Global Change Biology (2008) **14**, 1475–1487, doi: 10.1111/j.1365-2486.2008.01593.x

Large annual net ecosystem CO_2 uptake of a Mojave Desert ecosystem

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Abstract

The net ecosystem CO_2 exchange (NEE) between a Mojave Desert ecosystem and the atmosphere was measured over the course of 2 years at the Mojave Global Change Facility (MGCF, Nevada, USA) using the eddy covariance method. The investigated desert ecosystem was a sink for CO_2, taking up 102 ± 67 and $110 \pm 70\,g\,C\,m^{-2}$ during 2005 and 2006, respectively. A comprehensive uncertainty analysis showed that most of the uncertainty of the inferred sink strength was due to the need to account for the effects of air density fluctuations on CO_2 densities measured with an open-path infrared gas analyser. In order to keep this uncertainty within acceptable bounds, highest standards with regard to maintenance of instrumentation and flux measurement postprocessing have to be met. Most of the variability in half-hourly NEE was explained by the amount of incident photosynthetically active radiation (PAR). On a seasonal scale, PAR and soil water content were the most important determinants of NEE. Precipitation events resulted in an initial pulse of CO_2 to the atmosphere, temporarily reducing NEE or even causing it to switch sign. During summer, when soil moisture was low, a lag of 3–4 days was observed before the correlation between NEE and precipitation switched from positive to negative, as opposed to conditions of high soil water availability in spring, when this transition occurred within the same day the rain took place. Our results indicate that desert ecosystem CO_2 exchange may be playing a much larger role in global carbon cycling and in modulating atmospheric CO_2 levels than previously assumed – especially since arid and semiarid biomes make up $>30\%$ of Earth's land surface.

Keywords: eddy covariance, heterotrophic respiration, Mojave Global Change Facility (MGCF), photosynthesis, rain pulse, uncertainty analysis

Received 10 November 2006; revised version received 19 October 2007 and accepted 20 December 2007

Introduction

The extent to which deserts of the world currently modulate global atmospheric CO_2 levels is poorly understood. This is because of the worldwide paucity of empirical measurements of net ecosystem CO_2 exchange (NEE) in desert and semiarid biomes (Falge *et al*., 2002a, b; Law *et al*., 2002). This, in turn, is perhaps due to the perception that sparse vegetation cover and seemingly bare soil surfaces translate into a low net annual positive ecosystem CO_2 balance (net ecosystem productivity, NEP) or even to a neutral or negative balance. Certainly biomass carbon stocks of arid shrublands pale in comparison with forests hectare for hectare (Grace, 2004) and their net primary production (NPP) is considered among the lowest of any ecosystem type (Larcher, 2001). However, existing NEE and NEP data from sparsely covered (5–20% plant cover) arid shrublands – measured using repeated sampling with large static chambers over 2 full years (Jasoni *et al*., 2005; J. Arnone, personal communication), or using eddy covariance (Hastings *et al*., 2005; Scott *et al*., 2006; Luo *et al*., 2007) – indicate that deserts may rival or even exceed net CO_2 uptake by forests and grasslands, at least in some years (Baldocchi *et al*., 2001; Falge *et al*., 2002b). Thus, these high NEPs and the large global extent of the arid and semiarid biome ($>30\%$ of Earth's land surface; Lal, 2004) strongly suggest that deserts are playing a much larger role than previously expected in

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modulating atmospheric CO_2 levels. Expansion of arid shrubland vegetation cover, similar to that observed in the Mojave Desert of the southwestern United States over the past three decades (Webb *et al.*, 2003), or potential increases in the activity or land-area-based mass of cryptobiotic crust communities that cover large areas of desert soil (Evans & Johansen, 1999; Belnap *et al.*, 2004) may be contributing to the large positive NEPs that have been measured.

Measurement of NEE in deserts can be challenging. The eddy covariance technique (Baldocchi, 2003), while providing potentially continuous data integrated over a representative spatial area, must, when an open-path infrared gas analyser (IRGA) is used to measure CO_2 concentrations, take into account significant corrections. The need for these corrections arises from fluctuations in air density brought about by large daylight sensible heat fluxes, which may even cause the CO_2 flux to change sign (Webb *et al.*, 1980). In addition, it was recently discovered (Burba *et al.*, 2006) that self-heating of open-path IRGAs results in an additional sensible heat flux, which up to date has been rarely taken into account (Grelle & Burba, 2007). Static chamber measurements, while providing direct and very sensitive estimates of ecosystem fluxes even with large chambers (Arnone & Obrist, 2003) are challenged by undesirably low spatial replication and discrete temporal sampling even when attempting to capture both diel and seasonal variation in NEE (cf. Jasoni *et al.*, 2005). Gaps in NEE time series data, resulting from instrument failure and removal of inferior quality data through quality control of eddy covariance data, as well as discrete temporal sampling of NEE using chambers, necessitate imputation of missing values in order to derive daily and longer-term annual NEE estimates. Accurate gap-filling becomes all the more challenging because of uncertain responses of NEE to periodic rains of various amounts, intensities and frequencies that may define temporal variation in NEE (Huxman *et al.*, 2004a, b; Ivans *et al.*, 2006; Potts *et al.*, 2006a, b) that ultimately determine annual NEP.

The objectives of our study were (1) to quantify the uncertainty of eddy covariance measurements of NEE over the course of 2 years in a typical Mojave Desert sparse shrubland ecosystem, (2) to integrate NEE over the study period to quantify current ecosystem CO_2 sink or source strength and (3) to elucidate the role that environmental factors, especially rainfall, plays in defining NEE.

Materials and methods

Site description

The Mojave Global Change Facility (MGCF) is located on a broad, gently sloping bajada in northern Mojave Desert on the Nevada Test Site, 120 km northwest of Las Vegas, NV, USA (36°49′N, 115°55′W). Vegetation, average cover is 18%, is dominated by the evergreen shrub *Larrea tridentata* (DC.) Cov., with subdominant drought–deciduous shrub species [*Lycium andersonii* (A. Gray) and *Ambrosia dumosa* (A. Gray)], perennial grasses [*Achnatherum hymenoides* (Roemer & Schultes) Barkwood and *Pleuraphis rigidia* Thurber] and several annual and perennial forbs (Jasoni *et al.*, 2005). Soils have been classified as loamy sands (Meadows *et al.*, 2006) and have a biological crust composed of cyanobacteria, lichens and moss. Wind at the MGCF originates for 80% of the time between 90 and 270°, which provides undisturbed, fairly homogenous fetch conditions for several kilometres. Average maximum upwind distances for the measured flux to represent 90% of the surface flux (based on calculations with the footprint model of Hsieh *et al.*, 2000) range from 150 to 2300 m.

Previous research at the study site and the neighbouring Nevada Desert FACE Facility (NDFF) have examined plant gas exchange and soil respiration that are pertinent to the data reported here. These data show that the Mojave Desert has the capacity for multiple periods of biological uptake of carbon that is primarily determined by water availability and temperature. The evergreen species *L. tridentata* is photosynthetically active when air temperatures are above $-5\,^{\circ}C$ and soil water is not limiting (Naumburg *et al.*, 2004). Peak photosynthesis typically occurs in the spring and fall when soil water is available and plants are not under the more extreme vapour pressure deficits of summer (Hamerlynck *et al.*, 2000a, b; Naumburg *et al.*, 2003; Barker *et al.*, 2006). Net photosynthetic rates for these studies ranged up to $20\,\mu mol\,m^{-2}\,s^{-1}$. Huxman & Smith (2001) show peak net assimilation occurred in mid March for an annual grass and an herbaceous perennial, but germination of some annual species has been observed to occur as early as January following a significant precipitation event(s). Soil respiration is generally lower in canopy interspaces and during dry periods; after rains and below the evergreen *L. tridentata* and deciduous *A. dumosa* shrub canopies peak respiration rates of $1.5\,\mu mol\,m^{-2}\,s^{-1}$ are observed (de Soyza *et al.*, 2005).

Eddy covariance

Fluxes of CO_2, H_2O, energy and momentum were measured by means of the eddy covariance method (Aubinet *et al.*, 2000; Baldocchi, 2003) starting in March 2005. Here, we report the first full 2 years of measurements up to February 2007 – for simplicity, we will refer to the first and second year of measurements as 2005 and 2006, respectively.

The three wind components and the speed of sound were measured using a three-dimensional sonic anemometer (CSAT3, Campbell, Logan, UT, USA), CO_2 (and H_2O) mole densities using an open-path IRGA (Li-7500, LI-COR, Lincoln, NE, USA), both instruments being mounted at 1.5 m above zero-plane displacement height or 2 m above ground. The head of the sonic anemometer pointed towards south, the predominating wind direction. The open-path IRGA was mounted 0.3 m to the east and 0.1 m below the sonic anemometer. Raw data of the three wind components, the speed of sound, and CO_2 and H_2O mole densities were acquired at 10 Hz by a data logger (CR5000, Campbell). Using the postprocessing software EDIRE (University of Edinburgh), eddy fluxes were calculated as the covariance between turbulent fluctuations of the vertical wind speed and the scalar densities derived from Reynolds (block) averaging of 30 min blocks of data. The sonic anemometer's coordinate system was rotated during each averaging period by applying a double rotation, aligning the longitudinal wind component into the main wind direction and forcing the mean vertical wind speed to zero (Wilczak *et al*., 2001). Frequency response corrections were applied to raw eddy fluxes accounting for low-pass (lateral and longitudinal sensor separation, sensor time response, scalar and vector path averaging) and high-pass (block averaging) filtering following Massman (2000, 2001) using a site-specific cospectral reference model (Massman & Clement, 2004; Wohlfahrt *et al*., 2005). Experimentally derived frequency response correction factors, according to Aubinet *et al*. (2000, 2001), were used to assess the validity of the theoretical low-pass filtering correction method, as detailed in Wohlfahrt *et al*. (2005). Finally, CO_2 fluxes were corrected for the effect of air density fluctuations following Webb *et al*. (1980). Net ecosystem exchange of CO_2 was then calculated as the sum of the corrected vertical eddy covariance term and the storage flux, the latter being estimated from the time-rate-of-change in CO_2 concentration at the reference height (Wohlfahrt *et al*., 2005). Negative flux densities represent transport towards the surface, positive values the reverse.

In May/June 2007 a closed-path IRGA (Li-6262, LI-COR) was operated at the study site during a 2-week campaign for measurement of CO_2 and H_2O fluxes using a closed-path approach. The inlet of a 2.7 m Teflon tube (0.004 m inner diameter) was mounted 0.06 m North of the sonic anemometer volume. Air was sucked through the tube and the analysis cell of the IRGA by a pump (Model MOA, GAST Mfg Corp., Benton Harbor, MI, USA) at a flow rate of $10\,\mathrm{L\,min^{-1}}$, while the reference cell was flushed with 99.999 UHP N_2 from a gas cylinder which passed through a column of Drierite and Soda Lime at a flow rate of around $0.1\,\mathrm{L\,min^{-1}}$. Linearized voltage signals of the CO_2 and H_2O mole fractions were sampled by data logger at 10 Hz as above. Data processing was identical to that employed for the open-path system except that (i) the tube induced time delay of the CO_2 (1.0 s) and H_2O (1.1 s) signals was determined by optimizing the correlation coefficient with the vertical wind velocity within a given time window, (ii) frequency response corrections accounted for the attenuation of concentration fluctuations down the sampling tube, and (iii) corrections for air density fluctuations following Webb *et al*. (1980) accounted only for water vapour induced effects, because temperature fluctuations were assumed to be completely dampened out upon arrival of air in the infrared cell (Aubinet *et al*., 2000).

Quality control of the half-hourly flux data was exercised in a three-step procedure: First, periods were identified when the eddy covariance system would not work properly due to adverse environmental conditions (usually rain) or instrument malfunction. These data were excluded from any further analysis if $<90\%$ of the 18 000 possible data sets during each averaging period were available. In a second step, data were subject to the integral turbulence test (Foken & Wichura, 1996) and accepted only on the condition that they did not exceed the target value by $>60\%$ (Foken *et al*., 2004). This occurred mostly for flow from the northern sector, where the instrument tower is located. In a third step, night-time CO_2 flux data were analysed for potential biases in ecosystem respiration during periods of low and high turbulence (Gu *et al*., 2005). As shown in Fig. 1, night-time ecosystem respiration was independent of friction velocity (u^*), a measure of turbulent mixing, between 0.1 and $0.5\,\mathrm{m\,s^{-1}}$. Below and above these thresholds, flux measurements increased with u^*, which is currently understood to indicate advection and pressure pumping, respectively (Massman & Lee, 2002). As these processes, in particular the frequent flux underestimation during periods of low turbulence, would lead to a bias in night-time ecosystem respiration and, thus the daily and longer-term CO_2 balances (Goulden *et al*., 1996), data were excluded when u^* was outside these thresholds (17% of data).

Energy balance closure, quantified by regressing half-hourly available energy (net radiation minus soil heat flux) against the sum of latent and sensible energy fluxes, amounted to 82% ($r^2 = 0.72$; regression forced through origin), which is well within the range of values reported for most sites (cf. Wilson *et al*., 2002). Finally, quality-controlled mean daily NEE data were compared with NEE values measured using a large static chamber dome (Arnone & Obrist, 2003; Jasoni *et al*., 2005) at an adjacent site with the same plant community and ecosystem characteristics.

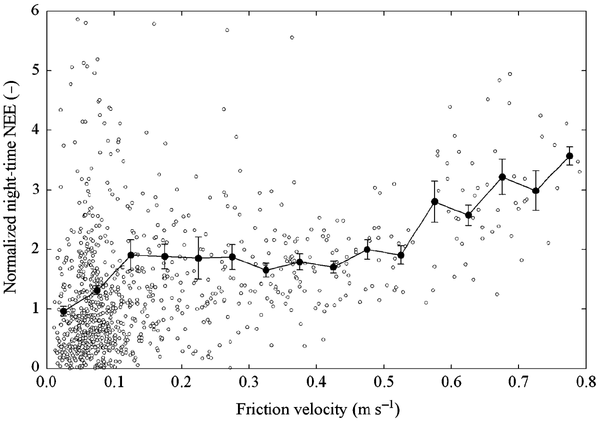

Fig. 1 Night-time ecosystem respiration normalised with a parametric model that relates soil temperature to ecosystem respiration, as a function of friction velocity. Open symbols represent half-hourly data from March–May 2005, closed symbols respective bin-averages of 0.05 m s^{-1} width. Error bars refer to ±1 standard error.

Ancillary data

Supporting environmental measurements of relevance for the present study included photosynthetically active radiation flux density (Li-190SA, LI-COR), air temperature and humidity (HMP45C, Campbell) at 2 m above ground, precipitation (TE525MM, Texas Electronics, Dallas, TX, USA), and two replicates of soil temperature (TCAV, Campbell) and water content (CS616, Campbell) at 0.04 m soil depth. These data were recorded by the data logger at 10 Hz and saved as half-hourly averages.

Gap-filling and uncertainty analysis

In order to derive continuous time series of NEE, required for calculating the annual CO_2 balance, the following procedure was employed to fill the gaps in the data resulting from instrument malfunction or quality control: Gaps <1 h were filled by linear interpolation. Larger gaps were filled by the mean diurnal variation method with a time window of one month (Falge *et al*., 2001). According to recent work by Moffat *et al.* (2007), who compared 15 different gap-filling methods, the mean diurnal variation method shows a moderate but consistent performance and, thus we did not attempt alternative gap-filling techniques. Altogether, 35% of the possible half-hourly NEE observations (49% and 21% in 2005 and 2006, respectively) were modelled this way during the 2-year study period. Gaps were distributed roughly equally between day and night; only 2% of the gaps occurred during rains.

An uncertainty analysis, accounting for both random and systematic errors (Moncrieff *et al*., 1996), was conducted in order to obtain confidence intervals for the annual CO_2 balance: The random uncertainty of the half-hourly CO_2 flux measurements was determined based on measurements under similar environmental conditions during adjacent days as devised by Hollinger & Richardson (2005) and Richardson & Hollinger (2005).

The systematic uncertainty of NEE was estimated by assessing the quality of the half-hourly flux measurements themselves, and issues related to postprocessing of data required for deriving annual CO_2 balances. When measuring CO_2 fluxes with open-path sensors under conditions of large sensible heat exchange, the largest source of uncertainty is due to the effect of concurrent air temperature and humidity fluctuations on CO_2 densities (ρ_c), which necessitate corrections after Webb *et al*. (1980):

$$F_c = \overline{w'\rho_c'} + \mu\frac{\rho_c}{\rho_a}\overline{w'\rho_v'} + \rho_c(1+\mu\delta)\frac{\overline{w'T'}}{T_a}, \qquad (1)$$

where μ and δ refer to the ratios of the molecular weights of air to water vapour and the densities of water vapour (ρ_v) to dry air (ρ_a), respectively; T_a to air temperature (°K); $\overline{w'\rho_c'}, \overline{w'T'}$ and $\overline{w'\rho_v'}$ to the CO_2, sensible and latent heat flux; F_c to the corrected CO_2 flux. The uncertainty introduced by applying Eqn (1) was estimated by defining a likely relative uncertainty for each independent input parameter and by applying this in turn to calculate annual NEE. Assuming that the various component uncertainties are independent, the combined uncertainty due to Eqn (1) was calculated by taking the square root of the sum of the squared individual uncertainties (the same approach was used to derive the overall random and systematic uncertainty).

Based on the manufacturers' specifications and on past experience with long-term sensor stability, the water vapour density, air temperature and static air pressure (which is required to derive ρ_a) were assigned uncertainties of 10% (Table 1). The measured CO_2 density was adjusted daily against the ambient CO_2 concentration measured at the nearby NDFF, which itself was calibrated monthly to a NIST traceable standard (Nor LAB, Boise, ID, USA), and thus we assigned a 5% uncertainty to ρ_c. Uncertainty in the sensible heat flux may arise from the fact that the sensible heat flux was measured based on speed of sound measurements, which has been shown by Loescher *et al.* (2005) to deviate from sensible heat flux derived from measurements of air temperature with a fast-response platinum resistance thermometer by up to 10% for this specific sonic model. On the other hand, Ham & Heilman (2003), again for the same sonic model used in this study, found extremely good correspondence between

Table 1 Estimates of random and systematic uncertainty of annual net ecosystem CO_2 exchange (NEE) ($g\,C\,m^{-2}\,yr^{-1}$)

Uncertainty analysis	2005	2006
Random uncertainty	1	1
Systematic uncertainty		
u^* (reference vs. no u^*-threshold)	22	19
Long gaps (1–2 months, summer-winter)	5*	NA
Precipitation (reference vs. exclude all)	3	1
Density correction Webb *et al.* (1980)		
T_{air} (10%)	6	6
ρ_v (10%)	4	2
P (10%)	1	1
ρ_c (5%)	36	37
F_H (5%)	34	36
F_{CO_2} and F_{H_2O} (5%)	39	42
Combined density corrections	63	67
Random and systematic uncertainty	67	70

*Assumed to equal the value determined for 2006.
Data in parenthesis give details on the assumptions (e.g. percentage error) under which uncertainties were derived. For further details refer to the text.

sonic- and thermocouple-derived sensible heat flux measurements. Additional uncertainty of the sensible heat flux arises from the choice of coordinate system (Lee *et al.*, 2004) and from the necessary (small) frequency response corrections (Massman, 2001). Based on the evidence presented above and some preliminary sensitivity tests with different coordinate systems (data not shown), we have assumed a 5% uncertainty for the sensible heat flux. Uncertainties of the uncorrected latent heat and CO_2 flux are likely to be similar in magnitude because these are measured by the same instruments and were thus dealt with jointly. We have also assumed a 5% uncertainty for the latent heat and CO_2 flux, intended to reflect uncertainties due to choice of the coordinate system and frequency response corrections. We based our frequency response corrections on a site-specific cospectral reference model (cf. Massman & Clement, 2004; Wohlfahrt *et al.*, 2005) that have been validated against experimentally derived frequency response correction factors following Aubinet *et al.* (2000, 2001) as described in Wohlfahrt *et al.* (2005). We, thus, believe our choice of 5% uncertainty to be justified, even if Massman & Clement (2004) report potential errors in frequency response correction factors of up to 30%. The systematic uncertainty associated with the choice of the u^* threshold was estimated by calculating annual NEE with and without filtering for u^* similar to the procedure used by Morgenstern *et al.* (2004). Long data gaps, as occurred during summer/autumn 2005 and winter 2006, may cause considerable uncertainty in annual NEE (Richardson & Hollinger, 2007). In order to quantify the uncertainty related to these gaps, we randomly introduced 1- and 2-month-long gaps to the July–December 2006 record (when the longest consecutive gap was <1 day). Eddy covariance measurements during and immediately after precipitation are unreliable because the quality of the data from the sonic anemometer and, particularly, from the open-path IRGA are compromised by the presence of water drops in the acoustic and optical paths. Because large emissions of CO_2 have been observed in semiarid ecosystems following precipitation events (Xu & Baldocchi, 2003; Veenendaal *et al.*, 2004; Hastings *et al.*, 2005; Kurc & Small, 2007), we quantified the resulting uncertainty by creating artificial gaps during and 2 h following precipitation events.

Another approach for determining the reliability of the open-path eddy covariance NEE flux measurements is to use independent methods for comparison. To this end we used NEE obtained concurrently with a closed-path eddy covariance system during a 2-week campaign in May/June 2007 (cf. Ocheltree & Loescher, 2007) and large geodesic ecosystem chambers at several occasions throughout 2005 (Arnone & Obrist, 2003; Jasoni *et al.*, 2005). Data from the open-path eddy covariance system have been processed both with and without accounting for the additional sensible heat flux induced by self-heating of the open-path IRGA (Burba *et al.*, 2006).

Results

Uncertainty analysis

The probability density distribution of the random CO_2 flux uncertainty, shown in Fig. 2a, was distributed in a double-exponential fashion, following a Laplace rather than a normal distribution. A good linear correlation between the random uncertainty and the magnitude of the CO_2 flux was found (Fig. 2b), which was subsequently used to estimate the random uncertainty of each valid half-hourly NEE measurement. Integration up to the annual scale resulted in a random NEE uncertainty of $1\,g\,C\,m^{-2}$ for each of the 2 study years (Table 1).

The systematic uncertainty of annual NEE due to the density correction terms in Eqn (1) was estimated as 63 and $67\,g\,C\,m^{-2}$ for 2005 and 2006, respectively (Table 1). The largest contributors to this overall uncertainty were the uncertainties in the quantification of the CO_2 density, the sensible heat and latent heat/CO_2 fluxes ($34–42\,g\,C\,m^{-2}$), while air temperature, water vapour density and static air pressure accounted for $<6\,g\,C\,m^{-2}$ uncertainty (Table 1). The systematic

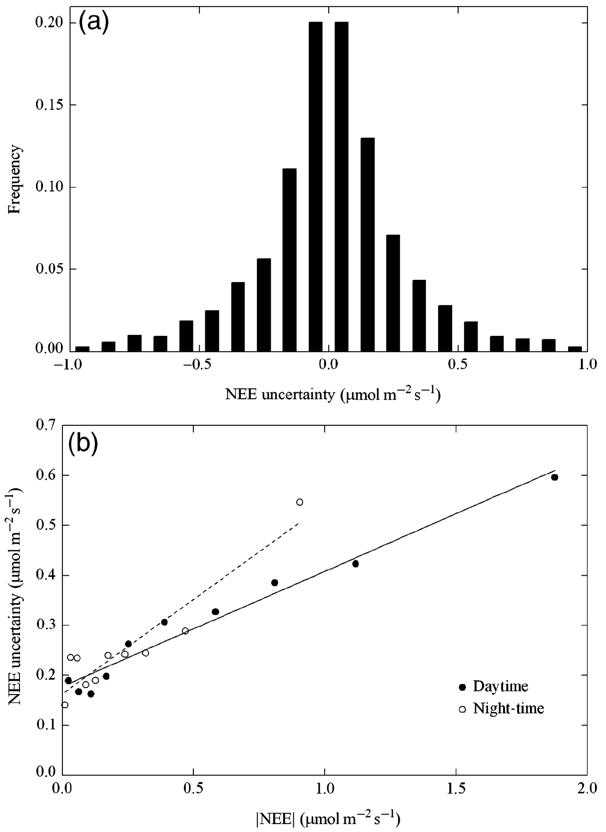

Fig. 2 Random uncertainty of the net ecosystem CO_2 exchange (NEE): Probability density distribution (a) and random uncertainty of NEE as a function of the absolute magnitude of NEE (b), separately for daytime (closed symbols) and night-time (open symbols) hours, calculated using the neighbouring days approach devised by Hollinger & Richardson (2005) and Richardson & Hollinger (2005). Lines in Fig. 2b represent linear best fits with the following equations: $y = -0.23x + 0.18$ (day, solid line, $r^2 = 0.98$) and $y = 0.38x + 0.16$ (night, dotted line, $r^2 = 0.88$).

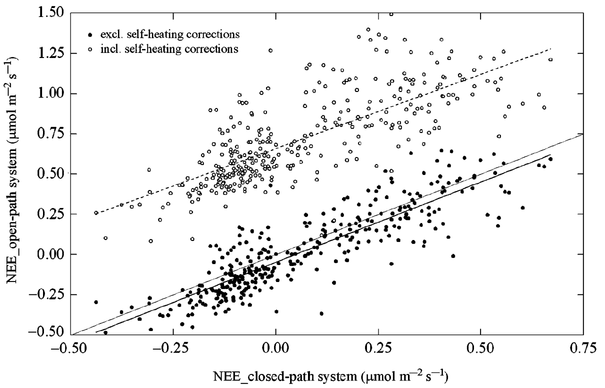

Fig. 3 Comparison between net ecosystem CO_2 exchange (NEE) measured by means of the eddy covariance technique using an closed- and an open-path IRGA connected to a common sonic anemometer. Flux data processing of the open-path system was conducted with and without taking into account the self-heating of the open-path IRGA (Burba *et al.*, 2006). Bold lines represent linear best fits with the following equations: $y = 1.00x + 0.05$ (exclusive self-heating corrections, solid line, $r^2 = 0.77$) and $y = 0.93x + 0.66$ (inclusive self-heating corrections, dotted line, $r^2 = 0.57$). One-to-one correspondence is indicated by the thin solid line.

uncertainty associated with the choice of the u^* threshold amounted to an uncertainty of 22 and 19 $\mathrm{g\,C\,m^{-2}}$ for 2005 and 2006, respectively; randomly introducing 1- and 2-month long gaps to the July–December 2006 record resulted in a maximum annual uncertainty of 5 $\mathrm{g\,C\,m^{-2}}$ (Table 1). Creating artificial gaps during and 2 h following rains yielded a total annual uncertainty of 3 and 1 $\mathrm{g\,C\,m^{-2}}$ for 2005 and 2006, respectively (Table 1). Assuming that these sources of systematic uncertainty are independent and combining these with the estimate of random uncertainty, we calculated an overall uncertainty of 67 and 70 $\mathrm{g\,C\,m^{-2}}$ for 2005 and 2006, respectively (Table 1).

NEEs obtained with the closed- and open-path IRGA systems – not accounting for self-heating of the open-path IRGA – corresponded very well (Fig. 3). NEE calculated using the closed-path IRGA were slightly higher than NEEs calculated using the open-path instrument. When integrated over 1 year, the difference amounted to 19 $\mathrm{g\,C\,m^{-2}}$. In contrast, including the corrections for self-heating of the open-path IRGA proposed by Burba *et al.* (2006) resulted in a gross underestimation of the closed-path NEE (Fig. 3) – when applied to the entire years of 2005 and 2006, the correction amounted to a shift towards net CO_2 release of 157 and 161 $\mathrm{g\,C\,m^{-2}}$, respectively, and a change in the sign of cumulated annual NEE for both years. NEEs measured using the open-path IRGA also corresponded closely to NEEs measured with large geodesic ecosystem chambers in the ambient plots of the nearby NDFF during seven campaigns throughout 2005 (Fig. 4). Given that NEEs measured with the chambers were outside the footprint of the eddy covariance system and derived from a totally independent method, the correspondence between the two data sets is encouraging (means not statistically different; $P = 0.71$; Mann–Whitney-*U* test). When the small mismatch between chamber and open-path NEE determined for the year 2005 (Fig. 4) is applied to the entire years of 2005 and 2006, annual NEE changes by 25 and 26 $\mathrm{g\,C\,m^{-2}}$, respectively. Because of the good correspondence of the open-path NEE exclusive the corrections proposed by Burba *et al.* (2006) and the closed-path (Fig. 3) and chamber-based NEE (Fig. 4), we chose not to apply these additional corrections.

Meteorological conditions during study period

PAR followed a clear sinusoidal pattern during the study period with maxima and minima of 64 and

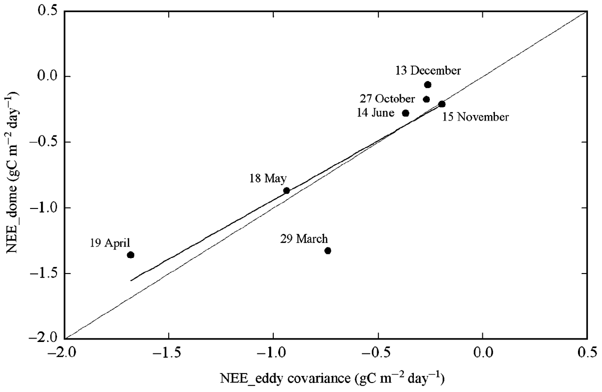

Fig. 4 Comparison between daily sums of net ecosystem CO_2 exchange (NEE) measured using eddy covariance at the MGCF site and large geodesic domes (Arnone & Obrist, 2003; Jasoni *et al.*, 2005) in the ambient plots of the nearby Nevada face facility (NDFF) during 2005. The bold line represents a linear best fit with the following equation: $y = 0.90x–0.04$ ($r^2 = 0.74$). One-to-one correspondence is indicated by the thin solid line.

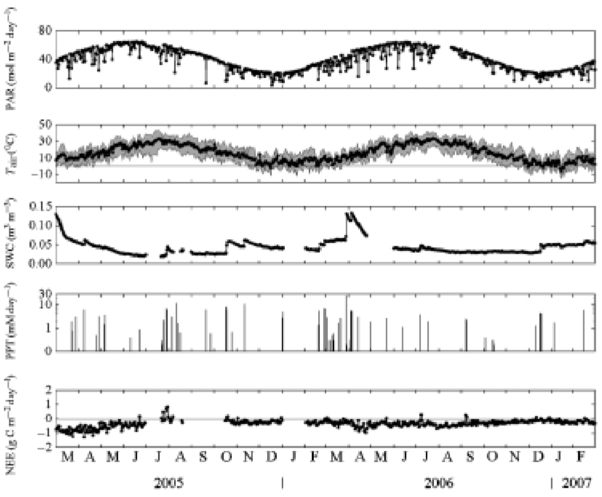

Fig. 5 Daily sums of photosynthetically active radiation (PAR), precipitation (PPT), the net ecosystem CO_2 exchange (NEE) and daily averages of air temperature (T_{air}) and soil water content (SWC) during the 2-year study period. Shaded areas in the second panel indicate the daily minimum to maximum temperature range.

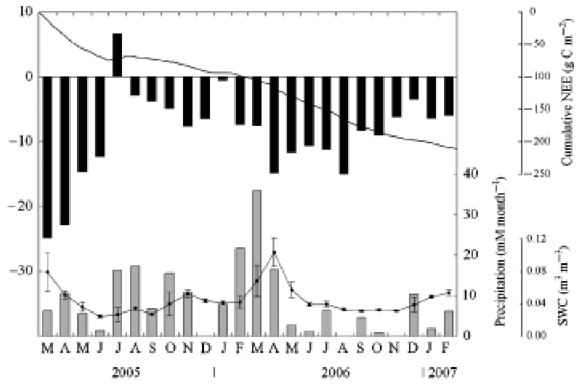

Fig. 6 Monthly net ecosystem CO_2 exchange (NEE, black bars), cumulative NEE (solid line), monthly precipitation (grey bars) and monthly averaged soil water content (solid line and filled symbols) during the 2-year study period. Error bars of the soil water content refer to the standard deviation around the mean.

22 mmol m^{-2} day^{-1} at summer and winter solstice, respectively, interrupted only by occasional cloud cover immediately surrounding rains (Fig. 5). Air temperature varied between 44 and −12 °C (Fig. 5), with annual averages of 15.8 and 15.9 °C in 2005 and 2006, respectively, which is close to the 1997–2005 mean of 15.4 °C measured at the nearby FACE site. During the 2-year study 74 discrete rainfall events were recorded at the eddy covariance site of which 55% delivered <2 mm and 22% >5 mm of rain (Fig. 5). Annual precipitation amounted to 120 and 86 mm in 2005 and 2006, respectively (1997–2005 annual average of 149 mm measured at the nearby FACE site). Following larger precipitation events, soil water content reached maximum values of 0.17 m^3 m^{-3} in spring, with minimum soil water contents down to 0.02 m^3 m^{-3} occurring during the summer months (Fig. 5). During summer, soil water content was less responsive to precipitation inputs (Fig. 5), indicating that parts of the rainfall evaporated before reaching 0.04 m soil depth.

Net ecosystem CO_2 exchange

Daily NEE during the 2-year study period (Fig. 5) ranged from an uptake of −1.7 g C m^{-2} day^{-1} (daily average NEE of −1.64 μmol m^{-2} s^{-1}) to a loss of 1.5 g C m^{-2} day^{-1} (daily average NEE of 1.45 μmol m^{-2} s^{-1}). The highest uptake rates were observed in March and April (Fig. 5), with NEE ranging between 1 and −4 μmol m^{-2} s^{-1}; the lowest uptake rates occurred between July and February, when daytime NEE hardly exceeded the range of 0.5 to −1.5 μmol m^{-2} s^{-1}. Days with a positive CO_2 balance occurred during any time of the year and were usually associated with rainfall events (Fig. 5). Gap-filled monthly NEE ranged from −25 g C m^{-2} month^{-1} in March 2005 to +7 g C m^{-2} month^{-1} in July 2005 (Fig. 6). Monthly NEE was significantly lower (i.e. more uptake) in March 2005 as compared with 2006, whereas July 2005 exhibited a significantly higher NEE ($P < 0.05$; Mann–Whitney-U test). The latter was associated with a series of rain events that delivered 16 mm of rain during the last week of July 2005 (Fig. 5). Annual NEE amounted to

Table 2 Regression statistics of independent variables against net ecosystem CO_2 exchange (NEE) for different integration periods (0.5 h to 20 days): Correlation coefficients of linear regression analysis are shown on the left and coefficients of determination of step-wise regression analysis on the right

		r					r^2
	n	PAR	T_{air}	T_{soil}	SWC	PPT	(step-wise regression)
0.5 h	22 292	−0.227***	−0.072***	−0.074***	−0.007	−0.003	0.05 (PAR, T_{air}, SWC)
1 day	530	−0.404***	0.058	−0.075*	−0.303***	0.116**	0.37 (PAR, T_{air}, SWC)
5 days	104	−0.454***	0.104	−0.105	−0.387***	0.164*	0.54 (PAR, SWC, PPT, T_{air})
10 days	51	−0.572***	0.239*	−0.224	−0.411***	0.066	0.58 (PAR, T_{soil}, SWC)
20 days	25	−0.605***	0.290	−0.256	−0.485**	−0.034	0.66 (PAR, SWC, T_{air})

Correlation coefficients are not significant except for: $^*P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$; results of step-wise regression are significant at $P<0.001$ (*n*, number of samples).
PAR, photosynthetically active radiation; SWC, soil water content; PPT, precipitation.

−102 and −110 g C m^{-2} in 2005 and 2006, respectively (Fig. 6).

Half-hourly NEE was significantly correlated with all investigated environmental variables except soil water content and precipitation, but these relationships possessed poor predictive power (Table 2). The predictive power of PAR and soil water content for explaining variations in NEE increased with increasing integration time, air and soil temperature possessed no significant relationship with NEE beyond 1 day integration (except 10 days: T_{air}), and precipitation exhibited a significant relationship with NEE only between 1 and 5 days integration (Table 2). PAR, soil water content and temperature were inversely correlated with NEE at all integration levels, whereas air temperature and precipitation were negatively correlated with NEE only at 1 day (and 20 days for precipitation) integration (Table 2). A step-wise regression analysis included PAR and soil water content at all integration levels, air temperature at all but 10 days integration (where soil temperature was included instead), and precipitation at the 5 days integration level (Table 2). The proportion of explained variance increased greatly with increasing integration time, a linear model including PAR, soil water content and air temperature explaining a maximum of 66% of the variability in data at 20 days integration (Table 2).

A cross correlation analysis on daily averaged data revealed no lagged effects for NEE (data not shown) except for precipitation (Fig. 7), which switched from a positive to a negative correlation 1 and 3–4 days after a precipitation event during spring (April–May) and summer (June–July), respectively. Responses of NEE to rains varied with season and soil moisture present (Fig. 8). For example, a sustained decrease in NEE (i.e. higher rates of net CO_2 uptake) followed the first spring rains (Fig. 8a), while similar amounts of precipitation resulted in the ecosystem turning from neutral to a source of CO_2 and back to neutral despite an increased moisture availability within a week during summer (Fig. 8b). In winter, virtually no change in NEE was observed in response to rains (Fig. 8c).

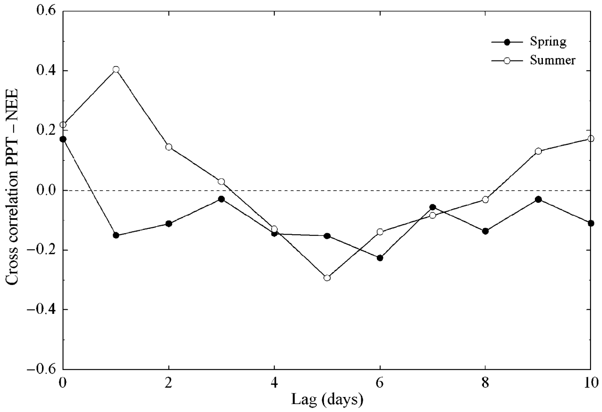

Fig. 7 Cross correlation of daily precipitation (PPT) and the net ecosystem CO_2 exchange (NEE) for spring (April–May 2006, closed symbols) and summer (June–July 2006, open symbols) conditions. Correlation coefficients are significant at $P<0.05$ when their absolute values exceed 0.25.

Discussion

With annual NEE of −102 ± 67 and −110 ± 70 g C m^{-2}, the Mojave Desert ecosystem we studied was a significant net sink for CO_2 during the 2-year study, corroborating the annual net gains of 127 ± 17 g C m^{-2} measured in 2004 by Jasoni *et al.* (2005) and the 185 ± 15 g C m^{-2} measured in 2005 (J. Arnone, personal communication) in the nearby ambient CO_2 FACE plots using large static ecosystem chambers (Arnone & Obrist, 2003). These sink strength estimates are in line with the few other studies available in the literature: −212 g C m^{-2} (March–

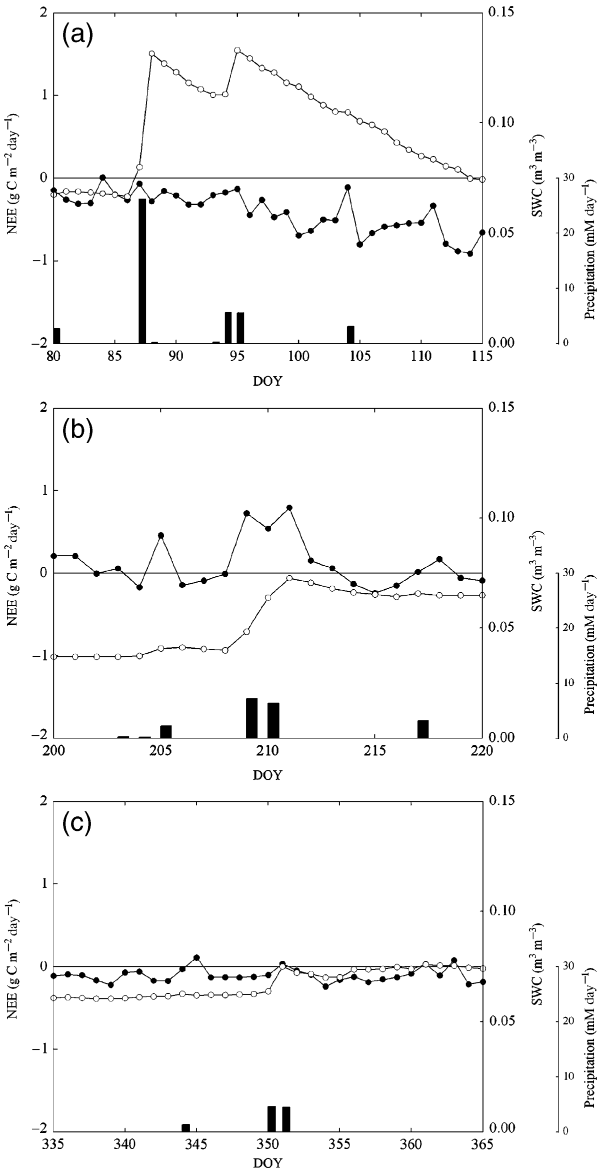

Fig. 8 Selected time series of daily sums of net ecosystem CO_2 exchange (NEE, filled symbols), daily precipitation (black bars) and daily average soil water content (SWC, open symbols) for illustrating precipitation effects on NEE. Time periods represent: March/April 2006 (a), July/August 2005 (b) and December 2006 (c).

December only) reported by Scott *et al.* (2006) for a semiarid riparian shrubland in Arizona (USA), −39 to $-52\,g\,C\,m^{-2}$ found by Hastings *et al.* (2005) for a desert shrub community in Baja California/Mexico, and −96 to $-155\,g\,C\,m^{-2}$ determined under normal weather conditions by Luo *et al.* (2007) for a mature semiarid chaparral ecosystem in California (USA). Emmerich (2003), though, reported a net annual loss of $144\,g\,C\,m^{-2}$ in a semiarid bush site in Arizona (USA), however this appears to stem from the large pool of soil inorganic carbon.

A comprehensive uncertainty analysis, accounting for both random and systematic sources of uncertainty (Moncrieff *et al.*, 1996), showed that quantification of NEE in semiarid climates with open-path IRGAs is challenging because the required density correction [Eqn (1); Webb *et al.*, 1980] is highly sensitive to uncertainties in the input parameters such as the CO_2 density, the sensible heat flux and the (uncorrected) CO_2 and latent heat fluxes. The resulting systematic uncertainty was an order of magnitude larger than the random uncertainty, and three times larger than the uncertainty resulting from the choice of the u* threshold, which very often constitutes the major source of uncertainty in annual NEE estimates (e.g. Anthoni *et al.*, 2004; Morgenstern *et al.*, 2004). The causes for this relatively large systematic uncertainty in semiarid climates are the low CO_2 fluxes and the relatively large density corrections needed as a result of the large sensible heat fluxes (Webb *et al.*, 1980). Both of these challenges require a high level of instrument/measurement accuracy (e.g. regular checks of the calibration of IRGAs) and a thorough postprocessing of EC data (especially frequency response corrections). The EC instrumentation used in our study was meticulously maintained and appropriately calibrated. Random uncertainty in our study was relatively small owing to the small magnitude of half-hourly NEEs at semiarid sites, compared with many mesic ecosystems that have larger CO_2 fluxes (Richardson *et al.*, 2006). In accordance with Richardson & Hollinger (2007), the uncertainty resulting from long gaps in the CO_2 flux record was relatively small as long as the gaps occurred during periods with small temporal variability.

Supporting evidence of the validity of our NEE estimates comes from the comparison with NEE measured by means of a closed-path EC system and large geodesic ecosystem chambers (Arnone & Obrist, 2003; Jasoni *et al.*, 2005), which showed close correspondence to the open-path system-based measurements. The comparison with the closed-path eddy covariance system revealed that the corrections for self-heating of the open-path IRGA proposed by Burba *et al.* (2006) seem to cause a significant underestimation of NEE at our site. This finding contrasts those reported by Grelle & Burba (2007) for a replanted forest site in Sweden. A possible reason for the apparent discrepancy between arid and high-latitude maritime forest sites might be that the parameterization of the gradients between air temperature and the open-path IRGA surface temperatures, to which the corrections are directly proportional and very sensitive and which were derived by Burba *et al.* (2006) with measurements in Nebraska (USA), does not hold for the climatic conditions in the Mojave Desert. Because our closed- vs. open-path IRGA comparison was conducted only under warm conditions (7–37 °C in late May and early June 2007; Fig. 3), we were unable to evaluate the self-heating corrections for cold periods when they may be quantitatively more important (Burba *et al*., 2006). These unquantified corrections must be considered, at least qualitatively, as contributing to the uncertainty of estimating annual NEE for each year. Ongoing measurements at our Mojave site will include further comparisons between open- and closed-path EC systems (Burba *et al*., 2006; Ocheltree & Loescher, 2007) and direct measurements of density fluctuations in the optical path of open-path IRGAs (Grelle & Burba, 2007) under different climatic conditions to quantify sensitivities of EC estimates of NEE across seasonal and interannual time scales. However, given the close agreement of NEE values measured with the closed-path and open-path eddy covariance methods (Fig. 3), and the very comparable NEE values calculated using EC and the chamber methods (Fig. 4), and the fact that applying the correction for self-heating would have led to unreasonably large changes in annual NEE, we feel confident in not applying this correction to the present data set.

The magnitude of our NEE estimates for this arid ecosystem is comparable to NEEs reported for many temperate forest and grassland ecosystems (Baldocchi *et al*., 2001; Falge *et al*., 2002b), which are characterized by a much higher NPP than deserts have (Larcher, 2001). Because NEP is the residual of NPP and heterotrophic respiration (R_h, Larcher, 2001), this suggests soil heterotrophic microbial respiration (R_h) to be very low in desert ecosystems. This idea is supported by Austin *et al*. (2004), Belnap *et al*. (2004), Cable & Huxman (2004), de Soyza *et al*. (2005), Miller *et al*. (2005) and Sponseller (2007), who showed that microbial activity in desert ecosystems is essentially confined to short time periods following rains, when the sudden moisture availability may result in a pulse in nutrient and substrate availability and subsequently of CO_2 efflux (Huxman *et al*., 2004a, b; Veenendaal *et al*., 2004; Hastings *et al*., 2005; Potts *et al*., 2006a, b; Kurc & Small, 2007). In contrast to previous studies (e.g. Huxman *et al*., 2004b), it is now well established that the physical displacement of soil CO_2 by rain water plays a minor role for the observed CO_2 pulses (Jassal *et al*., 2005). The magnitude and duration of these CO_2 efflux episodes depends on the amount of precipitation (Huxman *et al*., 2004b), the time between consecutive precipitation events (Sponseller, 2007) and antecedent soil moisture conditions (Potts *et al*., 2006a) and reflects trade-offs between autotrophic (i.e net CO_2 uptake) and heterotrophic (i.e. net CO_2 release) contributions (Huxman *et al*., 2004b): for example, small precipitation events wet only the upper soil and may activate only autotrophic (cyanobacteria, lichens and mosses) and heterotrophic surface soil organisms, but do not supply water to the roots of vascular plants (Huxman *et al*., 2004b). The magnitude of the CO_2 efflux in this case depends strongly on the ratio of activated autotrophic to heterotrophic soil organisms and thus the actual wetting depth (autotrophic soil organisms are located exclusively at or just below the soil surface; Cable & Huxman, 2004). Larger rains, sufficient to increase water availability in deeper soil layers, can stimulate gross photosynthesis of vascular plants which can result in a lagged and sustained period of net ecosystem carbon gain following an initial pulse of CO_2 efflux (Huxman *et al*., 2004a, b; Potts *et al*., 2006a, b). Respiration rates are greatly reduced in deeper soil layers (Sponseller, 2007). These two general types of responses may be modulated by the antecedent moisture conditions (i.e. whether a precipitation pulse occurs during a period of low or high soil water availability; Ignace *et al*., 2007). For example, during periods of low soil water availability, even large rains may not translate into a corresponding increase in carbon gain because: (i) leaf area of drought–deciduous plants may be low (Hamerlynck *et al*., 2002), (ii) annual plants are absent (Smith *et al*., 2000) or senescent (Ivans *et al*., 2006), and (iii) photosynthesis of evergreen plants may be colimited by biotic and environmental factors other than soil water availability (Potts *et al*., 2006a). In addition, the response of microbial respiration to wetting during periods of low soil water availability may be more intense because it involves the decomposition of accumulated labile soil organic matter and dead microbial biomass (Austin *et al*., 2004; Barker *et al*., 2005), but also the release of physically protected soil organic matter and the mineralization of microbial intracellular compounds (Fierer & Schimel, 2003). Particularly large CO_2 efflux episodes following rains after extended periods of low soil water availability have been reported by Hastings *et al*. (2005), Veenendaal *et al*. (2004) and Xu & Baldocchi (2003) and were observed in our study for July 2005 (Figs 5 and 8b). During these periods a lag of 3–4 days was observed before the correlation between NEE and precipitation switched from positive to negative, as opposed to conditions of high soil water availability when this transition occurred within the same day the rain took place (Fig. 7).

The large net annual carbon gains observed in this study and in the ambient CO_2 plots of the nearby FACE site (Jasoni e*t al*., 2005; J. Arnone, personal communication) prompt the question of where the fixed carbon is accruing within the ecosystem. Continuing accretion of vascular plant cover (NPP) may account for some of this carbon (Webb *et al*., 2003; R. Nowak, personal communication from FACE site). However, expansion and growth of cryptobiotic crust organisms (lichens, mosses, cyanobacteria) likely account for a significant portion of the carbon accretion. These organisms have, heretofore, been neglected as significant carbon pools in assessments of desert carbon pools. In fact, we could find no quantitative mass-based data on cryptobiotic crust productivity in the literature. In order to corroborate the inferred carbon sink strength of this Mojave Desert ecosystem using EC and chambers, however, changes in above- and below-ground carbon pools over time would need to be quantified.

Taken together, our results show that (i) during the 2-year study period Mojave Desert shrub ecosystem we investigated was a significant sink for CO_2 on an annual basis, corroborating earlier findings obtained with static chamber techniques at the nearby ambient CO_2 FACE site and several other studies of semiarid ecosystems; (ii) while the quality of our NEE measurements could be confirmed by two independent methods, our uncertainty analysis underlines the need for accurate instrument data (especially from the open-path IRGA) that are used to calculate the Webb *et al.* (1980) density corrections to NEE; (iii) seasonal variation in NEE primarily depends on soil moisture conditions and precipitation and their effects on vascular plant and cryptobiotic crust photosynthetic and respiratory activities and productivities; and (iv) desert shrubland ecosystems of the world may represent a potentially large global carbon sink that has been ignored until now and demands continuation of experimental studies (e.g. Jasoni *et al.*, 2005) aimed at quantifying ecosystem responses of deserts to global environmental change factors.

Acknowledgements

We are very grateful to T. Huxman for his advice on configuring and installing the eddy covariance system, E. Knight for maintaining (calibrating) the tower and equipment and acquiring data and S. Smith and R. Nowak for generating funding that supports the Mojave Desert Global Change Facility and the Nevada Desert Research Center. We especially thank the US National Science Foundation (DEB-0213055), the US Department of Energy Program for Ecosystem Research (DE-FG03-02ER63361) and the A. W. Mellon Foundation for research funding, and UNLV, UNR and the Desert Research Institute for equipment purchases. JAA III thanks the DRI supporting his 1-year sabbatical stay at the University of Innsbruck. G. W. acknowledges travel support to Reno (NV, USA) by the Office of Foreign Affairs of the University of Innsbruck. D. Baldocchi and five anonymous reviewers are acknowledged for their critical comments on earlier versions of this paper.

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