Controlling factors of the ecosystem and soil respiration in a xeric shrubland in the Chihuahuan Desert, Mexico

Factores que controlan la respiración del ecosistema y del suelo en un matorral xerófilo en el desierto de Chihuahua, México

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SUMMARY

In the terrestrial carbon cycle is very relevant to identify the influence of soil in the CO_2 released to the atmosphere, which is linked to multiple biotic and abiotic drivers. Arid ecosystems dominate the trend and interannual variability of the land CO_2 sink. This pattern is mainly controlled by temperature, precipitation, and shortwave radiation. Thus, these environments are characterized by a wide variability of water availability, which causes the CO_2 efflux to be highly variable in time, challenging our model capacities. This study aims to understand the ecosystem CO_2 fluxes and their controlling mechanisms from the Chihuahuan Desert in Northeast Mexico. We explore the average contribution of the R_{soil} (1.30 mmol m^{-2} s^{-1}) to R_{eco} (1.76 mmol m^{-2} s^{-1}), while identifying the controlling mechanisms of both on an annual scale. The structural equation model constructed showed a good fit for the data, explaining 50% and 93% of the annual variance of R_{soil} and R_{eco}, respectively. According to this model, R_{soil} was mainly controlled by the air temperature, and R_{eco} by soil water content. Unexpectedly, vapor pressure deficit was the most weight variable with a direct negative effect on R_{eco}, supporting the idea that the vegetation component has a crucial role in the CO_2 efflux of this ecosystem. This study highlights the importance of include multiple factors in the models of the C cycle.

Index words: *air temperature, ecosystem respiration, soil respiration, soil water content, structural equation models.*

RESUMEN

En el ciclo del carbono terrestre es muy relevante para identificar la influencia del suelo en el CO_2 liberado hacia la atmósfera, mismo que está vinculado a múltiples factores bióticos y abióticos. Los ecosistemas áridos dominan la tendencia y variabilidad interanual de los sumideros de CO_2 terrestre. Este patrón es principalmente controlado por la temperatura, precipitación y radiación de onda corta. De este modo, estos ambientes se caracterizan por una amplia variabilidad en la disponibilidad de agua, lo que hace que la emisión de CO_2 sea altamente variable en el tiempo, desafiando nuestra capacidad de modelación. El objetivo de este estudio es comprender los flujos ecosistémicos de CO_2 y los mecanismos que los controlan en el desierto de Chihuahua en el noreste de México. Exploramos la contribución promedio de R_{soil} (1.30 mmol m^{-2} s^{-1}) a R_{eco}(1.76 mmol m^{-2} s^{-1}), identificando los mecanismos de control de ambos en una escala anual. El modelo de ecuaciones estructurales construido mostró un buen ajuste de los datos, explicando 50 y 93% de la varianza anual de R_{soil} y R_{eco}, respectivamente. Según este modelo,

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R_{soil} fue controlado principalmente por la temperatura del aire y, R_{eco} por el contenido de agua en el suelo. Inesperadamente, el déficit de la presión de vapor fue la variable con el efecto negativo de mayor peso sobre R_{eco}, sustentando la idea de que el componente vegetal tiene un rol crucial en el flujo de CO_2 en este ecosistema. Este estudio destaca la importancia de incluir múltiples factores en los modelos del ciclo del carbono.

Palabras clave: *contenido de agua del suelo, modelos de ecuaciones estructurales, respiración del ecosistema, respiración del suelo, temperatura del aire.*

INTRODUCTION

The Net Ecosystem Exchange (NEE) is defined as the difference between the gross ecosystem productivity (GEP, photosynthetic assimilation of carbon dioxide -CO_2-) and the ecosystem respiration (R_{eco}). R_{eco} is the sum of different biological and non-biological CO_2 sources, grouped into above-ground respiration and below-ground respiration (Luo and Zhou, 2006). Above-ground respiration includes that from leaves and woody tissues, whereas below-ground respiration refers that produced by the soil respiration (R_{soil}), subterranean ventilation, carbonate weathering, or photo-degradation (Bond-Lamberty, Wang, and Gower, 2004; Brüggemann *et al*., 2011; Rey, 2015). Thus, R_{soil} is defined as the efflux rate measured at the soil surface as a result of the autotrophic (roots, mycorrhizae, endophytes, etc.) and heterotrophic (soil fauna) respiration (Phillips and Nickerson, 2015).

Soil carbon (C) reserves on the first meters of the earth's surface contain between 1500 and 2400 PgC, representing twice to three times the amount of atmospheric C (~829 PgC). This is mirrored in the soil CO_2 emissions (118.7 Pg per year) from the soil to the atmosphere, turning the R_{soil} into the largest terrestrial source of CO_2 (Ciais *et al*., 2013; Bispo *et al*., 2017). Furthermore, global changes in temperature, moisture (Bond-Lamberty and Thomson, 2010; Hursh *et al*., 2017), vegetation composition (Vargas, Detto, Baldocchi, and Allen, 2010; Roby, Scott, Barron, Hamerlynck, and Moore, 2019), and land-use (Post and Kwon, 2000) alters the R_{soil}, and subsequently the R_{eco}. Therefore, atmospheric CO_2 concentrations have increased in the last decades, raising concerns about global warming and further releasing CO_2, particularly from soils (Rustad, Huntington, and Boone, 2000).

Despite the importance of studying the R_{eco} and R_{soil} dynamics, their knowledge is biased to temperate ecosystems, at latitudes above 30º, being the tropical and arid ones least investigated (Baldocchi *et al*., 2001; Bond-Lamberty and Thomson, 2018). Among the latter, arid ecosystems cover roughly 47.2% of the earth's surface, having a key role in terrestrial C cycling since those dominate the trend and interannual variability of the land CO_2 uptake, acting as a C sink (Poulter *et al*., 2014; Ahlström *et al*., 2015). This behavior is at the same time controlled to a greater extent by the temperature, precipitation, and shortwave radiation (Ahlström *et al*., 2015). Similarly, 65% of the Mexican territory corresponds to arid lands (CONAFOR-UACh, 2013), which posses wide variability in the seasonal and inter-annual rainfall, precipitation pulses (Pontifes, García, Gómez, Monterroso, and Caso, 2018), and high plant diversity (~6000 species and 50% of endemicity) (Rzedowski, 2006). The aforementioned makes R_{soil} and R_{eco} highly variable over time and space, and strongly associated with the biological activity and vegetation variation (de Graaff, Throop, Verburg, Arnone III, and Campos, 2014; Montaño *et al*., 2016).

Studies that analyze the C flux in arid Mexican lands have focused on the NEE controllers, with the information about the R_{eco} and R_{soil} being scant (Cueva-Rodríguez, Robles, Garatuza, and Yépez, 2016; Montaño *et al*., 2016). Regarding R_{eco}, it has been shown precipitation legacies control the C uptake and R_{eco} of the next seasons, with GEP being more sensitive to precipitation than R_{eco} (Delgado-Balbuena *et al*., 2019) and that shifts in soil moisture and temperature drive the monthly variations of R_{eco} (Hastings, Oechel, and Muhlia, 2005; Bell, Menzer, Troyo, and Oechel, 2012). Whereas for R_{soil}, the main study topic has been the spatial heterogeneity linked to different vegetation types (Cueva-Rodríguez, Yépez, Garatuza, Watts, and Rodríguez, 2012) or land uses (Yáñez-Díaz, Cantú, González, Jurado, and Gómez, 2017). Nevertheless, monthly precipitation and soil temperature have been recorded as the primary drivers of R_{soil} in semiarid shrubland from Baja California (Leon *et al*., 2014).

While R_{eco}, in Mexican arid zones, is mainly measured using the eddy covariance method (Vargas *et al*., 2013), chamber-based methods are widely used to measure the R_{soil} (Cueva-Rodríguez *et al*., 2016). In general, it has been shown the eddy covariance method has lower fluxes than chamber-based methods, with the contribution of the R_{soil} to R_{eco} being quite heterogeneous, depending on the vegetation type, plant age, or the site biomass (Wang, Wang, and Bond, 2017b). Since R_{soil} is the main component of R_{eco}, theoretically, R_{soil} cannot be larger than R_{eco} (Luo and Zhou, 2006). Nevertheless, current studies have not yet confirmed that R_{eco} is consistently higher than R_{soil} at different spatial and temporal scales, indicating inconsistencies in measurement footprints, biases in the R_{eco} or R_{soil} measurements, or both (Barba *et al*., 2018).

The wide range of interactions among the different variables and the spatial and seasonal variability in arid ecosystems has made it challenging to develop consistent models to identify the control factors that lead to their C balance (Roby *et al*., 2019; Estruch, Macek, Armas, Pistón, and Pugnaire, 2020). Structural equation modeling (SEM) allows exploring potential direct and indirect controls over R_{eco} and R_{soil}, with an aprioristic model in which the causal relationships among variables are included (Shipley, 2002; Iriondo, Albert, and Escudero, 2003). SEM aims to systematically study the impacts imposed by multi-factors and evaluate the overall model performance instead of studying the individual effects (Grace, 2006; Eisenhauer, Bowker, Grace, and Powell, 2015; Wang, Zhou, Jia, and Ping, 2019b). Several studies have proven SEM to successfully find the controlling mechanisms of R_{soil} obtained from field estimates (Matías, Castro, and Zamora, 2012; Flores-Rentería *et al*., 2018; Curiel-Yuste *et al*., 2019). On the other hand, the number of studies that have applied the SEM methodology to explore the controlling mechanisms of the C fluxes with eddy covariance data has been increasing in the last decades (Chen, Yang, and Robinson, 2014; Wang, Zhou, Ping, Jia, and Li, 2018; Wang *et al*., 2019b).

This study investigates the controlling mechanism of R_{eco} and R_{soil} in a xeric shrubland in the Chihuahuan Desert of Northeast Mexico, and indagate the relationship between both parameters. Specifically, we answer the following questions: 1) Is the R_{eco} value consistently higher than R_{soil} through a year? 2) Are the precipitation, soil temperature, and photosynthetic active radiation the main causal controllers of R_{eco} and R_{soil}? Therefore, the following predictions were made: 1) Since R_{eco} is the sum of above-ground and below-ground respiration, which includes R_{soil} (Luo and Zhou, 2006; Phillips and Nickerson, 2015), it is expected R_{eco} values are consistently higher than the R_{soil}; 2) As precipitation, soil temperature, and shortwave radiation are the main CO_2 balance controllers in arid ecosystems (Poulter *et al*., 2014; Ahlström *et al*., 2015), it is expected those variables have a direct causal effect on the R_{eco} and R_{soil}.

MATERIALS AND METHODS

Site Description

Our study was carried out in the southeast of the Chihuahuan Desert, at General Cepeda municipality, in Coahuila de Zaragoza, México. Valleys and gentle hills characterize the topography. Climate conditions are dry, mean annual temperature is 17.5 °C with a maximum of 31.4 ºC in the warmest month and a minimum of 3.3 ºC in the coldest month (Fick and Hijmans, 2017). Mean annual precipitation is 493 mm, with the highest rainfall during July, August, and September (Fick and Hijmans, 2017). The dominant soils are leptosols (INEGI, 2007), very shallow with highly calcareous material (IUSS Working Group WRB, 2007). In this xeric semiarid shrubland, the dominant vegetation is composed of *Fouquieria splendens*, *Larrea tridentata, Yucca carnerosana, Yucca filifera, Dasylirion cedrosanum,* and several species of the Cactecaea family, such as *Echinocactus* spp., *Echinocereus* spp., *Mammillaria* spp., *Opuntia* spp., etc. (Granados-Sánchez, Sánchez, Granados, and Borja, 2011).

Soil Respiration Measurements

Six field campaigns were conducted every two months, from June 2019 to April 2020. Soil respiration (R_{soil}) was determined with a steady-state infrared gas analyzer (EGM-5; PP Systems, Amesbury, MA) and a portable dynamic closed chamber (SRC-1, PP Systems, Amesbury, MA, USA). Ten external PVC collars (10 cm diameter × 5 cm height at 3 cm depth into the soil) were inserted 24 h previous to the measurements. Two permanent 100 m lineal transects (20 m apart from each other) were established inside the footprint area of the micrometeorological tower. Five collars were inserted (spaced every 20 m) along each transect. The purpose of each collar's temporary insertion was to minimize the impact of the soil alteration (*e. g.*, underestimate R_{soil} from roots) (Davidson, Savage, Verchot, and Navarro, 2002; Heinemeyer *et al*., 2011). Each collar was re-inserted near the previous point at each new sampling event (30 cm). R_{soil} measurements (60 sec) were carried out between 12:00-15:00 h at maximum daily soil temperature (Matías *et al*., 2012). Additionally, soil temperature and soil moisture at 8 cm depth (Hydra Probe II, Stevens Water Monitoring Systems, Inc., Portland, USA), ambient temperature, ambient relative humidity (WatchDog 1450 Micro Station, Spectrum Technologies, Inc., Illinois, USA), and photosynthetically active radiation (PAR, MQ-200 sensor, Apogee Instruments, Utah, USA) were recorded at each R_{soil} sample point.

Soil Physicochemical Characterization

After R_{soil} measurements, soil cores (2 cm in diameter) were taken from a depth of 0-15 cm in dry and rainy seasons (February and August, respectively). Soils were sieved (<2 mm) and air-dried. Soil pH was determined in a 1:2 (w:v) aqueous suspension (Orion Star A211, ThermoFisher Scientific, Inc, California, USA). Soil organic matter (SOM) was assessed by loss on ignition at 400 °C for 4 hours.

Ecosystem-Scale Measurements

We installed a 3.5 m micrometeorological tower near the San Isidro community (25º 18′ 1.6″ N, 101º 23′ 32.51″ W, 1703 m elevation). The eddy covariance system (LI-7900, LI-COR Biosciences, Lincoln, Nebraska, USA) consisted of an open path infrared gas analyzer (LI-7500DS) and a three-dimensional sonic anemometer (WindMaster Pro, Gill Instruments, Lymington, UK). Flux data were sampled at 10 Hz and stored in a 16 GB USB device in the SmartFlux® 3 system, storing files in intervals of 30 min from May 2019 to May 2020. During the same period, meteorological variables were collected continuously at a rate of 1 s and averaged at 30 min intervals using a Datalogger (Sutron Xlite 9210, Sutron Corporation, USA). Relative humidity (RH) and air temperature (Tair) (Vaisala HMP155, Vaisala Corporation, Helsinki, Finland), net radiation was measured with a radiometer (NR-Lite2, Kipp & Zonen, Delft, Netherlands), and PAR was measured with a quantum sensor (LI-190R-SMV-5, LI-COR Biosciences, Lincoln, Nebraska, USA) and a pyranometer sensor (LI-200R-SMV-5, LI-COR Biosciences, Lincoln, Nebraska, USA). Soil heat flux measurements were implemented with three soil heat flux plates (HFP01, Hukseflux Thermal Sensors BV, Delft, Netherlands) at 8 cm depth. Additionally, three soil moisture and temperature probes (Hydra Probe II, Stevens Water Monitoring Systems, Inc., Portland, USA) were placed at 5 cm depth next to the heat plates, and a tipping bucket rain gauge (TE525, Texas Electronics, Dallas, USA) was installed three meters away from the micrometeorological tower. Meteorological and soil variables were measured every five seconds, averaged, and stored to half-hour intervals; rainfall was accumulated for the same time period.

Raw eddy covariance data were processed in EddyPro® software version 7.0.6 (https://www.licor.com/env/support/EddyPro/software.html), following standard procedures (Delgado-Balbuena *et al*., 2019). Wind velocities, sonic temperature, [CO_2], and [H_2O] signals were despiked considering outliers those values greater than ±3.5 SD (Vickers and Mahrt, 1997). Double rotation was applied to sonic anemometer wind velocities. Lags between the vertical wind velocity and scalars were removed with a cross-correlation procedure. C flux was estimated using a 30 min block average, and then they were corrected for air density fluctuations (WLP correction, Webb, Pearman, and Leuning, 1980). Fluxes were subjected to quality control procedures: i) stationarity (<50 %, Foken and Wichura, 1996), ii) integral turbulence characteristics (<50%), iii) flags of IRGA and sonic anemometer (Mauder and Foken, 2006), iv) range tests (±20 μmol CO_2 m^{-2} s^{-1}) (Taylor and Loescher, 2013), v) a threshold of u*= 0.12 m s^{-1}, which was defined through the 99% threshold criterion after Reichstein *et al.* (2005) and nighttime fluxes below the threshold were removed (Zhu et al., 2006), and vi) 90% of cumulative fluxes (> 200 m, footprint model, (Kljun, Calanca, Rotach, and Schmid, 2004). In the data period, 35% of half-hour data were lost after quality filtering. Closure of energy balance was > 90% for the whole period. Storage flux was not estimated because of the low vegetation stature, and we assumed it would be 0 over a 24-h period (Loescher *et al*., 2006).

Data gaps were filled with the Marginal Distribution Sampling algorithm (MDS, Reichstein *et al*., 2005). The online MPI Jena tool, www.bgc-jena.mpg.de/REddyProc/brew/REddyProc.rhtml, based on the REddyProc R package (Wutzler *et al*., 2018), was used for this gap-filling procedure and the flux partitioning of NEE. Ecosystem respiration (R_{eco}), *i. e.*, outflux from the land surface (µmol m^{-2} s^{-1} as NEE), was estimated using the air temperature by the night-time-based flux-partitioning algorithm (Reichstein *et al*., 2005).

Data Analyses

R_{soil} rates measured with EMG-5 (g CO_2 m^{-2} h^{-1}) were converted to micromoles of carbon dioxide per square meter per second (µmol CO_2 m^{-2} s^{-1}), dividing by the conversion factor 0.1584 (Lamptey, Li, and Xie, 2018). From the ecosystem scale measurements, only the R_{eco} data from the days of the field campaigns of R_{soil}, only ten half-hours were used (12:00-16:30). In these days/hours, non-gap-filling data were used. These ten values per campaign were compared with the ten R_{soil} sample points.

The difference between respiration (soil *vs.* ecosystem) at each field campaign was determined using a two-way Analysis of Variance (ANOVA) ($P < 0.05$). The assumption of normality of residuals and homoscedasticity of the variance was met. Tukey's honesty test was used to detect any significant differences between means. All ANOVAs were run in R (R-Core-Team, 2020).

To test the direct and indirect influence of the abiotic factors over R_{soil} and R_{eco}, and the relationship between those two C fluxes, computing structural equation models (SEMs) were implemented. Our model was a path analysis (Figure 1) which considered a complete set of hypotheses based on literature and own previous experience (Flores-Rentería *et al*., 2018; Curiel-Yuste *et al*., 2019; Wang *et al*., 2019b). In short, we hypothesized that radiation (PAR) would influence both air and soil temperature (Tair), as well as the soil water content (SWC; Jia *et al*., 2018; Wang *et al*., 2018). The air temperature would influence the vapor pressure deficit (VPD), which, in turn, controls the soil temperature (Tsoil), SWC, R_{soil} and R_{eco} (Wang *et al*., 2018; Wang *et al*., 2019b). A correlation between soil temperature and soil moisture, both affecting R_{soil} and R_{eco} was also taken into account (Flores-Rentería *et al*., 2018; Wang *et al*., 2018; Wang *et al*., 2019b). Additionally, soil pH could influence the R_{soil} because it potentially reflects the punctual concentration of labile carbon (Phillips and Nickerson, 2015). Non-significant loadings and pathways were sequentially eliminated by dropping the path with the largest nonsignificant *P*-value each time, and the new model was re-parameterized. For instance, relative humidity (RH), had a non-significant effect over R_{soil} and R_{eco};

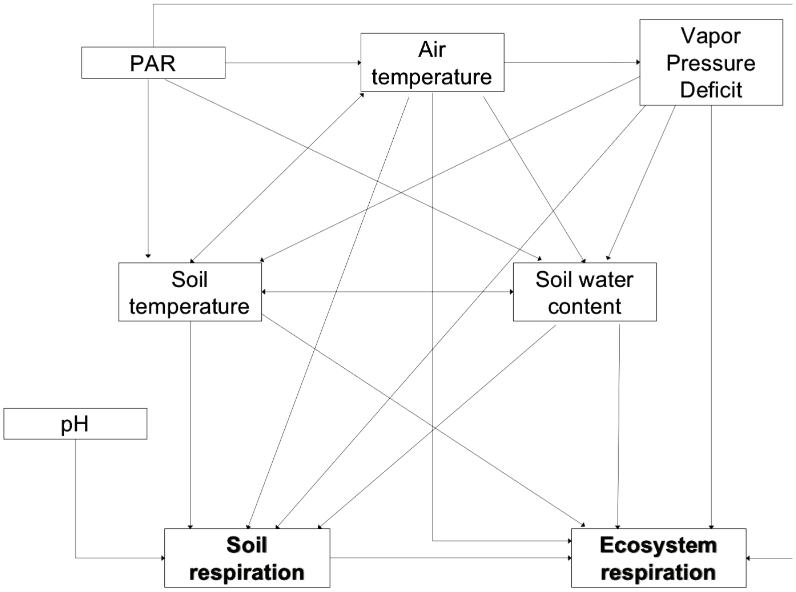

Figure 1. General model of the path analyses representing hypothesized causal relationships among the environmental factors, soil, and ecosystem respiration.

thus, this variable was no longer included in the model. Goodness-of-fit χ^2 was used to select the final model, according to the covariance proximity between observed and expected data. Bentler and Bonett's normed-fit index (NFI) was used to assess the data fit of the general model, where values >0.9 indicate an acceptable fit (Iriondo *et al*., 2003). Additionally, the root mean square error of approximation statistic (RMSEA) was used to assess the degree of fit between observed and expected structure of the covariance, where values <0.08 indicate a good fit (Steiger, 1990; Maccallum, Browne, and Sugawara, 1996). In all models, standardized path coefficients were estimated by using the maximum likelihood algorithm (Shipley, 2002). SEM analyses were performed by using SPSS® and SPSS® AMOS 20.0 software (IBM Corporation Software Group, Somers, NY).

RESULTS AND DISCUSSION

Regarding variables had direct and indirect influences on the respiration rates in the SEM analyses, the soil pH and SOM on the study site had a mean of 7.96 and 3.82%. Those values were higher for the pH, but lower for the SOM than the annual mean recorded in another shrubland (7.6 and 6.1%, respectively) and grassland (7.61 and 4.6% respectively) in the region (Yáñez-Díaz *et al*., 2017). Similar differences are observed when means for Tair, Tsoil, VPD, SWC, and PAR were compared regarding other arid ecosystems (Table 1). Table 1 enhance the high heterogeneity on those variables, particularly in North of Mexico, showing a large variety variation on the vegetation and orography (mirrored by differences in the elevation) among study sites as mentioned by larger scales studies (Anderson-Teixeira, Delong, Fox, Brese, and Litvak, 2011; Montaño *et al*., 2016).

The soil pH on the study site was slightly basic in February (7.99 ± 0.08) compared to the one recorded in August (7.93 ± 0.11). On the other hand, the SOM was slightly higher during February (4.00 ± 0.24%) in comparison with the one from August (3.64 ± 0.77%). Temporal variation is also evident when means of Tair, Tsoil, VPD, SWC, and PAR are compared among the different sampling dates (Figure 2). These results agree with long-term studies that analyze soil properties in the region, that have found important seasonal variations on these soil properties and environmental variables (Vargas *et al*., 2010; Lüneberg, Schneider, Siebe, and Daniel, 2018; Pontifes *et al*., 2018; Delgado-Balbuena *et al*., 2019). Further studies in the study site should test the seasonal variations on such variables in deep.

Table 1. Means on pH, soil organic matter (SOM), air temperature (Tair), soil temperature (Tsoil), vapor pressure deficit (VPD), soil water content (SWC), and photosynthetic active radiation (PAR) of comparable studies carried out in the Chihuahuan Desert and North of Mexico.

Variable/Source	This study	Hastings *et al.* (2005)	Anderson-Texeira *et al.* (2011)		Leon *et al.* (2014)	Yáñez-Díaz *et al.* (2017)	
Altitude (m)	1703	19	1596	1605	406	380	380
pH	7.96	NA	NA	NA	7	7.6	7.61
SOM (%)	3.82	0.21	NA	NA	NA	6.1	4.6
Tair (ºC)	25.28	23.87	13.46	13.4	17	20.79	20.79
Tsoil (%)	29.9	NA	NA	NA	21.04	22.51	25
VPD (hPa)	23.27	28.12	NA	NA	NA	NA	NA
SWC (%)	6.66	NA	NA	NA	NA	NA	NA
PAR (Wm^{-2})	1412.98	1700.34	NA	NA	NA	NA	NA
Vegetation	Xeric shrubland	Sarcocaulescent shrubland	Grassland	Shrubland	Xeric shrubland	Thornscrub	Grassland
Location	Chihuahua, Mexico	Baja California, Mexico	New Mexico, USA		Baja California, Mexico	Nuevo Leon, Mexico	

NA = not available data.

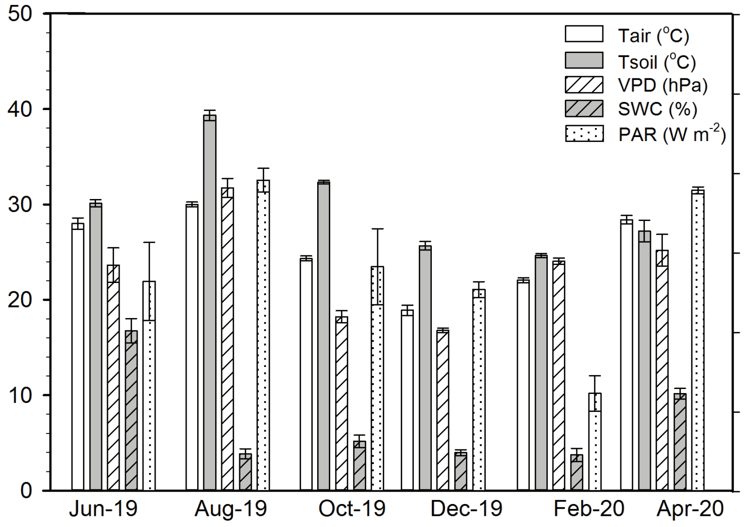

Figure 2. Variation of environmental factors along the year in the southeast of the Chihuahuan Desert in the moment of the soil (R_{soil}) and ecosystem (R_{eco}) respiration measurements. Data = mean ± standard error; Tair = air temperature; Tsoil = soil temperature; VPD = vapor pressure deficit; SWC = soil water content; PAR = photosynthetic active radiation.

Ecosystem Respiration Versus Soil Respiration

Annual mean R_{soil} was 1.3 ± 0.14 mmol m^{-2} s^{-1}, and R_{eco} of 1.76 ± 0.12 mmol m^{-2} s^{-1}, in this first study measuring the CO_2 flux annual variation in a xeric shrubland in the Chihuahuan Desert in northeastern Mexico. R_{soil} obtained in our study show a lower respiration annual rate than the one recorded in shrublands and grasslands from Nuevo Leon state (6.17 mmol m^{-2} s^{-1} and 4.61 mmol m^{-2} s^{-1}, respectively; Yáñez-Díaz *et al*., 2017), but nearest to the one recorded in shrublands from Baja California state (0.97 mmol m^{-2} s^{-1}; Leon *et al*., 2014). On the other hand, the comparison between R_{soil} and R_{eco} shows that both C fluxes exhibit a similar tendency throughout the year. Thus, the highest respiration rates (2.58 ± 0.32 and 3.50 ± 0.05 mmol m^{-2} s^{-1} for R_{soil} y $R_{eco,}$ respectively) were reached in June to decreasing until their lowest values in December (R_{eco} 0.75 ± 0.01 mmol m^{-2} s^{-1}) and February (R_{soil} 0.57 ± 0.10 mmol m^{-2} s^{-1}), and finally showing a new increase in April (Figure 3). This intra-annual respiration pattern contrast with those obtained for R_{soil} in other arid shrubs and grasslands from Northern Mexico, where the maximum and minimum values are registered in different months: September/October/November (maximum) and April/May/August (minimum) (Leon *et al*., 2014; Yáñez-Díaz *et al*., 2017). Similar differences in the intra-annual R_{eco} can be inferred from other Mexican arid zones by showing different peaks throughout their NEE values: July/August (maximum) and January/February (minimum) for a grassland in Jalisco state (Delgado-Balbuena *et al*., 2019), and December (maximum) and July (minimum) for a shrubland in Baja California state (Hastings *et al*., 2005). It is possible variations in vegetation and climate (Salinas-Zavala, Douglas, and Diaz, 2002; Encina *et al*., 2016; Pontifes *et al*., 2018) might explain, in part, the aforementioned differences and similarities among respiration rates, as suggested in large scale studies (Vargas *et al*., 2010; de Graaff *et al*., 2014; Cueva-Rodríguez *et al*., 2016; Montaño *et al*., 2016).

Our results show R_{eco} tend to have a higher respiration rate than R_{soil} throughout the analyzed period with a R_{soil}: R_{eco} annual mean ratio of 0.72. Nevertheless, lower values of R_{eco} regarding R_{soil} were observed in April 2020, recording a contribution ratio of 1.33 (Figure 3). Studies that compare the contribution ratio of R_{soil} to R_{eco}, using chamber based and eddy covariance methods suggest that can be highly variable even in the same ecosystem (*i. e*., 0.37 to 1.38 in temperate forests) (Janssens *et al*., 2001; Pilegaard, Hummelshøj, Jensen, and Chen, 2001; Curiel-Yuste, Nagy, Janssens, Carrara, and Ceulemans, 2005).

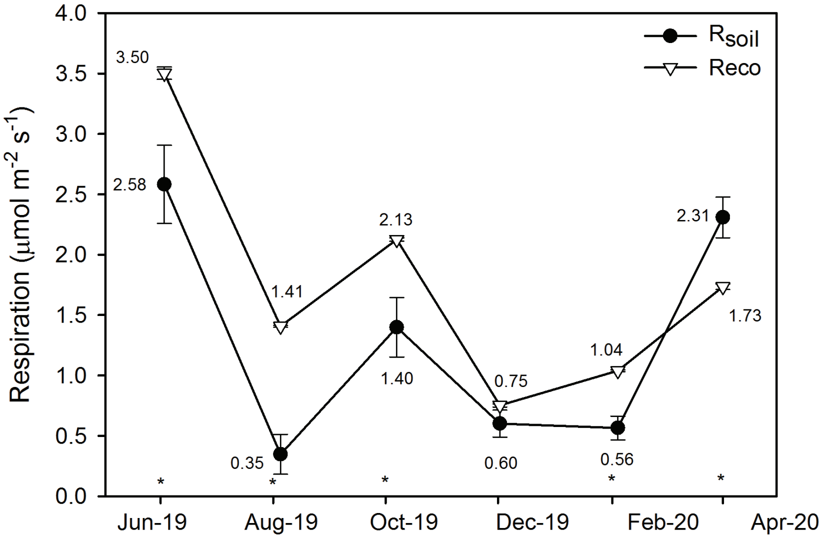

Figure 3. Soil (R_{soil}) and ecosystem (R_{eco}) respiration along the year in the southeast of the Chihuahuan Desert. Triangles and circles represent mean values. Error bars represent standard errors. Significant differences between respirations for a given sampling event are indicated with asterisks on the X axis, according to Tukey's post-hoc ($P < 0.05$) comparison of the two-way ANOVA results.

As a result of the spatial-temporal heterogeneity in small scales, biophysical parameters (*e. g*., vegetation type, plant age, site biomass, SWC, soil C content among others) have a strong influence on soil respiration, making the eddy covariance method has lower fluxes than chamber-based methods (de Graaff *et al*., 2014; Wang *et al*., 2017b). Particularly, rain pulses that increase SWC, hot spots, or hot moments have direct effect on the R_{soil} of arid ecosystems (Huxman *et al*., 2004; Leon *et al*., 2014; Salazar, Sulman, and Dukes, 2018). Thus, the higher $R_{soil,}$ regarding R_{eco}, recorded in April may be due to the SWC and temperature increasing in that moment (Figure 2), which may not be considered in the data partition of the eddy covariance method and subsequently no reflected in the calculated R_{eco} (Reichstein *et al*., 2005).

Even though the bias caused by the collars' insertions in the R_{soil} measurements was controlled, in part, by a shallow insertion (<5 cm) and measuring 24 h after inserting them (Heinemeyer *et al*., 2011), it has been shown that steady-state-dynamic chambers tend to generate insufficient or excessive turbulence inside the camera, resulting in measurement biases ranging from –21% to 33% of the known flux rate (Xu *et al*., 2006). Similarly, the poor representation of the spatial variability and a small area of measurement also have been identified as other factors in the bias of R_{soil} estimations (Savage and Davidson, 2003). Regarding the R_{eco} measurements, a low atmospheric mixing at night has been argued as the largest limitation in Eddy Covariance CO_2 measurements (Burba and Andersen, 2010; Burba, 2013). Thus, R_{eco} estimation method based on the light response curve (NEE~Radiation; Lasslop *et al*., 2010) might result in consistently highest R_{eco} values. Finally, the high R_{soil} registered in April may be due to a non-biological CO_2 source such as the carbonate weathering, as has been observed in other semiarid ecosystems with calcareous or carbonate-rich soils during dry periods (Emmerich, 2003; Ma, Wang, Stevenson, Zheng, and Li, 2013). Discrepancies on the R_{soil} contribution to R_{eco} are not yet clear, and the analysis of those is beyond the reach of this study. Nevertheless, considering the large proportion of R_{eco} values were explained at this half-hourly scale (Figure 3), it is possible that the mismatch of the R_{eco} and R_{soil} observed in our study may have been caused by altering the diffusive regime in the chamber measurements for R_{soil} (Phillips *et al*., 2017).

The intra-annual tendency of both measurements approaches observed in our results was similar (Figure 3), showing the higher values during the rainy season (June to October) compared to the dry one, except R_{soil} in April 2020. This pattern of higher CO_2 releasing throughout the rainy season is in agreement with the observed in studies where high root respiration has been described (Wang and Guo, 2006; Chen *et al*., 2014; Leon *et al*., 2014; Li *et al*., 2018; Roby *et al*., 2019). Therefore, here is reinforced the idea that R_{soil} depends on the frequency of rain events (Montaño *et al*., 2016; Roby *et al*., 2019; Wang, Chen, Li, Qian, and Yu, 2019a; Estruch *et al*., 2020).

Controlling Factors

SEM analysis was performed with data corresponding to the campaign where R_{soil} was measured to explore its relationship with R_{eco}, along with the controlling mechanism of both fluxes. A crucial role in the soil dynamics has been shown for the SOM in other environments of the region (*e. g*., Hernández-Becerra *et al*., 2016; García-Oliva, Elser, and Souza, 2018). Nevertheless, this variable coupled with RH did not have significant effects on the R_{soil} in our study, being excluded from the subsequent SEM analyses (Figure 4). The model shows a good data fit (*P* = 0.95, NFI = 0.99, GFI = 0.99 and RMSEA < 0.001), explaining a high proportion of variance of R_{soil} (R^2 = 0.50), and R_{eco} (R^2 = 0.93; Figure 4). The explained variance by the SEM is comparable with previous studies analyzing the causal relationships among environmental factors and CO_2 flux, specifically in arid ecosystems (Matías *et al*., 2012; Shao *et al*., 2016; Flores-Rentería *et al*., 2018; Yang, Ali, Xu, Jiang, and Lv, 2019).

R_{soil} was affected by the Tair followed by VPD (negatively), Tsoil (negatively), SWC, and pH (negatively). R_{eco} was controlled by SWC followed by Tair, VDP (negatively), R_{soil}, and Tsoil. The total effects showed that VPD has both direct and indirect effects over R_{eco} and R_{soil} (Table 2), accounting for the total effect over these; when VPD increases, both fluxes decrease on a daily scale. The VDP is considered a proxy for plant water stress because it controls stomatal water loss and plant carbon absorption (Hashimoto *et al*., 2008). When VPD increases, the stomatal closure affects both autotrophic and heterotrophic respiration (Shao *et al*., 2016; Roby *et al*., 2019). On the other hand,

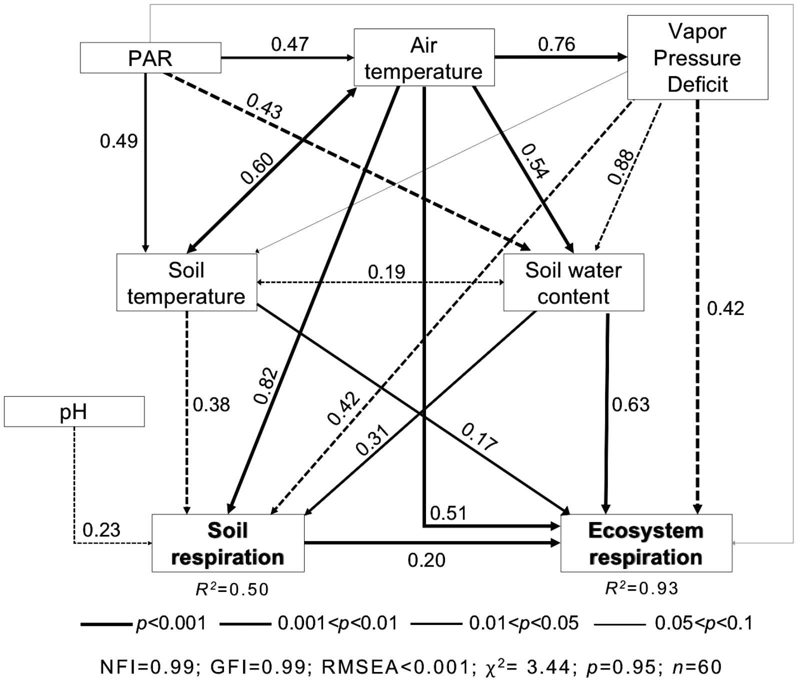

Figure 4. Structural equation models representing hypothesized causal relationships among the environmental factors, soil, and ecosystem respiration. Arrows represent causal relationships: positive (solid lines) and negative (dashed lines) effects, with numbers indicating standardized estimated regression weights (SRW). Arrow widths are proportional to significance values according to the legend. Paths with coefficients non-significant are in gray. NFI = 0.99; GFI = 0.99; RMSEA < 0.001; χ^2 = 3.44; p = 0.95; n = 60. PAR = photosynthetic active radiation.

radiation (*i. e.*, PAR) showed only weak indirect effects over R_{eco} and R_{soil} through its effect on Tair, Tsoil, and SWC. Furthermore, the estimated regression weight of Tair on both R_{soil} and R_{eco} was higher in comparison with Tsoil (Figure 4). A higher carbon input into the soil could explain this higher positive effect over Rsoil, instead of the release of stored older carbon (Bond-Lamberty and Thomson, 2010).

The two primary environmental drivers of biological soil and ecosystem respiration are temperature and moisture, but whit different contribution depending on the type of ecosystem. It is also known that soil dynamics in arid ecosystems tend to exhibit a higher spatial and temporal variability associated with the biological activity of soil microorganism, biocrusts, and plant roots (Sponseller, 2007; Cable *et al*., 2012; Phillips and Nickerson, 2015; Wang *et al*., 2017a). These variables act directly over the root and microbial respiration and indirectly regulating respiration derived by photosynthesis and plant growth (Davidson, Janssens, and Luo, 2006; Davidson, Samanta, Caramori, and Savage, 2012). Thus, the strong effect of Tair, SWC, and VPD over the R_{soil} and R_{eco} observed in our results reinforces the idea that the plant component plays a crucial role in the control of CO_2 efflux of this ecosystem (Vargas *et al*., 2011; Estruch *et al*., 2020). This strong vegetation influence over the CO_2 efflux, both R_{soil} and R_{eco} in the semiarid ecosystems, has been consistently described (Vargas *et al*., 2011; Cable *et al*., 2012; Delgado-Balbuena *et al*., 2019; Roby *et al*., 2019; Yang *et al*., 2019; Estruch *et al*., 2020).

CONCLUSIONS

The studied xeric shrubland in the Chihuahuan Desert had a R_{eco} mean of 1.76 ± 0.12 mmol m^{-2} s^{-1}, with 1.3 ± 0.14 mmol m^{-2} s^{-1} of R_{soil} contribution (71.94%). As expected, R_{eco} values were larger than R_{soil} throughout most of the analyzed period, except in April measurements. So far, inconsistencies of the R_{soil} contribution to the R_{eco} have been mainly recorded in temperate forests. The structural equation models explained 93% and 50% of the R_{eco} and R_{soil} total variance, respectively. Tair was found as the most weight R_{soil} controller, whereas the SWC was it for the $R_{eco,}$ both having positive direct effect. Unexpectedly, VPD was the most weight variable with a direct negative effect on R_{eco}, supporting the idea that the vegetation component has a crucial role in the CO_2 efflux of this ecosystem. In order to reach a better understanding of the CO_2 dynamics and their components in this environment, further studies should explore the R_{eco} long-term patterns, including the seasonal tendency. In addition, partitioning the R_{soil} contribution to R_{eco}, or testing another R_{eco} estimation method (*e. g.*, based on the light response curve, NEE~Radiation) might improve the R_{eco} values, and subsequently, the estimation of the R_{soil} : R_{eco} ratio.

ETHICS STATEMENT

Not applicable.

Table 2. Standardized direct, indirect, and total effects of environmental factors for soil and ecosystem respiration (See Figure 4). Significant direct effects are indicated in bold.

	Effect	Tair	PAR	VPD	SWC	Tsoil	pH
R_{soil}	Direct	**0.815**	---	**-0.419**	**0.31**	**-0.381**	**-0.23**
	Indirect	-0.179	-0.071	-0.102	---	---	---
	Total	0.636	-0.071	-0.522	0.31	-0.381	-0.23
R_{eco}	Direct	**0.512**	0.071	**-0.421**	**0.625**	**0.168**	---
	Indirect	0.081	-0.107	-0.31	0.062	-0.076	-0.046
	Total	0.593	-0.036	-0.731	0.687	0.092	-0.046

R_{eco} = ecosystem respiration; R_{soil} = soil respiration; Tair = air temperature; PAR = photosynthetically active radiation; VPD = vapor pressure deficit; SWC = soil water content; and Tsoil = soil temperature.

CONSENT FOR PUBLICATION

Not applicable.

AVAILABILITY OF SUPPORTING DATA

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

COMPETING INTERESTS

The authors declare that they have no competing interests.

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AUTHORS' CONTRIBUTIONS

Conceptualization: D.F.R. Methodology: E.C. and D.F.R. Software: E.C., J.D.B., and D.F.R. Validation: E.C., J.D.B., and D.F.R. Formal analysis: E.C. and D.F.R. Investigation: E.C. and D.F.R. Resources: D.F.R. Data curation: E.C. and D.F.R. Writing-original draft preparation: E.C. and D.F.R. Writing-review and editing: E.C., J.D.B., and D.F.R. Visualization: E.C. and D.F.R. Supervision: E.C. and D.F.R. Project administration: D.F.R. Funding acquisition: D.F.R.

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