# Soil respiration in Mexico: Advances and future directions

## Respiración de suelo en México: Avances y direcciones futuras

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## SUMMARY

Soil respiration ($R_S$) is a $CO_2$ efflux from the soil to the atmosphere defined as the sum of autotrophic (respiration by roots and mycorrhizae), and heterotrophic (respiration of microorganisms that decompose fractions of organic matter and of soil fauna) respiration. Globally, $R_S$ is considered to be the second largest flux of C to the atmosphere. From published literature it is clear that its main controls are soil temperature, soil moisture, photosynthesis, organic matter inputs and soil biota composition. Despite its relevance in C cycle science, there have been only twenty eight studies in Mexico in the last decade where direct measurement of gas exchange was conducted in the field. These studies were held mostly in agricultural and forest ecosystems, in Central and Southern Mexico where mild subtropical conditions prevail. However, arid, semi-arid, tropical and wetland ecosystems may have an important role in Mexico's $CO_2$ emissions because of their extent and extensive land use changes. From the twenty eight studies, only two provided continuous measurements of $R_S$ with high temporal resolution, highlighting the need for long-term studies to evaluate the complex biophysical controls of this flux and associated processes over different ecological succession stages. We conclude that Mexico represents an important opportunity to understand its complex dynamics, in national and global context, as ecosystems in the country cover a wide range of climatic conditions. This is particularly important because deforestation and degradation of Mexican ecosystems is rapidly increasing along with expected changes in climate.

***Index words:*** *biogeosciences; carbon cycle; soil* $CO_2$ *efflux; soil temperature; soil moisture.*

## RESUMEN

La respiración del suelo ($R_S$) se define como la suma de la respiración autótrofa (raíces y micorrizas) y la respiración heterótrofa (la de los microorganismos del suelo que descomponen materia orgánica y de la fauna del suelo). A nivel global, a $R_S$ se le considera el segundo flujo de C más importante hacia la atmósfera. La literatura denota que sus principales controles son la temperatura y humedad del suelo, la fotosíntesis, la disponibilidad de materia orgánica y la composición de la biota del suelo. A pesar de su relevancia en la ciencia del ciclo del C, ha habido solamente 28 estudios publicados en revistas indizadas en México en la última década, en los cuales se llevaron a cabo mediciones directas de intercambio de gases en campo. Estos estudios principalmente representan sistemas agrícolas y bosques en el centro y sur del país. Los ecosistemas áridos y semiáridos, tropicales y los humedales requieren atención debido a su cobertura espacial, su variación de temperatura y humedad, y la amenaza de los cambios de uso de suelo. De los 28 trabajos en la literatura, sólo en dos midieron $R_S$ de manera continua, remarcando la necesidad de llevar a cabo estudios a largo plazo para evaluar los complejos controles biofísicos y procesos asociados a este flujo en distintas fases de sucesión ecológica. Concluimos que México representa una oportunidad importante para entender la compleja dinámica de $R_S$, relevante en contextos nacionales e internacionales, debido a la fuerte estacionalidad que gobierna en la mayoría de

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los ecosistemas mexicanos. Esto es particularmente relevante ya que la deforestación y la degradación en los ecosistemas mexicanos están incrementando rápidamente mientras que se avizoran cambios importantes en la climatología del país.

***Palabras clave:*** *biogeociencias; ciclo de carbono; flujo de* $CO_2$ *del suelo; temperatura de suelo; humedad de suelo.*

## INTRODUCTION

Soil respiration ($R_S$, also known as soil $CO_2$ efflux) is the second largest carbon (C) flux between terrestrial ecosystem and the atmosphere (Raich and Schlesinger 1992; Bond-Lamberty and Thomson 2010). Globally, it exceeds the input of carbon dioxide ($CO_2$) by anthropogenic fossil fuels combustion to the atmosphere by an order of magnitude (Reichstein and Beer, 2008). Then, the importance of understand the dynamics and controls of $R_S$ is that it represents a net loss of C from the soils (Lal, 2004), and even a small change in this pool could represent a significant feedback to the Earth system (Reichstein *et al.*, 2003).

There is a growing community across the globe interested in measuring and understanding soil C fluxes. Furthermore, there are growing databases for ecosystem $CO_2$ fluxes (e.g., FLUXNET, AmeriFlux, MexFlux) (Baldocchi *et al.,* 2001; Vargas *et al.,* 2013) and $R_S$ (Bond-Lamberty and Thomson, 2014). However, most of the studies had been carried out in Europe and the United States (Bond-Lamberty and Thomson, 2010) at latitudes above 30° N. Ecosystems in those regions are characterized by temperate climates, with mean annual temperatures between 5-17 °C and annual rainfall above 600 mm; in contrast, arid, semiarid, tropical, and subtropical regions have been poorly represented, denoting that more tropical countries are underrepresented in continental-to-global understanding of the C cycle (Vargas *et al.*, 2012).This bias has regional, continental, and global implications, from scientific understanding to policy making and management that could be reduced if more spatially refined and *equally* distributed estimations and measurements exists, to improve our knowledge of the factors that govern $R_S$ across time and space (King *et al*., 2015).

Mexico has many contrasting ecosystems, spanning from arid deserts to evergreen and tropical forest. Besides, Mexico exhibits heterogeneous landscapes due to land use change, mainly from deforestation, and livestock grassing (Vargas *et al*., 2012). Furthermore, Mexico is prone to natural hidrometeorological disturbances, such as the North American Monsson across the Pacific Ocean, and tropical cyclones occurring in the Caribbean and the Gulf of Mexico. Despite the great opportunity describe natural phenomena in contrasting gradients (e.g., altitudinal, disturbances) and the potential for manipulative experiments, Mexican scientists have barely studied the dynamics of $R_S$ and other ecosystem C fluxes (Escobar *et al*., 2008).

The main objective of this paper is to highlight the opportunities that scientists interested in $R_S$ (e.g., biologists, ecologists, soil scientists, hydrologists, modelers) have to advance on the knowledge of soil C cycle science. We first review the global literature of $R_S$ in order to give a brief description of the main mechanisms that controls $R_S$, as well as common methodologies to measure it. Then, we make a synthesis from $R_S$ studies held in Mexico, to discuss the state of the art in this topic in the country. For the latter, we only focused on published literature where fluxes where measured or sampled in the field, excluding studies where soil samples were incubated in the laboratory.

## MECHANISMS

Soil respiration ($R_S$) is a composite of two main $CO_2$ sources (Ryan and Law, 2005): i) autotrophic respiration, the respiration by roots and mycorrhizae, and ii) heterotrophic respiration, the respiration of microorganisms within the soil that decompose fractions of organic matter plus the respiration of soil fauna. In view of the latter, $R_S$ exhibits complex dynamics across different spatio-temporal scales (Vargas *et al*., 2010b). The main abiotic controls of $R_S$ are soil temperature (Lloyd and Taylor, 1994; Davidson and Janssens, 2006) and soil moisture (Kim *et al*., 2012), while soil physical characteristics (Pumpanen *et al*., 2003) and organic matter inputs (Curiel Yuste *et al*., 2007) influence the composition of soil biota (Nannipieri *et al*., 2003). Although $R_S$ is the main $CO_2$ efflux from the soil to the atmosphere, other non-biological processes contributes to $CO_2$ emissions (Rey, 2015). An example of the latter is the chemical weathering of calcium carbonate (Ca $CO_3$) (Serrano-Ortiz *et al*., 2010; Hamerlynck *et al*., 2013) and pore degassing following major inputs of water (Liu *et al*., 2002; Lee *et al*., 2004).

## Biophysical Controls

At different spatial scales (e.g., plot to continental), soil temperature and soil moisture have been considered the main abiotic factors that account for the major temporal variability of $R_S$ (Subke and Bahn, 2010). Although the temperature dependence of $R_S$ has been greatly studied, there is still an open discussion about the temperature sensitivity of soil organic matter (SOM) decomposition (Giardina and Ryan, 2000; Davidson and Janssens, 2006; Conant *et al.,* 2011), and the dependence of $R_S$ on soil moisture is not well understood (Moyano *et al.,* 2012; Vicca *et al*., 2014). Furthermore, studies in the last two decades have demonstrated that photosynthesis plays also a key role regulating $R_S$ (Högberg *et al*., 2001; Vargas *et al.,* 2011). Thus, the interactions among these factors across temporal scales cause great uncertainties in estimations of $R_S$, and it becomes difficult to extrapolate site measurements to the estimation of C budgets at different spatial scales.

## Temperature

In most of the global literature, the variation of $R_S$ has been treated as a function of soil temperature (Lloyd and Taylor, 1994), the most widely used equations being those of van't Hoff and Arrhenius (Sierra *et al.,* 2011). The temperature dependence of $R_S$ reflects the effect of temperature on microbial metabolism which is derived from enzymatic kinetics (Schipper *et al.,* 2014). This temperature dependence of $R_S$ had received much attention in recent years due to contradictory results (von Lützow and Kögel-Knabner, 2009) resulting from different methods, such as incubation experiments, field measurements (Rinkes *et al.,* 2013), different substrate pools [e.g., high-quality-labile-fresh or low-quality-recalcitrant-old (Van Hees *et al*., 2005)], different metabolic temperature sensitivities of autotrophic or heterotrophic components (Boone *et al*., 1998), or different indices or empirical relations used to describe this relationship (Sierra, 2012). An important factor is the heterogeneity of abiotic and biotic factors within the soil profile (texture, temperature, moisture, microorganism composition, life strategies, acclimatization delays, root composition and distribution).

In temperate ecosystems, the diurnal increase and decrease of soil temperature is generally reflected in $R_S$ (Xu and Qi, 2001; Subke *et al.,* 2003). Some researchers have observed diel hysteresis and two arguments have been proposed to explain this phenomenon: i) environmental variables such as photosynthate production, litterfall, and soil organic carbon (SOC) availability may oscillate out of phase with soil temperature (Carbone *et al*., 2008; Vargas and Allen, 2008a); ii) soil temperature is measured at a fixed depth but $CO_2$ efflux represents a profile, leading to differences in magnitude and phase (Lasslop *et al*., 2012). Of course, $CO_2$ production has an intrinsic lag with surface efflux, dependent on depth and diffusion (Vargas *et al.,* 2010a). The temperature response of $R_S$ has concerned the scientific community because climate change would lead to positive feedback of $CO_2$ emission to the atmosphere (Fang and Moncrieff, 2001).

## Moisture

Microbial decomposition as well as root respiration may be limited by water availability. Global patterns of precipitation are changing in terms of number of events, event size, and the number of dry days between events (Knapp *et al*., 2015). However, the response of $R_S$ to precipitation events, or soil moisture, is relatively unknown (Kim *et al*., 2012).

For these reason researches had proposed several explanations and hypothesis of what could be happening after rain events: i) a rapid degasification of soil air-filled pore spaces (Yépez and Williams, 2009), ii) a re-hydration of dormant fungi and microbes and an increase of their biomass *(*Chowdhury *et al*., 2011), iii) microbial cell lysis due to a osmotic shock (Van Gestel *et al*., 1992), iv) release of microbial osmolytes that may support broader increases in metabolism (*metabolic hypothesis*) (Xiang *et al.,* 2008), v) rewetting of old, non-available or recalcitrant compounds (*physical hypothesis* or *priming effect*) (Kuzyakov, 2010). Also, root respiration should affected by the return of moist conditions. Ecosystems with highly seasonal hydrology are common in Mexico, so soil moisture is likely to be a key limiting factor in many processes controlling $R_S$ in Mexican ecosystems.

Mexico has a coastline of 12 122 km, where other non-rainfall inputs of water could influence the C exchange from terrestrial ecosystems to the atmosphere. Reimer *et al.* (2015) found that sea surface temperature could influence gross primary productivity (GPP) trough fog formation in the Baja California Peninsula; fog is an important non-rainfall water input in tropical cloud forests in Veracruz, as well in the deserts across Baja California, but it has not being linked with $R_S$ yet. Carbone *et al*. (2011) found in the Santa Cruz Island in California that seasonal and episodic moisture inputs from fog can influence the magnitude of $R_S$. Thus, it is important to recognize that not only water inputs from precipitation triggers $R_S$, but other non-rainfall inputs, such as dew or fog could influence $R_S$.

## Photosynthesis

Although temperature and moisture are the main temporal controls of $R_S$, recent studies provide evidence that plant photosynthesis influence $R_S$ at different temporal scales, challenging the assumption that most of the soil $CO_2$ efflux is microbial-derived (Kuzyakov and Gavrichkova, 2010; Mencuccini and Hölttä, 2010; Brüggemann *et al*., 2011; Vargas *et al.*, 2011). For example, there is evidence that >60% of the C released by $R_S$ in a temperate forest could be related to recent photo-assimilates transported belowground (Taneva *et al.*, 2006), and root respiration could be insensitive to decreasing temperatures while microbial metabolism is inhibited (Singh *et al.*, 2003).

This relationship of $R_S$ with photosynthesis showed temporal lags and phase differences from hours to days. However, these relations depend on ecosystem type, as well as vegetation phenology. For example, Vargas *et al*. (2011) showed that different forest types (e.g., Mediterranean, temperate, boreal) could present the same temporal lag between photosynthesis and $R_S$ (i.e., one day) but the duration (in days) of the effect differed. In contrast, grasslands used photoassimilates produced the same day for root respiration (Tang *et al.*, 2005; Bahn *et al.*, 2009).

## Temporal Variation

Seasonal variation of $R_S$ has been observed in almost every ecosystem. This variation is driven by seasonality of temperature, light, soil moisture, and the derived growing seasons of the vegetation and soil biota. This variation can be explained by leaf area index (LAI), litter production and root biomass (Thomas *et al.*, 2000). Phenology plays a key role, mainly through the timing of litterfall, labile C fraction availability, and root turnover (Curiel Yuste *et al.*, 2004). In special cases like wetlands, the main factor controlling $R_S$ is the tidal fluctuation where spring-neap tide cycles results in a fluctuating soil $O_2$ concentration, which limits or enhances both microbial and root activity and thus $R_S$ (Lovelock, 2008).

Successional changes in an ecosystem also drive variability of $R_S$ during long-time scales (Chapin *et al.,* 2002). During secondary succession, $R_S$ may rise substantially because some disturbances (e.g., logging, hurricanes, floods, but not fire) may input large amounts of labile C into the soil (Vargas, 2012a). This enhancement of $R_S$ eventually subsides (Luo and Zhou, 2006). In late succession, $R_S$ is expected to be high due to litter production and accumulation, and root density (Kolari *et al.,* 2004; Luo and Zhou, 2006, Kopittke *et al.*, 2013).

## Spatial Variation

Soil properties and dynamics are vertically and horizontally heterogeneous across the landscape, changing within a few centimeters (Figure 1). Soil texture and tortuosity affect the diffusion rate of the gases within the soil (Moldrup *et al.,* 2001). The local availability of nutrients affects soil microbiota composition and activity, influencing $R_S$ rates (Lipson *et al.,* 2005; Almagro *et al.,* 2013). Soil temperature and moisture are spatially heterogeneous (Huxman *et al.*, 2004), creating spots where the metabolic activity of microbes and fine roots are higher or lower (Jenerette *et al.*, 2008) producing hot spots and hot moments of $R_S$ across the landscape (Leon *et al.*, 2014). Special attention has been paid to the effect of vegetation on $R_S$. For example, Barron-Gafford *et al.* (2011) studied the dynamics of $R_S$ under different cover types (under grasses or mesquites, and inter-canopy), Tang and Baldocchi (2005) evaluated the influence of the proximity of trees on $R_S$, Cable *et al.* (2011) compared $R_S$ in seven different deserts, and Rochette *et al.* (1991) evaluated the influence of different crops on the efflux of $CO_2$ from the soil.

# METHODS AND TECHNIQUES TO MEASURE AND ESTIMATE SOIL RESPIRATION

There are different approaches to measure $R_S$ in the field (Figure 2): i) $CO_2$ trapping, ii) measurement of

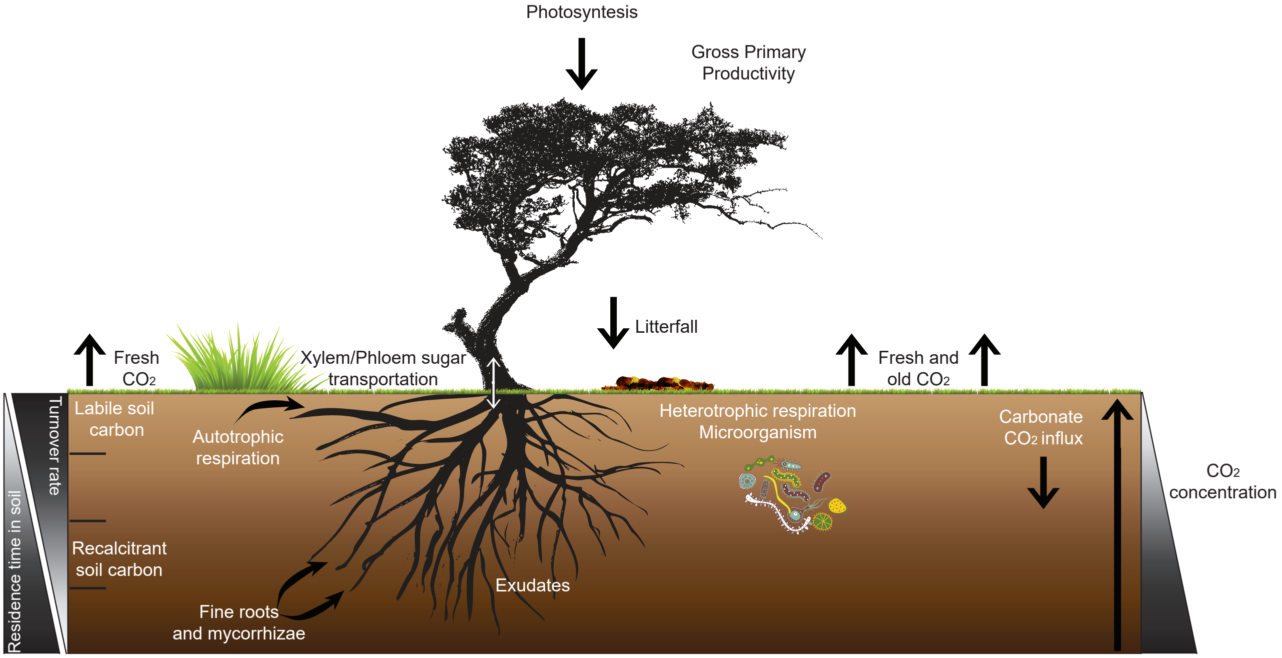

**Figure 1. Schematic representation of the main components of soil respiration. Autotrophic respiration is mainly controlled by carbon allocation by the xylem/phloem transport, meanwhile heterotrophic respiration is controlled by substrate availability; however, both fluxes are temperature and moisture dependent. The scales on the sides represent a gradient, being darker the highest and clearer the lowest. This figure was recreated after the conceptual models of Ryan and Law 2005; Kuzyakov and Gavrichkova, 2010; Brüggemann *et al.,* 2011. Figure produced by Lluvia B. Vargas-Gastélum.**

surface concentration changes, and iii) measurement of $CO_2$ along soil profiles. These techniques had been widely used elsewhere but seldom in Mexico. Here we briefly describe their operational principles. The first two are typically used with a ring inserted several centimeters into the ground and projecting above the surface, defining both a surface and its lower entry, installed some weeks in advance of measurements to allow acclimation of the soil system to the disturbance.

The trapping technique consists of placing a chamber hermetically in the soil ring, collecting air or $CO_2$ after some time interval for further analysis in the lab. Collecting devices are typically syringes or alkali. With syringes, the $CO_2$ concentration is measured using a gas chromatograph; for the alkali trap, $CO_2$ is measured by simple chemical procedures.

For estimation from the rate of change of $CO_2$ concentration, a chamber placed on the soil ring, attached to an Infra-Red Gas Analyzer (IRGA), air is circulated actively or passively in the system and $CO_2$ concentration is measured repeatedly (for a few minutes) through its adsorption of specific bands of light (Cueva-Rodríguez *et al*., 2012).

The gradient method is based on the Fick's law of diffusion and consists of measuring $CO_2$ concentrations at several depths in the soil profile with solid-state non-dispersive infrared $CO_2$ sensors (De Jong and Schappert 1972; Tang *et al.,* 2003; Maier and Schack-Kirchner, 2014). Measurements are made often over weeks or months (after acclimation to the installation).

These methods have errors, both systematic (Davidson *et al*., 2002; Pumpanen *et al.,* 2004) and random (Savage *et al.,* 2008; Cueva *et al.,* 2015), but the former are relatively well-studied (Simunek and Suarez, 1993; Fang and Moncrieff, 1996; Janssens *et al.,* 2000; Rayment, 2000; Davidson *et al.,* 2002; Pumpanen *et al*., 2003, 2004; Pingintha *et al*., 2010; Heinemeyer *et al.,* 2011; Maier and Schack-Kirchner, 2014). While systematic errors are related to improper calibration, instrument malfunction, or mistakes in data handling, random errors are caused by unknown and unpredictable sources (Cueva *et al*., 2015).

## SOIL RESPIRATION IN MEXICO

While gas emissions from soils have been measured since almost 90 years ago (Lundegårdh, 1927), the first measurements of soil gas exchange published in peer review literature from Mexico were in the early 90s, (Davidson *et al.,* 1991, 1993; García-

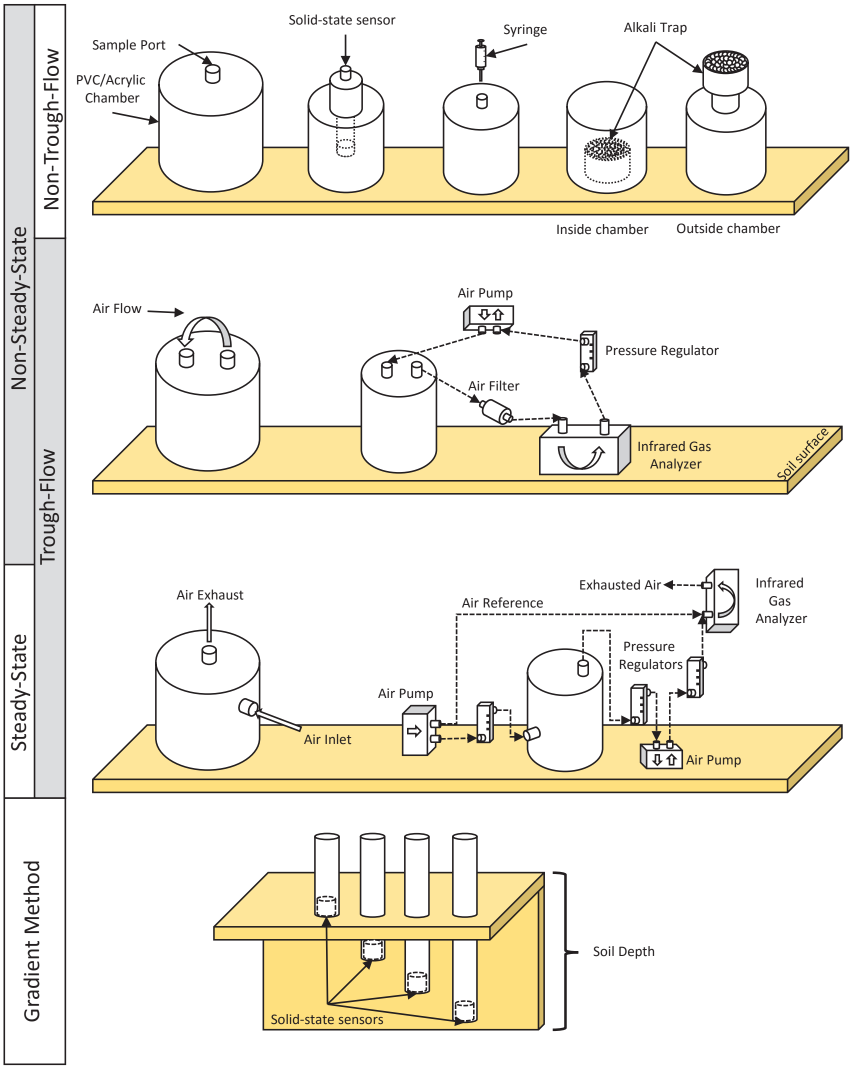

**Figure 2. Schematic representation of the different methods and techniques to measure and estimate soil respiration. See Section 3 for further explanation. Figure based on Livingston and Hutchinson, 1995; Luo and Zhou, 2006; Vargas and Allen, 2008c; Risk *et al.*, 2011; Cueva-Rodríguez *et al.*, 2012.**

Méndez *et al.,* 1991). The first measurements of soil $CO_2$ efflux were reported in 2004 (Table 1). Most of the research on $R_S$ in Mexico had been carried out in agroecosystems, followed by forests, shrublands, grasslands, and wetlands (Table 1). The most common method to estimate soil gas emissions had been the syringe method, followed by the IRGA-based (closed system) method, and least-used have been the alkali and gradient methods. It must be emphasized that most of the studies have focused on spatial variation or the effect of a treatment, and few studies had been about the temporal variation of $R_S$.

The $R_S$ research in Mexico for agroecosystems have been focused on amending crops yields without increasing soil $CO_2$ emissions. It is known that the conversion from natural to managed ecosystems (e.g., agroecosystems) causes depletion of SOC (Guo and Gifford, 2002), due to the alteration of the balance between C inputs (e.g., GPP, photosynthesis, litterfall) and outputs (e.g., $R_S$, photodegradation) of (Kim and Kirschbaum, 2015). This type of research has been preponderant in Mexico, reflecting the high rate of land use change (Balbontín *et al.*, 2009; Sánchez-Colón *et al*., 2009).

Changes in soil $CO_2$ efflux have also been examined for different management practices in agricultural land. For example, the addition of fertilizers increased soil $CO_2$ efflux in bean and maize cultivations (Fernández-

**Table 1. Soil respiration studies in Mexico.**

| Reference | Method | Measurement type | Ecosystem type(s) | Question type | Scale |
|---|---|---|---|---|---|
| Campos, 2004 | NSS-NTF | Alkali | Agroecosystem (C), tropical cloud forest | TV, SV | Season |
| Campos, 2006 | NSS-NTF | Alkali | Agroecosystem (C), grassland, tropical cloud forest | TV, SV | Year |
| Vargas and Allen, 2008b | GM | IRGA | Tropical forest | TV | Year |
| Covaleda *et al*., 2009 | NSS-TF | IRGA | Oak-pine forest, grassland | TV, SV | Year |
| Fernández-Luqueño *et al*., 2009 | NSS-NTF | Syringe | Agroecosystem (C) | ET, TV | Season |
| Fernández-Luqueño *et al*., 2010 | NSS-NTF | Syringe | Agroecosystem (C) | ET, TV | Season |
| López-Valdez *et al*., 2011 | NSS-NTF | Syringe | Agroecosystem (C) | ET, TV | Season |
| Aguilar-Chávez *et al*., 2012 | NSS-NTF | Syringe | Agroecosystem (C) | ET, TV | Season |
| Báez-Pérez *et al*., 2012 | NSS-TF | IRGA | Agroecosystem (C) | | |
| Cueva-Rodríguez *et al*., 2012 | NSS-TF | IRGA | Semiarid shrubland | TV,SV | Days |
| Dendooven *et al*., 2012 | NSS-NTF | Syringe | Agroecosystem (C) | TV, SV | Years |
| Fuentes *et al*., 2012 | NSS-TF | IRGA | Agroecosystem (C) | TV, SV | Year |
| Juárez-Rodríguez *et al*., 2012 | NSS-NTF | Syringe | Agroecosystem (C) | ET, TV | Days |
| Ruiz-Vega *et al*., 2012 | NSS-TF | IRGA | Agroecosystem (C) | ET, TV | Season |
| Vargas, 2012 | GM | IRGA | Tropical Forest | TV | Year |
| Vargas, 2012 | GM | IRGA | Tropical Forest | TV | Year |
| Ikkonen *et al*., 2013 | NSS-NTF | Syringe | Montane Cloud Forest | TV, SV | Day |
| Ruíz-Valdiviezo *et al*., 2013 | NSS-NTF | Syringe | Agroecosystem (C) | ET, TV | Season |
| Báez-Pérez *et al*., 2014 | NSS-TF | IRGA | Agroecosystem (C) | ET, TV | Season |
| Campos, 2014 | NSS-NTF | Alkali | Agroecosystem (C), coniferous forest, tropical cloud forest | SV, TV | Year |
| Díaz-Rojas *et al*., 2014 | NSS-NTF | Syringe | Agroecosystem (C) | ET, TV | Season |
| Hernandez *et al*., 2014 | NSS-NTF | Syringe | Wetland | SV, TV | Season |
| Hernández-Alarcón and Córdova, 2014 | NSS-NTF | Syringe | Cloud forest, Agroecosystem (C,F) | | |
| Leon *et al*., 2014 | NSS-TF | IRGA | Semiarid shrubland | SV, TV | Year |
| Robles-Zazueta *et al*., 2014 | GM | IRGA | Semiarid shrubland | TV, SV | Year |
| Villanueva-López *et al*., 2014 | NSS-TF | IRGA | Agroecosystem (C,F) | ET, TV | Season |
| González-Méndez *et al*., 2015 | NSS-NTF | Syringe | Agroecosystem (C) | TV, SV | Season |
| Marín-Muñiz *et al*., 2015 | NSS-NTF | Syringe | Wetland | TV, SV | Years |

(N)SS = (Non-) Steady-State; (N) TF = (Non-) Trough-Flow; C = Cropland; F = Farmland; TV = Temporal Variation; SV = Spatial Variation; ET = Effect Treatment.

Luqueño *et al.,* 2009, 2010), but had no effect in a sunflower cultivation (López-Valdez *et al.,* 2011). The addition of charcoal reduced $CO_2$ emissions (Aguilar-Chávez *et al*., 2012). Contrasting results were found in comparison between conventional and conservational agricultural practices, such as no changes in either maize or wheat cultivations (Dendooven *et al*., 2012; Ruiz-Vega *et al.,* 2012), but reduced emissions with the reduction of mechanical disturbance and the retention of crop residues after harvest (Fuentes *et al*., 2012). Despite of the negative, null or positive effect on $R_S$, many of the latter studies coincide that SOC increased when fertilizers or charcoal (e.g., urea, waste water, biochar) were added, and where little or no disturbance was present (e.g., reduced or zero tillage).

The first $R_S$ study in México was conducted in a tropical cloud forest (Table 1). It is important to highlight that several of the studies in forest landscapes Mexico deal with the effects of land use changes, where $R_S$ increases while SOC decreases (Campos, 2004, 2006, 2014; Covaleda *et al*., 2009). It is also noteworthy that the highest $R_S$ rates reported globally was from a Mexican tropical deciduous forest in the Yucatan Peninsula, after perturbation occasioned by Hurricane Wilma (Table 2; Vargas and Allen, 2008b; Bond-Lamberty and Thomson, 2010). The influence of the hurricane enhanced $R_S$ due to plant defoliation (Vargas, 2012b). Thus, we highlight the importance of high-frequency (e.g., 30, 60 min) and also opportunistic measurements, to understand the effects of diurnal, seasonal, and inter-annual variations because they offer the opportunity to understand the effects of extreme events on ecosystem´s carbon fluxes.

Although almost half of the Mexican territory is arid or semiarid, only a few studies of $R_S$ had been carried out in these regions. Because ecosystems in these climates are characterized by patchy vegetation patterns, soil physical characteristics (e.g*.,* moisture and temperature) that vary greatly across only a few meters. The complex spatio-temporal dynamics in soil processes can include ephemeral periods with very high $R_S$ rates (Table 2). For example, in a subtropical shrubland in Sonora, Robles-Zazueta *et al*. (2014) estimated $R_S$ under woody canopies and exposed patches (bare soil) over the growing season of 2012, finding evidence for a strong but differentiated control of precipitation pulses over $R_S$ during the rainy season. Although no explicit measurements were carried to explain the $R_S$ differences between the vegetated and the exposed patches, the larger $R_S$ fluxes following precipitation events in bare patches (Figure 3) are probably explained by rainfall not reaching the ground due to canopy interception in vegetated patches. On the same study site, Cueva-Rodríguez *et al*. (2012) found spatial differences in $R_S$ related to different plant species. Also in a mediterranean-climate shrubland in Baja California, Leon *et al*. (2014) found that $R_S$ increased by 522% after rewetting of the soil following the dry season but remained elevated during part of the growing season. Here, spatial variability was strong and best-related to local soil moisture and litter accumulation. These studies coincide that the main driver of $R_S$ was water availability, while soil temperature only extended an influence when water was present. It has recently demonstrated that arid and semiarid ecosystems play a key role on the global carbon cycle (Poulter *et al.,* 2014), emphasizing the importance of studies that would propose alternative models to describe the functional controls on $R_S$ water limited ecosystems

Hernández *et al*. (2014) measured $CO_2$ emissions in freshwater wetlands and flooded grasslands in Veracruz. $CO_2$ emissions were higher during the dry season and decreased during the rainy season, with rates similar to the windy season. In adjacent freshwater marshes and swamps Marín-Muñiz *et al*. (2015) measured $R_S$ during two years, over the dry, rainy and windy seasons. The highest rates of emission were measured during the dry season, followed by the rainy season, and the lowest rates during the windy season. Soil $CO_2$ emissions

**Table 2. Minimum and maximum values reported for soil respiration rates in Mexico (g C m$^{-2}$ d$^{-1}$).**

| Reference | Agricultural | Forest | Grassland | Shrubland | Wetland |
|---|---|---|---|---|---|
| Campos, 2004 | 2.76-8.45 | 1.8-5.22 | | | |
| Campos, 2006 | 0.43-3.07 | 0.54-2.21 | 1.51-4.87 | | |
| Cueva-Rodríguez *et al*., 2012 | | | | 0.52-9.34 | |
| Vargas, 2012 | | 3.11-13.71 | | | |
| Dendooven *et al*., 2012 | 0.1-1.8 | | | | |
| Fuentes *et al*., 2012 | 2.4-38.4 | | | | |
| Campos, 2014 | 0.43-3.1 | 0.54-2.15 | 1.51-4.87 | | |
| Leon *et al*., 2014 | | | | 0.41-2.18 | |
| Robles-Zazueta *et al*., 2014 | | | | 0.01-3.31 | |
| Villanueva-López *et al*., 2014 | 0.93-1.4 | | | | |
| González-Méndez *et al*., 2015 | 0.24-5.52 | | | | |
| Hernandez *et al*., 2014 | | | | | 1.25-7.2 |
| Marín-Muñiz *et al*., 2015 | | | | | 0.13-4.91 |

from wetlands have been related to biological variables (SOC quality and availability, dissolved organic carbon (DOC); McLeod *et al.,* 2011), as well as to physical variables such as dissolved oxygen, hydroperiod, temperature, salinity, electrical conductivity and pH (Alongi, 2014).

While most research on $R_S$ has been carried out in agroecosystems and forests, and many ecosystems have been poorly represented in Mexico some commonalities emerge across the available studies. For example, in most of the ecosystem presented in this manuscript $R_S$ could be coupled with soil temperature, as long as moisture is not a limiting factor. However, since most of the studies of $R_S$ in Mexico had been based in low frequency measurements, we cannot know which could be the threshold of soil moisture to become a limiting factor. Related to the latter, Kim *et al*. (2012) suggested the designs of manipulative experiments that could enhance our knowledge about the interaction of soil rewetting. Furthermore, also Kim *et al*. (2012) highlighted that most of the studies that explores the effect of soil moisture on $R_S$ are carried out on small spatial scales, and that is critical to scale up these interactions at ecosystem level.

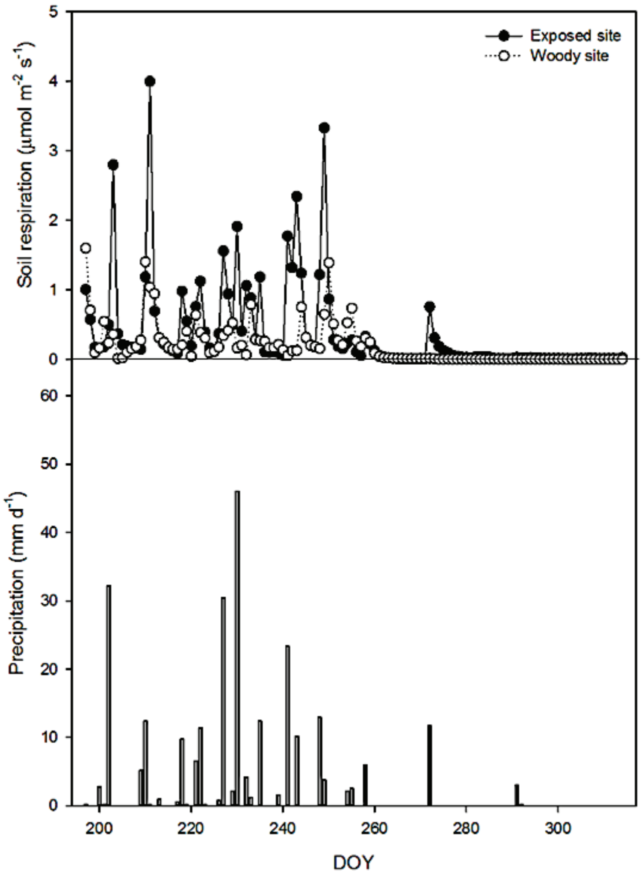

**Figure 3. Seasonal variation of RS in a subtropical shrubland of Sonora. Estimates of RS were conducted with the gradient method during the rainy season of 2012 (Robles-Zazueta *et al*., 2014).**

Mexico is a country with high rates of land use change, mainly by deforestation and livestock grassing. Thus, intensive agricultural practices could enhance $R_S$ and deplete SOC pools, while conservation agricultural practices could decrease $R_S$ and increase the SOC. However, despite that most of the studies of $R_S$ in Mexico had been carried out in agroecosystems, few of them had compared the trade-off of converting natural to managed ecosystems.

## FUTURE DIRECTIONS OF SOIL RESPIRATION RESEARCH IN MEXICO

The Mexican Carbon Program (Programa Mexicano del Carbono; PMC) has developed databases and improved techniques and methodologies related to SOC stocks (Fuentes-Ponce *et al*., 2012), however, these stocks result from different processes, both aboveground (e.g., photosynthesis) and belowground (e.g., decomposition) that are not well described in Mexican ecosystems. For example, although in Mexico exists long-term observations of above-ground production and below-ground decomposition (e.g., Anaya *et al*., 2012), high-frequency measurements (e.g., every 30-60 min) are needed to understand short-term processes on an hourly-to-daily basis (Carbone and Vargas, 2008).

Most of the studies of C exchange between the ecosystems and the atmosphere in Mexico had been originated from individual efforts (Vargas *et al.*, 2013), and it is reflected in the $R_S$ research in Mexico: few sites with various publications or many sites with one publication. Furthermore, most of the studies presented in this review do not meet the criteria to be included in global databases, being only the studies of Campos (2006) and Vargas and Allen (2008c) included on the Global Database of Soil Respiration Data (V 3.0, Bond-Lamberty and Thomson, 2014). This situation reflects that most of the studies of $R_S$ in Mexico had been conducted on short-term scales (e.g., days, weeks, and season), making a poor representation of the country in continental-to-global synthesis.

For these reasons, is preponderant to adopt knowledge from global experiences and develop expertise across the country to acquire long-term $R_S$ data and fulfill national needs to study the C cycle in Mexico. For example, methodologies should incorporate long-term high-and-low frequency measurement protocols, with criteria to study the spatial heterogeneity and a strategy to integrate high frequency measurements. Furthermore, it should be a priority for Mexican C cycle scientists to develop technologies that reduce costs to transfer these technologies from developed countries (i.e., Cueva-Rodríguez *et al.*, 2012). Meanwhile, we need to develop a strategic plan to advance on the $R_S$ research in Mexico, as well as collaborative research groups.

It is noteworthy that none of the peer-reviewed studies of $R_S$ in Mexico has been carried out in a Mexican Long-Term Ecological-Research site (Mex-LTER). Incorporating long-term measurements in Mex-LTER sites would offer a great variety of contrasting ecosystems with a natural altitudinal gradient, as well as an integrative framework between ecologists and social scientists (Maass *et al.*, 2010). Thus, long-term $R_S$ studies in Mex-LTER sites could provide baseline information to identify the responses from ecosystems after low-but-constant or fast-and-rare disturbances (Turner *et al.,* 2003). However, little has been done in Mexico about how disturbances affects functional processes in ecosystems (Calderon-Aguilera *et al.,* 2012). For example, tropical cyclones and hurricanes are fast-and-rare natural disturbances that have a strong influence on terrestrial vegetation across Mexico (Farfán *et al.,* 2014). Vargas (2012a) highlighted the importance of high-frequency measurements in a fast-and-rare disturbance, documenting the legacies of a hurricane on $R_S$ in the Yucatan Peninsula. However, if Vargas (2012a) had had only low-frequency measurements we would only know the status of the ecosystem *before*-and-*after* the hurricane, leading only to infer what happened *during* the hurricane.

MexFlux sites (Vargas *et al*., 2013) also offer an opportunity to carry out $R_S$ measurements across Mexican ecosystems. Since $R_S$ estimates at the represented ecosystems would be accompanied by estimates the net ecosystem exchange of matter (e.g., $CO_2$, $CH_4$) and energy (e.g., $H_2O$) between the ecosystem and the atmosphere and combined efforts will allow more refined estimates of ecosystem fluxes by empirical models (e.g., Reichstein *et al*., 2005; Lasslop *et al*., 2010). Flux partitioning of different C fluxes within the ecosystem had been commonly compared with $R_S$ measurements as a proxy of ecosystem respiration. Moreover, data of $R_S$ in conjunction with net ecosystem exchange (NEE) measurements to estimate ecosystem respiration could provide insights for partitioning of ecosystem respiration on its, heterotrophic and autotrophic components, which reminds as a central question in C cycle research.

Thus, the future directions on $R_S$ research in Mexico should be:

a) Develop a base-line understanding of the biophysical controls of $R_S$ across different ecosystems in Mexico, including the responses when a land use change occurs,

b) establish long-term (>5 years) observatory networks to measure $R_S$ across different ecosystems and management schemes,

c) within the latter, establish manipulative experiments to obtain mechanistic knowledge of how different scenarios (e.g., increasing temperature or changing timing and magnitude of precipitation) could affect $R_S$ (Norby and Luo, 2004),

d) when an array of long-term measurements has been established, large-scale modelling of $R_S$ using satellite data could be carried out (i.e., Wu *et al*., 2014),

e) develop a Mexican database of $R_S$ records, with a quality assurance and quality control (QA/QC) protocols (Carbone and Vargas, 2008),

f) integrate aboveground phenological measurements and net fluxes (e.g., phenocams, Richardson *et al*., 2007; Vargas *et al*., 2013),

g) integrate belowground phenological measurements (e.g., minirhizotrons, (Hasselquist *et al*., 2009),

h) integrate emerging disciplines to explain patterns and mechanisms (e.g., ecological genomics, Escalante *et al*., 2014),

i) isolate autotrophic and heterotrophic respiration from total $R_S$ (Hanson *et al*., 2000),

j) integrate other greenhouse gases related to $R_S$ measurements (e.g., $CH_4$, NO, $NO_2$),

k) continuous interaction of universities, research centers, and government agencies, as well as with other networks (e.g., MexFlux, Mex-LTER).

Coupled with the lack of knowledge of $R_S$ in Mexican ecosystems, predicted and actual temperature changes across the country (Diffenbaugh *et al*., 2008; Tejeda-Martínez *et al.,* 2008; Pavia *et al*., 2009; García-Cueto *et al*., 2010), as well as changes in precipitation patterns (Arriaga-Ramírez and Cavazos, 2010; Pérez-Morga *et al*., 2013) with less frequent but more intense precipitation events (Cavazos, 2012), longer and drier dry seasons, and increasing water stress across the country (Fuentes-Franco *et al.,* 2015), urges the Mexican scientific community to increase its interest and efforts in studying ecosystem C fluxes. We believe that strong synergies could become fruitful if interdisciplinary research in this field is carried out. Concluding, this review should not be considered as a baseline of the knowledge on $R_S$ in Mexico, but it should be re-evaluated on the middle (e.g., 5 years) and long (e.g., 10 years) term to know what progresses had been made.

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