | | | | 18.5 | 29 |
| | APR | -0.54 | 2.48 | 1.94 | 18.3 | 16 |
| | MAY | 0.05 | 2.86 | 2.91 | 20.6 | 31 |
| | JUN | 0.38 | 4.21 | 4.59 | 19.3 | 73 |
| | JUL | -1.00 | 1.78 | 0.77 | 17.1 | 96 |
| | AGO | | | | | 75 |
| | SEP | | | | | 179 |
| | OCT | -1.26 | 5.25 | 3.99 | 15.3 | 52 |
| | NOV | -0.13 | 2.65 | 2.52 | 14.4 | 0 |
| | DEC | 0.04 | 1.80 | 1.84 | 13.8 | 0 |
| **2018** | JAN | -0.05 | 1.29 | 1.24 | 11.1 | 0 |
| | FEB | 0.06 | 1.88 | 1.94 | 15.5 | 12 |
| | MAR | -0.94 | 2.45 | 1.51 | 18.8 | 0 |
| | APR | -0.58 | 2.87 | 2.29 | 18.5 | 32 |
| | MAY | -0.29 | 3.77 | 3.48 | 19.5 | 66 |
| | JUN | -2.52 | 4.33 | 1.81 | 19.5 | 206 |
| | JUL | -2.83 | 8.23 | 5.41 | 18.9 | 6 |
| | AGO | -1.93 | 9.21 | 7.28 | 17.0 | 77 |