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Isolating the effect of subterranean ventilation on CO_2 emissions from drylands to the atmosphere

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ABSTRACT

Recent studies show the importance of CO_2 exchange processes by subterranean ventilation, not directly related to concurrent biological activity, in net ecosystem exchanges between drylands and the atmosphere. We present seven years of eddy covariance measurements over a carbonate ecosystem in southern Spain and offer a practical, empirical approach that isolates such processes. Net fluxes represent emissions by ecosystem respiration and subterranean ventilation (V_s), reduced by the gross photosynthetic flux ($F_c = -F_{gp} + R_{eco} + V_s$). Large daytime emissions due to decreases in subterranean storage ($S_s < 0$) – destocking subterranean CO_2 ($-S_s = V_s$) – are hypothesized as the dominant process decoupling F_c from biological sources (R_{eco}) and sinks (F_{gp}) during dry periods. Since the latter are regulated by stomatal conductance (g_s), and can be characterized in terms of evapotranspiration (E), our approach exploits the extreme seasonality of gas exchanges in such ecosystems to disentangle the role of V_s in eddy fluxes.

Diurnal trends in F_c and g_s were strongly linked during growing periods. During dry periods however, daytime CO_2 emissions greatly exceeding modelled R_{eco} when g_s was low, precluded physiological interpretation of the negative quantity ($R_{eco} - F_c$) as F_{gp}. Since physiological inhibition of photosynthesis by drought coincided with large CO_2 emissions, V_s was isolated as $F_c - R_{eco}$. Analysis of different environmental factors showed that wind speed is most strongly correlated with V_s over the dataset. Although the ecosystem under study was nearly carbon neutral annually ($R_{eco} \approx F_{gp} + S_s$; all respired CO_2 is either offset by photosynthetic uptake or stored underground), during long periods with dry soils and wind, V_s represented up to 62% of annual emissions. Once the effects of subterranean ventilation are considered, net exchanges correspond credibly to a net flux due to concurrent biological processes that can be better decomposed into F_{gp} and R_{eco}. These findings suggest that the flux-partitioning and gap-filling models used by the FLUXNET community require adaptation to explicitly account for such processes in drylands.

1. Introduction

Because of the societal goal of reducing CO_2 emissions, a major scientific challenge of the 21st century is the categorization – as sources or sinks of this greenhouse gas – of major land surface types including shrublands. Characterizing CO_2 exchanges at continental/global scales depends on accurate knowledge at the ecosystem scale, and integrations are hindered by poorly characterized ecosystem types such as shrublands (Janssens et al., 2003). Often thriving on carbonate soils, shrublands are dominant only in habitats under substantial stress such as those influenced by drought/aridity, nutrient-poor soils, fire, winter cold, short growing seasons, or wind (McArthur et al., 2007). Many of these environmental conditions are relevant to arid and semi-arid continental climates, where direct measurements of CO_2 exchanges have been scarce in comparison with well-studied forest and agricultural lands (Domingo et al., 2011).

Net fluxes of CO_2 (F_c), water vapour and energy between the atmosphere and terrestrial ecosystems – such as those measured by the eddy covariance technique (Baldocchi et al., 2001) – require partitioning into component processes. In the context of FLUXNET, a "network of regional networks" (Baldocchi et al., 2001), a combination of detailed field measurements, improved understanding and model development is crucial to close the global carbon cycle

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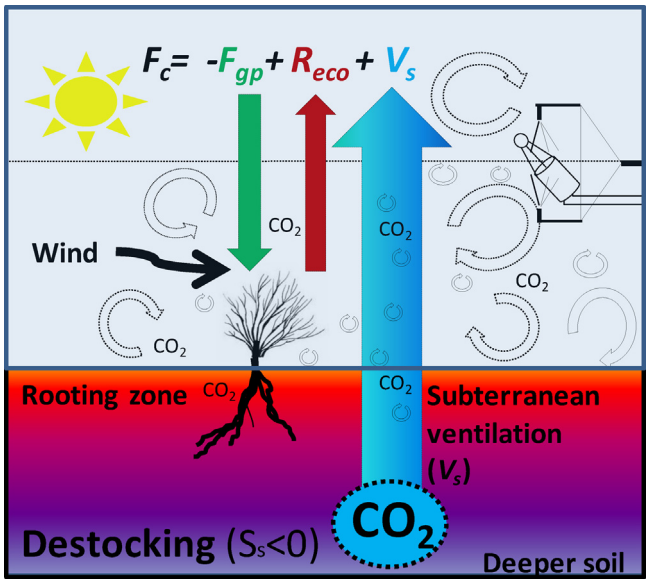

Fig. 1. Schematic of mechanisms and processes involved in net ecosystem CO_2 exchanges – F_c – over an ecosystem with carbonate soil. In dry periods, subterranean ventilative fluxes (V_s), affecting daytime F_c, dominate both concurrent biological processes: ecosystem respiration (R_{eco}) and photosynthesis (F_{gp}). A negative subterranean storage of CO_2 (S_s < 0) by V_s represents destocking. Higher soil temperatures are denoted in red while lower temperatures appear in violet. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

(Baldocchi et al., 1996). In terms of net ecosystem CO_2 source or sink behaviour, eddy covariance partitioning techniques usually interpret F_c as a biological flux defined by the difference between two components: the gross photosynthetic flux (F_{gp},) and ecosystem respiration (R_{eco}, by plants and soil; Lasslop et al., 2010; Reichstein et al., 2005; Stoy et al., 2006):

$$F_c = -F_{gp} + R_{eco} \quad (1)$$

Generally, F_c must be partitioned into its components, and the dependencies of R_{eco} and F_{gp} on biotic and environmental variables must be determined to interpret and extrapolate flux results, understand the mechanics of spatial and temporal variations in carbon budgets, and enable modelling (Smith et al., 2010).

Recent publications from different Mediterranean ecosystems suggest that Eq. (1), which is limited to concurrent biological processes, may not describe all of the components of F_c (Ferlan et al., 2011; Kowalski et al., 2008; Were et al., 2010; Plestenjak et al., 2012). For such ecosystems, eddy covariance partitioning and gap-filling have to be applied very carefully, and established techniques (e.g. Reichstein et al., 2005; Lasslop et al., 2010) may require adaptation to take into account additional processes. In this regard, 'anomalous' CO_2 fluxes measured by the flux tower community have been reviewed recently by Serrano-Ortiz et al. (2010). This review found that some carbonate ecosystems, characterized by cracks and pores, can temporally store large amounts of CO_2 below ground.

Accumulated CO_2 in the subsoil can be vented, causing emissions to the atmosphere (Fig. 1), apparently only during daytime (Kowalski et al., 2008; Sánchez-Cañete et al., 2011). Such subterranean ventilation (V_s) depends on both meteorological conditions such as rainfall events, changes in temperature and pressure, atmospheric stability, and wind speed (Ek and Gewelt, 1985; Emmerich, 2003; Kowalski et al., 2008; Mielnick et al., 2005; Rey et al., 2012; Weisbrod et al., 2009), and also the degree of connection between macro-pores, fissures and cavities with the atmosphere (Serrano-Ortiz et al., 2010). Soil air with high CO_2 concentrations is denser, and thus tends to percolate downward (Kowalski and Sánchez-Cañete, 2010), promoting storage. The non-negligible role of subterranean (micro- and macro-) pores as a temporal storehouse of CO_2, whether coming from biological and/or geochemical processes, is still poorly understood, as are the main drivers controlling their ventilation.

In this study, subterranean storage (S_s) of CO_2, both positive (stocking during winter and wet periods) and negative (degassing or ventilation during summer and dry periods) is hypothesized to be the main process decoupling the magnitude and timing of F_c from concurrent biological CO_2 sources and sinks. Thus, F_c may be expressed as:

$$F_c = -F_{gp} + R_{eco} - S_s \quad (2)$$

with the latter two terms predominantly representing soil processes. In an edaphic context, a positive value of S_s represents the difference between soil respiration and soil CO_2 effluxes (Maier et al., 2011). During destocking, since subterranean ventilation (V_s) causes degassing, for dry periods we can write

$$V_s = -S_s \quad (3)$$

Gas exchange by Mediterranean shrubs is reduced via physiological control mechanisms during summer drought (Tenhunen et al., 1981), coincidentally when V_s can dominate F_c (Kowalski et al., 2008; Serrano-Ortiz et al., 2009). The approach put forth here exploits the extreme seasonality of both ventilative (V_s) and biological (F_{gp}) gas exchanges, the latter regulated by stomatal control that can be characterized in terms of evapotranspiration. We assess stomatal conductance (g_s) via evapotranspiration data to establish a threshold in g_s to define periods with negligible F_{gp}, and thereby isolate moments dominated by V_s.

The overall objective of this study is to establish an empirical approach to disentangle biological and degassing processes involved in eddy fluxes in drylands. To do this we aim to:

(a) assess environmental drivers and physiological mechanisms that regulate CO_2 and water vapour exchange in a semi-arid ecosystem;
(b) evaluate an empirical approach – based on the role of stomata in regulating plant transpiration and photosynthesis – to isolate the contribution of ventilative processes involved in net CO_2 fluxes;
(c) assess site-specific empirical relationships between subterranean ventilation and environmental drivers; and
(d) estimate the contribution of CO_2 released to the atmosphere by subterranean ventilation in annual emissions.

2. Materials and methods

2.1. Study site

This study focused on "El Llano de los Juanes", a Mediterranean shrubland plateau at 1600 m altitude and 25 km from the coast, located in the Sierra de Gádor (Almería, Southeast Spain; 36°55.596′ N; 2°45.127′ W). "El Llano de los Juanes" is characterized by a sub-humid montane Mediterranean climate with a mean annual temperature of 12 °C and mean annual precipitation of ca. 475 mm, falling mostly from November until May, and by a very dry summer. The dominant ground cover is bare soil, gravel and rock (49.1%). The vegetation is diverse but sparse, with predominance of three perennial species, *Festuca scariosa* (Lag.) Hackel (18.8%), *Hormathophilla spinosa* (L.) Küpfer (6.8%) and *Genista pumila* (Vierh) ssp. pumila (5.5%). More detailed site information can be found in Serrano-Ortiz et al. (2007).

The parent soil material of the Sierra de Gádor consists of Triassic carbonate rocks (Vallejos et al., 1997); in "El Llano de los

Juanes" these carbonate rocks are mainly dark limestones, with 98 ± 2% calcite. Soils are classified as Lithic Haploxeroll (Soil Survey Staff, 1999) with silt loam texture (15 ± 1% clay, 37 ± 5% loam and 48 ± 5% silt) and neutral pH (7.5 ± 0.1); the apparent density is 1.05 ± 0.01 g cm^{-3} and C/N is 15 ± 5 (50 ± 10 g kg^{-1} of carbon and 3.2 ± 0.4 g kg^{-1} of nitrogen); the bicarbonate content at the surface is 2.1 ± 1.8% (Oyonarte et al., 1994). There are two horizons: surface "A" (0–10 cm) and subsurface "B" (variable, from 10 to 30 or even 150 cm) including a petrocalcic horizon. Soil water content at the wilting point (0.10 m^3 m^{-3}) and the field capacity (0.35 m^3 m^{-3}) were estimated using established water retention curves at the site (Oyonarte et al., 1998).

The leaf area index (LAI) was estimated from the normalized difference vegetation index (NDVI), obtained from an Agricultural Digital Camera (ADC, Dycam Inc., Woodland Hills, CA, USA), and validated by destructive sampling. Ecosystem LAI was estimated using individual values measured per species, together with information regarding percentage of cover, and ranged seasonally from 1.31 to 2.71 m^2 m^{-2}. The average height of the canopy is 0.5 m.

2.2. Eddy covariance data

Measurements of CO_2, water vapour and energy exchange were made from May 2004 to December 2010 with an eddy covariance system installed atop a 2.5 m tower. Additional variables measured can be found in Table 1. The open-path infrared gas analyser was calibrated monthly using an N_2 standard for zero and (variable but known) 500 μmol (CO_2) mol^{-1} gas standards for span. A data logger (CR3000, Campbell Scientific, Logan, UT, USA) managed the measurements and recorded the data.

Means, variances, and covariances of 10 Hz data were calculated and stored every 30 min; raw 10 Hz data also were stored. Environmental and soil measurements made every 10 s were stored as 30 min averages. Sonic temperatures were corrected for humidity effects (Schotanus et al., 1983) prior to calculating the heat flux. Eddy flux corrections for density perturbations (Webb et al., 1980) and double coordinate rotations were carried out in post processing (Kowalski et al., 1997), as was the conversion to half-hour means following Reynolds' rules (Moncrieff et al., 1997).

When applying the density corrections, to avoid CO_2 density (ρ_c) underestimations due to open-path IRGA lens contamination and resulting errors in fluxes, the IRGA lenses were cleaned periodically and mean gas densities were corrected using thermohygrometer humidity data (Serrano-Ortiz et al., 2008).

Quality control of the half-hourly flux data was applied in a two-step procedure. First, we detect periods when the eddy covariance system did not work properly due to dew or dirty rain events, or to instrument malfunction; data from the open-path IRGA were rejected if <75% of 18,000 possible data sets during each averaging period were available. Half-hour periods marked by changes in the diagnostic parameter for window purity (AGC) were considered unreliable in terms of fluctuations in CO_2 density (fluxes rejected); by contrast, when AGC was constant but above the baseline for window purity, CO_2 fluctuations were accepted whereas the mean CO_2 density was not (Serrano-Ortiz et al., 2009). Secondly, averaging periods with low turbulence (friction velocity, $u_* < 0.2$ m s^{-1}) were rejected according to Gu et al. (2005). The contribution of aboveground storage to net CO_2 exchange, very small for low measurement heights and aerodynamically simple surfaces (Suyker and Verma, 2001), was neglected (Kowalski et al., 2003).

2.3. Isolating subterranean ventilative processes in net ecosystem CO_2 fluxes

For ecosystems with carbonate soils, the net ecosystem CO_2 exchange measured by eddy covariance (F_c) may be partitioned into subterranean ventilation – V_s, destocking subterranean CO_2 – and biological CO_2 sources (R_{eco}) and sinks (F_{gp}), the latter regulated by stomatal conductance (g_s, defined below). At night, the measured F_c is composed entirely of R_{eco} since F_{gp} is null in the dark, subterranean ventilation (V_s) does not occur (Kowalski et al., 2008; Sánchez-Cañete et al., 2011), and soil CO_2 effluxes very closely approximate soil respiration (Maier et al., 2011).

According to the procedure of Reichstein et al. (2005), we use an adaptation of the Arrhenius equation (Lloyd and Taylor, 1994) to describe the temperature dependence of R_{eco} as follows;

$$R_{eco} = R_b e^{E_0\left(\frac{1}{T_{ref}-T_0}\right)-\left(\frac{1}{T_{air}-T_0}\right)} \quad (4)$$

where T_{air} and T_{ref} (10 °C) are the air and reference temperatures, respectively, and R_b (μmol m^{-2} s^{-1}) is the basal respiration rate, E_o (°C) the temperature sensitivity, and T_o parameter taken as −46.02 °C (Lloyd and Taylor, 1994). To minimise the dependence of R_{eco} on other processes not included in the model (e.g. soil water content), R_b and E_o are estimated every two days with a 4-day moving window using night time data. The temperature dependence of R_{eco} was fit and extrapolated to daytime periods. Thus, when subtracting estimated R_{eco} from measured daytime F_c, a negative result corresponds to photosynthesis, whereas strongly positive values must be explained in terms of other processes, namely subterranean ventilation (V_s) representing emissions due to subsurface degassing processes.

To optimize carbon gains while minimizing water loss, plants control gas exchanges via stomatal conductance, with highly proportionate effects on both evapotranspiration (E) and F_{gp} over short time scales (Cowan, 1978). By inspection of the relationship between g_s and the difference $F_c - R_{eco}$, we define a basal conductance as the relative value below which $F_c - R_{eco}$ becomes independent of g_s and sizeable positive fluxes are found (V_s explains $F_c - R_{eco}$) since photosynthesis is strongly reduced. This takes advantage of the extreme seasonality of gas exchanges in semi-arid climates, with subterranean ventilation occurring mainly during dry periods, as discernible when F_{gp} is limited by

Table 1
List of variables measured in "El Llano de los Juanes".

Measurements	Sensor	Height (m)
Open-path eddy system (10 Hz)		
CO_2 and H_2O vapor densities	Open-path infrared gas analyzer (Li-Cor 7500, Lincoln, NE, USA)	2.5
Wind speed (3D) and Sonic temperature	Three-axis sonic anemometer (CSAT-3, Campbell Scientific, Logan, UT, USA)	2.5
Environmental and soil measurements (10 Hz)		
Air temperature	Thermohygrometer (HMP35-C, Campbell Scientific)	1.5
Relative humidity	Thermohygrometer (HMP35-C, Campbell Scientific)	1.5
Photon flux density (up and down)	PAR sensors (Li-190, Li-Cor)	1.5
Net radiation	Net radiometer (NR Lite, Kipp & Zonen, Delft, Netherlands)	1.5
Soil water content	Water Content Reflectometer (CS615, Campbell Scientific)	−0.15
Soil temperature	TCAV (Campbell Scientific)	(−0.01, −0.03, −0.05, −0.07)
Soil heat flux plates (2)	(HFP01, Hukseflux, Delft, Netherlands)	−0.08
Rain tipping bucket (0.2 mm)	Rain gauge (model 785 M, Davis Instruments Corp., Hayward, CA, USA)	1

stomatal control. Since g_s can be characterized in terms of E, the approach applied here is to isolate subterranean ventilative fluxes from photosynthetic fluxes by identifying light-saturating periods ($R_n > 300\,\mathrm{Wm^{-2}}$) when E (and thus F_{gp}) is strongly restricted by stomatal control in response to drought. Therefore, subterranean ventilation of CO_2 can be isolated as:

$$V_s = F_c - R_{eco} \tag{5}$$

After isolating subterranean ventilative fluxes and determining their main environmental drivers through site-specific empirical relationships, operative only during daytime, the percentage of CO_2 released to the atmosphere during dry periods in the annual emissions was calculated as:

$$\varepsilon_r = \frac{V_s}{R_{eco} + V_s} \tag{6}$$

Dry periods were defined when the Bowen ratio (β; calculated as the ratio between daily average sensible to latent heat fluxes) is higher than 4 and soil water content lower than $0.15\,\mathrm{m^3\,m^{-3}}$ (Serrano-Ortiz et al., 2009). A flow chart (Fig. 2) illustrates the hypothesised flux contributions and summarises the empirical approach applied.

2.4. Estimating stomatal conductance

Evapotranspiration (E) from a vegetated ecosystem is the sum of the contributions from the canopy (E_c) and soil (E_s). Since evaporation from bare soil or canopy interception can result in incorrect estimates of g_s (Rambal et al., 2003), but are negligible when excluding wet periods (Villagarcía et al., 2010), data taken on rainy and subsequent days (1–8 days based on inspection for realistic values of stomatal conductance; and a threshold in SWC > $0.30\,\mathrm{m^3\,m^{-3}}$) were not considered. Then, according to McNaughton and Jarvis (1984), E was quantified rewriting the Penman–Monteith equation as the sum of imposed ($E_{imposed}$) and equilibrium ($E_{equilibrium}$) components. The degree of stomatal control of E and the coupling between vegetation and atmosphere were studied through the decoupling coefficient (Ω). In the sparse shrubland under study, where boundary layer conductance is large (Were et al., 2010), stomata play a dominant role in controlling E. During dry periods, when available energy is maximum, Ω is near 0 and subsequently E is strictly restricted by stomatal conductance (g_s). Therefore, g_s was calculated by inverting the $E_{imposed}$ term as:

$$g_s = E_{imposed}\left(\frac{\lambda\gamma}{\rho_a c_p}\right) D^{-1} \tag{7}$$

where ρ_a the air density, C_p the specific heat of air at constant pressure, λ the latent heat of vaporisation of water, γ the psychrometer constant and D the vapour pressure deficit of the ambient air. The relative stomatal conductance (σ) is then defined as g_s normalized by the maximum observed value ($g_{s,max}$).

3. Results

3.1. Environmental and physiological control of net ecosystem CO_2 exchange

Photosynthesis-dominated (biological) uptake of CO_2 ($F_c < 0$) occurred consistently in May–June with daily averages near $-1.5\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ during such growing periods and sometimes smaller uptake during autumn–winter (Fig. 3A). Positive values of F_c from 0.5 up to more than $2\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ were observed during dry periods (regularly from July to September), and sizeable CO_2 emissions sometimes followed precipitation pulses. Overall, rain was concentrated from autumn to spring and followed by long dry periods from July to October (Fig. 3E). While the maxima of daily average E were observed at the end of spring, with values around $70\,\mathrm{W\,m^{-2}}$, maximum estimated $E_{equilibrium}$ occurred in late summer with up to $150\,\mathrm{W\,m^{-2}}$ (Fig. 3B). In almost all seven years, daytime average g_s showed the following seasonal pattern (Fig. 3C): high values during growing periods, exceeding $2.5\,\mathrm{mm\,s^{-1}}$ in early May, but falling abruptly by as much as 90% during summer, and then sometimes (with favourable soil moisture and weather) returning to high values in autumn (when rain caused much missing g_s data, as well as scatter).

The Bowen ratio (β) maintained quasi-stable values below 4 from autumn through winter into spring, but peaked to exceed 10 during the dry summer in every year (Fig. 3D) when soil water content dropped below $0.15\,\mathrm{m^3\,m^{-3}}$ (Fig. 3E). The effect of g_s on E during drought is clearly visible in the gap between E and $E_{equilibrium}$ whenever SWC was lower than $0.15\,\mathrm{m^3\,m^{-3}}$ and $\beta > 4$. Additionally, F_c was negative (CO_2 uptake) when g_s and E were high, but clearly positive when g_s and SWC were low.

While half-hour carbon and water fluxes exhibited tight coupling during the growing period, dry periods were characterized by very low E (limited by stomatal control and very low or null soil evaporation), and high CO_2 emissions. Fig. 4 shows characteristic daily time courses of F_c and g_s over two four-day periods during one growing (5–9 May) and one dry period (21–25 July) in 2009, when the ecosystem behaved as a net carbon sink ($F_c < 0$) and net source ($F_c > 0$), respectively. For the growing period, F_c and g_s followed similar patterns: g_s peaked in the morning and decreased in the afternoon until sunset, a pattern mirrored by F_c but with positive values around $0.5\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ during night. During the dry period when the ecosystem acted as a carbon source, F_c showed high rates of CO_2 release ($F_c > 0$) during daytime, a $6\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$

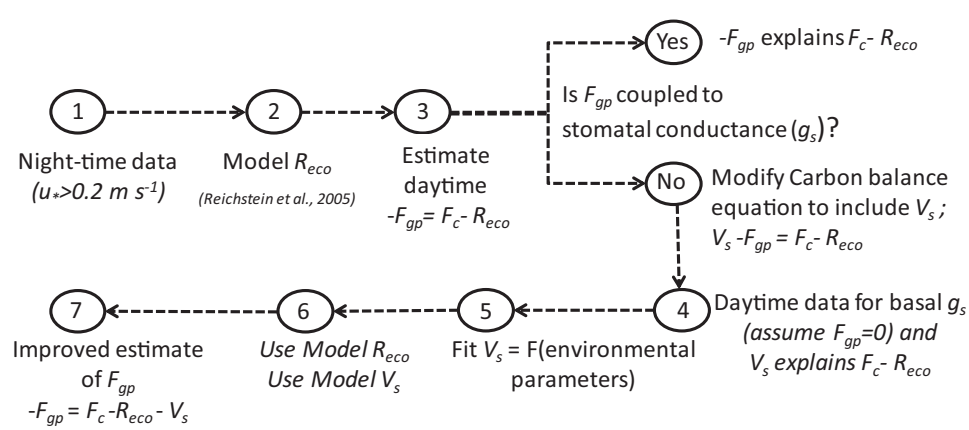

Fig. 2. Flow chart describing the approach proposed to segregate the hypothesized subterranean ventilation processes affecting F_c in ecosystems with carbonate soils.

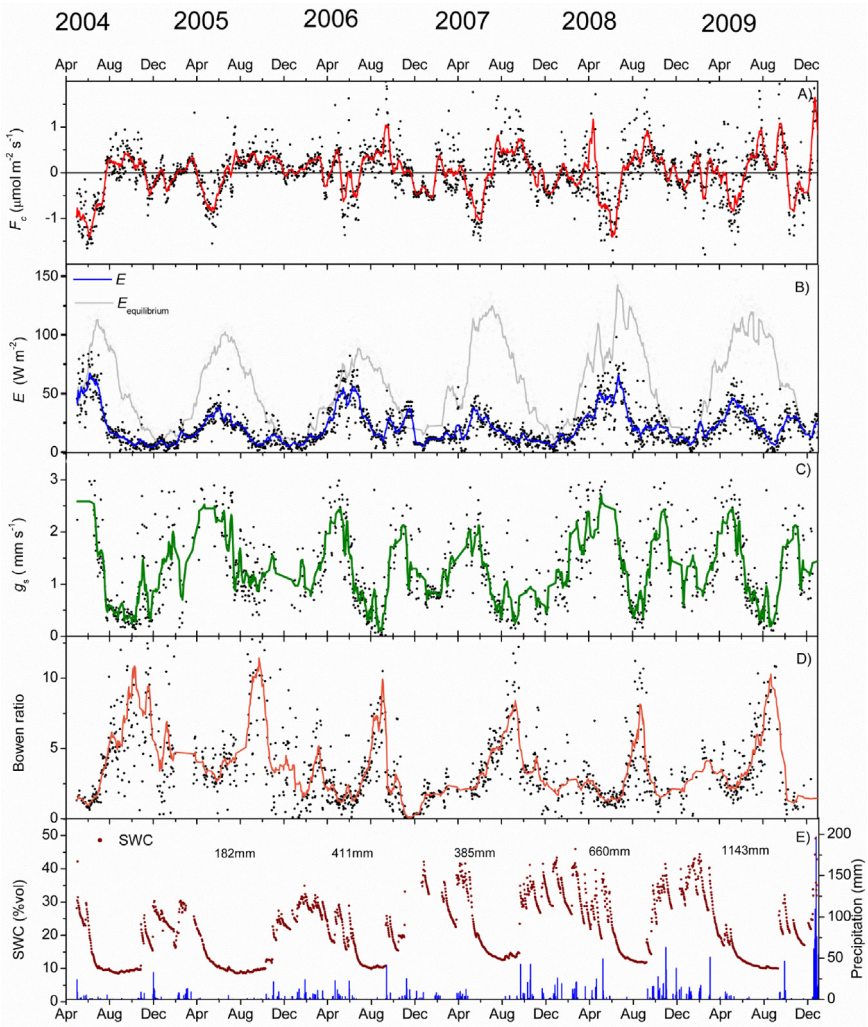

Fig. 3. Daily averages of net ecosystem CO_2 exchange (F_c; panel A), evapotranspiration (E) and equilibrium evapotranspiration ($E_{equilibrium}$; panel B), average daytime stomatal conductance (g_s; panel C), Bowen ratio (panel D), volumetric soil water content (SWC; 0.15 m depth) and daily precipitation (panel E) for measurements taken from May-2004 to December-2009. Lines represent the 15-day running average during the experiment.

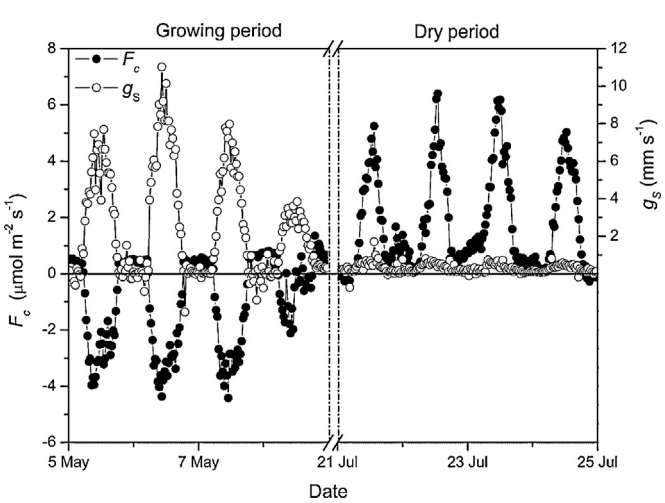

Fig. 4. Characteristic time course of net ecosystem CO_2 exchange (F_c) and stomatal conductance (g_s) over two four-day periods during one growing (5–9 May) and one dry period (21–25 July) in 2009.

maximum near mid-day, and near zero exchange at night. There was a clear effect of water deficit on g_s, which was 95% lower than during the growing period but still with an asymmetric pattern with maximum values in the morning.

3.2. *Biological and subterranean ventilative processes involved in eddy fluxes*

Traditional interpretations of net CO_2 fluxes, according to Eq. (1), yield unrealistic results, requiring the recognition of subterranean ventilative contributions. For example, the Reichstein et al. (2005) flux decomposition methodology would interpret any daytime emissions, which exceed night time respiration and occur during periods of stomatal restriction, as a negative value of photosynthesis ($F_{gp} < 0$), which is biologically implausible. Fig. 5 shows that, when g_s is low, the term $F_c - R_{eco}$ presents large positive values ($F_{gp} < 0$; magnitudes up to 6 μmol m^{-2} s^{-1}) that are not correlated with relative stomatal conductance, which suggests that they have no physiological sense. On the contrary, the term has consistently negative values ($F_{gp} > 0$) that correlated to σ during the growing period.

On the basis of Fig. 5, a criterion based on σ – taken as $\sigma_b = 0.05$, when g_s is reduced to 5% of its maximum value in response to drought, strongly inhibiting F_{gp} – may be used to identify

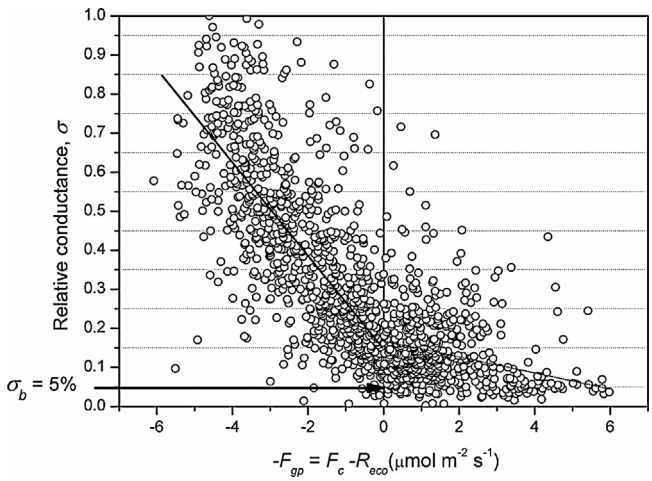

Fig. 5. Relationship between relative values of light-saturated stomatal conductance (σ) and a term, calculated as the difference between the measured net ecosystem CO_2 exchange and estimated daytime respiration ($F_c - R_{eco}$), representing the combined contributions of photosynthesis (F_{gp}, dominant for negative values) and subterranean ventilation (V_s, dominant for positive values) for measurement taken between May and July 2009. For negative values of $F_c - R_{eco}$, the solid line results from regression fitting as $y = -0.11 \times x + 0.16$ ($R^2 = 0.5$, $N = 821$), while for, positive the dashed line is $y = -0.019 \times x + 0.17$ ($R^2 = 0.05$, $N = 531$).

periods when subterranean ventilative fluxes (V_s) dominate $F_c - R_{eco}$ (Eq. (5)). Therefore, values of $F_c - R_{eco}$ with $\sigma < \sigma_b$ are assumed to be entirely due to V_s. Comparable results were found for all years following this inspection-analysis and the basal conductance value was extrapolated to dry and light-saturated conditions to study the main drivers controlling subterranean ventilative processes and quantify the role of subterranean CO_2 ventilation (V_s) in the net ecosystem carbon balance.

3.3. Subterranean ventilative CO_2 fluxes and their drivers

A strong correlation between subterranean ventilative fluxes (V_s) and wind speed (u) is shown in Fig. 6 for half-hour measurements taken from May 2004 to December 2010, excluding 2009 (to be used for validation). The resulting linear regression equations was $V_s = 0.94 \times u - 1$ ($R^2 = 0.8$; $n = 153$). Although restricted to

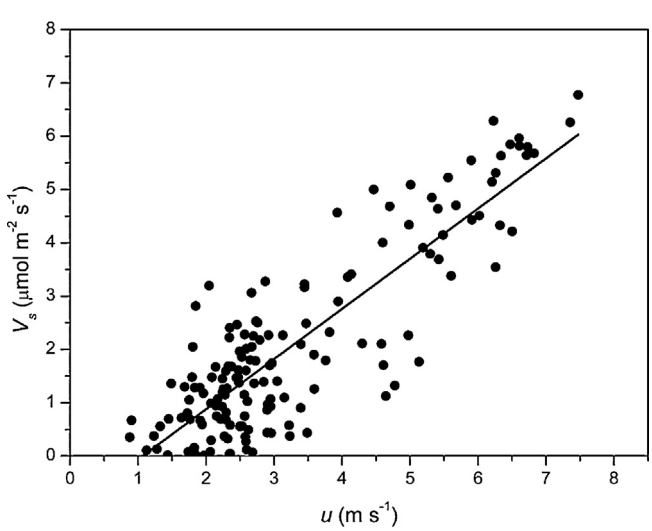

Fig. 6. Relationship between subterranean ventilative fluxes (V_s) and wind speed (u) for light-saturated ($R_n > 300\,W\,m^{-2}$) conditions of stomatal inhibition (relative stomatal $\sigma_b = 0.05$) taken from May 2004 to December 2010, excluding 2009. The regression equations is $V_s = 0.94 \times u - 1$ ($R^2 = 0.8$; $n = 153$).

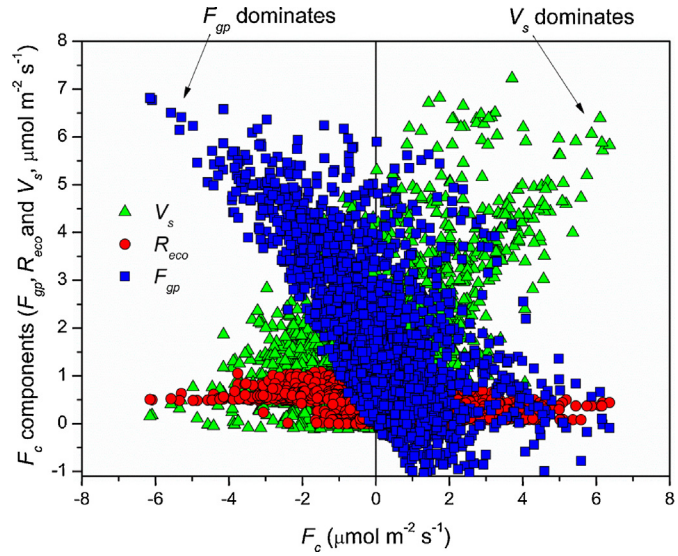

Fig. 7. Relationship between net ecosystem CO_2 flux (F_c, X axis) and the partitioned F_c components (Y axis): modelled subterranean ventilation (V_s, green triangles), ecosystem respiration (R_{eco}, red circles) and gross photosynthetic fluxes ($-F_{gp}$, blue squares,) during the dry period of 2009. Estimated V_s was obtained using the relationship between V_s and wind speed (u; $m\,s^{-1}$) obtained from the entire data set (2004–2010, excluding 2009; $V_s = 0.94 \times u - 1$; $\mu mol\,m^{-2}\,s^{-1}$, $R^2 = 0.8$). Estimated $-F_{gp}$ was calculated as $F_c - R_{eco} - V_s$. Arrows highlight times when F_{gp} (negative fluxes) and V_s (positive fluxes) dominate F_c.

basal values of stomatal conductance–as reflected in the ranges of Ω (<0.08), soil water content (<0.15 $m^3\,m^{-3}$), and LE (<38 $W\,m^{-2}$) – and high Bowen ratio (20.2 on average), the range of environmental variables for which this relation holds is nonetheless broad. These include soil temperatures (21–30 °C), sensible heat fluxes (130–454 $W\,m^{-2}$) and relative humidity (8.2–54%). This proportionality was used to estimate subterranean ventilative fluxes over the 2009 dry period (daily $\beta > 4$; SWC < 0.15 $m^3\,m^{-3}$). Fig. 7 shows the relationship between directly measured F_c (independent variable) and its components as modelled: V_s according to Fig. 6, R_{eco} from Eq. (4) and F_{gp} calculated as the residual $F_c - R_{eco} + V_s$. During moments when F_c achieves its highest positive values (up to 7 $\mu mol\,m^{-2}\,s^{-1}$), since R_{eco} and F_{gp} were of the same magnitude (about 0.5 $\mu mol\,m^{-2}\,s^{-1}$), V_s dominates F_c. By contrast, when F_c is very negative, exchanges are dominated by F_{gp} and emissions ($R_{eco} + V_s$) are small. Both large, measured CO_2 emissions ($F_c > 0$) and uptake ($F_c < 0$) are in good agreement with predicted V_s and F_{gp}, respectively.

3.4. Annual estimation of photosynthesis, respiration and subterranean ventilation

Annual exchanges varied greatly (Table 2), consistent with typical climatic variability in Mediterranean rainfall. Precipitation varied from very dry years with 182 mm in 2005 (Fig. 3E) – much lower than the climatic mean of 475 mm – to very rainy years with 1143 and 1008 mm in 2009 and 2010, respectively. Evapotranspiration (E) varied between 218 mm in 2005 and 337 mm in 2008. Net ecosystem carbon exchanges varied indistinctly from net source to sink, averaging 6 $g\,C\,m^{-2}$ (a nearly neutral net carbon source). Subterranean ventilation (V_s) and its fractional contribution to annual emissions (ε_r) were estimated to vary over a wide range from 39 $g\,C\,m^{-2}\,year^{-1}$ ($\varepsilon_r = 19\%$) in 2006 to 108 $g\,C\,m^{-2}\,year^{-1}$ ($\varepsilon_r = 62\%$) in 2005. Traditional neglect of V_s when decomposing F_c (Reichstein et al., 2005) would result in underestimating annual photosynthesis (F_{gp}), generally by about a quarter, but by as much as 62% for the extreme drought year of 2005.

Table 2
Six years of measurements taken in "El Llano de los Juanes" between 2005 and 2010. Annual ecosystem exchanges corresponding to (unshaded columns) directly measured fluxes of evapotranspiration (E) and net ecosystem C exchange (F_c), (grey shaded columns) modelled C emissions by ecosystem respiration (R_{eco}) and ventilation (V_s) for dry periods (daily Bowen ratio > 4, SWC < 0.15 $m^3 m^{-3}$)]; and (dark grey shaded columns) C assimilation as the residual according to the partitioning method. The fractional contribution to annual emissions of V_s is calculated as $\varepsilon_r = V_s/(R_{eco} + V_s)$.

Year	Evapotranspiration	Annual F_c budget	Emissions (modelled)			Assimilation (residual)	
	E (mm)	F_c (gC m^{-2})	R_{eco} (gC m^{-2})	V_s (gC m^{-2})	ε_r (%)	$F_{gp} = -F_c + R_{eco} + V_s$ (gC m^{-2})	$F_{gp} = -F_c + R_{eco}$ (Reichstein et al., 2005) (gC m^{-2})
2005	218	1	67	108	62	174	66
2006	317	31	166	39	19	174	135
2007	200	−5	144	45	24	194	149
2008	337	−13	173	46	21	232	186
2009	301	26	193	72	27	239	167
2010	267	−7	202	75	27	284	209

4. Discussion

This study presents a practical, empirical approach aimed to separately account for biological and subterranean ventilative processes affecting atmospheric carbon exchanges with drylands. Carbonate soils, characterized by the presence of subterranean pores and cavities capable of subsurface CO_2 storage and subsequent degassing, decouple the magnitude and timing of net carbon exchanges (F_c) from concurrent biological sinks (F_{gp}) and sources (R_{eco}). The easy-to-use method put forth successfully isolates subterranean ventilative fluxes by identifying periods when F_{gp} is restricted by stomatal control. The ecosystem under study was nearly carbon neutral ($R_{eco} \approx F_{gp} + S_s$). During long dry periods with soil moisture deficits, high temperatures and wind, CO_2 released to the atmosphere by subterranean ventilation represented up to 62% of the annual emissions. These results suggest that, for some ecosystems, traditional flux partitioning and gap-filling models commonly used by the FLUXNET community (e.g. Lasslop et al., 2010; Reichstein et al., 2005; Yi et al., 2004) may lead to erroneous interpretations of biological fluxes – as shown in Table 2, errors in F_{gp} when neglecting ventilation fluxes are on average about 42% (64 gC m^{-2} $year^{-1}$) – and require modification to account for temporal changes in the subterranean CO_2 storage processes.

In the semi-arid ecosystem under study, seasonal coupling between CO_2 and latent heat fluxes during the growing period, and decoupling during dry periods, allowed discernment between biological versus subterranean ventilative influences on F_c. In physiological terms, stomatal conductance (g_s) and evapotranspiration (E) were higher during growing periods than during dry periods due to drought effects induced by soil moisture deficits. Diurnal courses of F_c and g_s were strongly coupled during growing periods and markedly decoupled by sizeable daytime CO_2 emissions to the atmosphere in dry periods. Therefore, the ecosystem acted as a net carbon sink ($F_c < 0$) during growing periods but as a net carbon source ($F_c > 0$) during dry periods.

Over dry periods, when stomatal conductance decreased greatly ($\sigma < 0.05$), large mid-day CO_2 emissions – vastly exceeding modelled R_{eco} – were physiologically impossible to interpret, and must be due to subterranean ventilation. The strong decrease of g_s and E led to a larger portion of available energy being used for sensible heating, and consequently the Bowen ratio reached values up to 17.5 on average. These episodes of sizeable CO_2 emission to the atmosphere during dry periods might be explained by drought effects that induce atmospheric boundary layer growth and enable convective exchange mechanisms between cavities and the atmosphere. Subterranean ventilation of CO_2 stored below ground may depend on atmospheric parameters – such as stability (Rey et al., 2012; i.e., the convective/mechanical nature of the turbulence) and thus eddy size and/or soil characteristics like porosity, moisture, or other factors affecting the interconnectivity between micropores and cavities (Ek and Gewelt, 1985; Emmerich, 2003; Mielnick et al., 2005; Kowalski et al., 2008; Weisbrod et al., 2009; Cuezva et al., 2011). These interrelated mechanisms complicate accurate estimates of surface CO_2 exchange at larger spatial and temporal scales, requiring better integrative knowledge of factors governing changes in the subterranean CO_2 storage by ventilation processes, and thus further research.

Analyses of different environmental factors determined that wind speed was most correlated with subterranean ventilation for all data taken between May 2004 and December 2010 with sub-basal stomatal conductance. At this site, Sánchez-Cañete et al. (2011) found that large CO_2 emissions detected in eddy fluxes to the atmosphere were related to decreases in CO_2 molar fractions measured in both the soil and a borehole, each occurring with high friction velocities. Similarly, Kowalski et al. (2008) assessed eddy fluxes for a temperate pasture overlying a karstic substrate with an accessible cave. They observed large CO_2 emissions coinciding with periods when changes in the CO_2 storage were detected inside the subterranean cavity. In good agreement with this result, Rey et al. (2012) found a similar relationship between both daily average F_c and winds in a semiarid Mediterranean steppe in the southeast of Spain.

The CO_2 efflux from the soil surface is driven simultaneously by two processes in carbonate soils: respired CO_2 from the organic soil layer that is released to the atmosphere by molecular diffusion, and advective transport of CO_2 from subterranean cavities forced by wind. Observations indicated that subterranean ventilation processes occur only during daytime and not during night. Although this phenomenon remains poorly understood, the main causes could be associated with nocturnal soil rehydration processes that block the advective exchange between subterranean cavities and the atmosphere. Considering that accumulated CO_2 within the soil increases with depth worldwide (Amundson and Davidson, 1990), many short-term estimates of R_{eco} are likely underestimated unless changes in the amount of CO_2 stored in soil pores is explicitly taken into account (Maier et al., 2011). However, here we assume that such underestimation of R_{eco} is small compared with errors in daytime CO_2 exchange processes (F_{gp} and R_{eco}) derived from partitioning net fluxes while neglecting the role of subterranean ventilation.

The empirical relation where subterranean ventilation is a function of the easy-to-obtain wind speed appears to be valid throughout dry periods over seven years, and was used to estimate the magnitude of this component of the annual carbon balance. We observed coherence between measured F_c and estimated V_s for entire dry periods (as shown in Fig. 7). Thus, this approach represents a step forward regarding modelling of carbon fluxes in biomes thriving on carbonate soils.

Accounting for ventilative fluxes predicted by the wind-dependent model improves the interpretability of biological fluxes. Fig. 8 shows the daily time-courses of measured F_c from Fig. 4 and subterranean ventilation modelled empirically based on wind

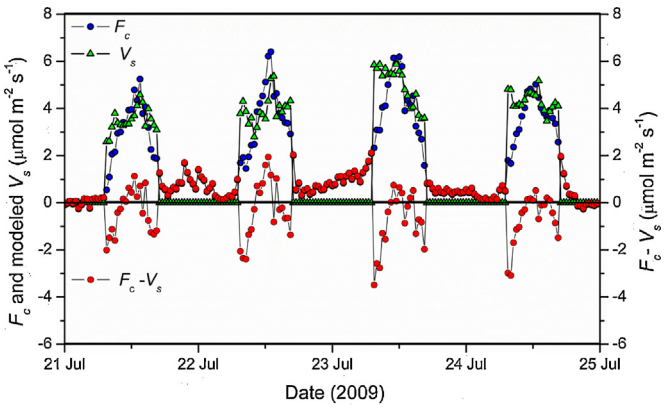

Fig. 8. Daily time course of the net ecosystem CO_2 exchange (F_c; blue circles) and estimated subterranean ventilation (V_s; green triangles) for the dry period presented in Fig. 4. An improved physiological interpretation of F_c in terms of photosynthesis and respiration is achieved after deducting the subterranean ventilation component (red circles). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

speed. During dry periods (July), the model succeeds in recovering the diurnal course of biological fluxes ($F_c - V_s$), which are coupled to g_s as shown in Fig. 4. Although there was a clear effect of drought on gas exchanges by vegetation, with g_s decreasing as much as 95% compared to the growing period, the asymmetric pattern during the growing period was reproduced with maximum values in the morning and lower during the afternoon, with perhaps small uptake in the early evening. Marked seasonal differences in photosynthetic rates have been characterized at the leaf level in Mediterranean sclerophyll shrubs, as a clear response to wet and drought periods (Flexas and Medrano, 2002; Tenhunen et al., 1981, 1990).

An improved physiological interpretation in terms of the gross photosynthetic fluxes and stomatal conductance is achieved after deducting the subterranean ventilation component (Fig. 9). The consistency in these results suggests the potential to use this methodology successfully to quantify changes in the subterranean CO_2 storage using eddy covariance towers. This approach should be tested in humid and temperate ecosystems, where the effect of drought on CO_2 exchange processes is comparatively unpredictable in timing, duration and intensity (Baldocchi, 2008). Accurate estimates of carbon balances at larger (regional) spatial scales for carbonate ecosystems require better integrative knowledge of the biological/geological origin of subterranean CO_2 storage and mechanisms associated with degassing or subterranean ventilation processes across climate zones. In this regard, alternative methods such as underground CO_2 molar fraction measurements in soil and boreholes (Sánchez-Cañete et al., 2011), chamber-based measurements (Pérez-Priego et al., 2010) and (stable) isotopic labelling (Yakir and Sternberg, 2000) may help to disentangle components from net fluxes and validate eddy flux results and canopy/soil gas exchange models.

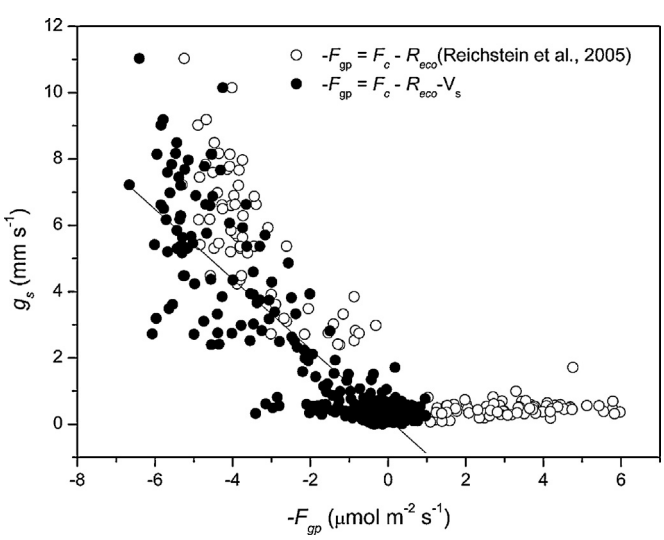

Fig. 9. Relationship between stomatal conductance (g_s) and photosynthesis (F_{gp}) after correcting for subterranean ventilation fluxes (black circles) and those obtained using traditional flux partitioning technique (e.g. Reichstein et al., 2005) that would represent the combined contributions of photosynthesis (dominant for negative values) and subterranean ventilation (V_s, dominant for positive values) for the same period presented in Fig. 4.

5. Conclusions

Subterranean emissions influencing net ecosystem CO_2 exchange (F_c) by a semi-arid shrubland have been segregated via a discrimination strategy, based on the stomatal conductance described by evapo-transpiration and environmental data. Interpreted as due to subterranean ventilation, such emissions are clearly correlated with wind speed, and explain from 1/4 to 2/3 of annual CO_2 released to the atmosphere by the ecosystem examined. Uncertainties remain regarding the possible extrapolation of such behaviour to larger spatial scales, as well as the mechanisms causing accumulation of CO_2 underground.

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