

# Cross validation of open-top chamber and eddy covariance measurements of ecosystem CO<sub>2</sub> exchange in a Florida scrub-oak ecosystem

SABINA DORE\*, GRAHAM J. HYMUS†, DAVID P. JOHNSON†, C. R. HINKLE‡, RICCARDO VALENTINI§ and BERT G. DRAKE†

\*National Research Council, Mail Code DYN-2, Kennedy Space Center, Florida 32899 USA, †Smithsonian Environmental Research Center, PO Box 28, Edgewater MD 21037, USA, ‡Dynamac Corporation, Mail Code DYN-1, Kennedy Space Center, Florida 32899 USA, §University of Tuscia, Department of Forest Sciences and Resources, via S Camillo De Lellis, 01100 Viterbo, Italy

## Abstract

Simultaneous measurements of net ecosystem CO<sub>2</sub> exchange (NEE) were made in a Florida scrub-oak ecosystem in August 1997 and then every month between April 2000 to July 2001, using open top chambers (NEE<sub>O</sub>) and eddy covariance (NEE<sub>E</sub>). This study provided a cross validation of these two different techniques for measuring NEE. Unique characteristics of the comparison were that the measurements were made simultaneously, in the same stand, with large replicated chambers enclosing a representative portion of the ecosystem (75 m<sup>2</sup>, compared to approximately 1–2 ha measured by the eddy covariance system). The value of the comparison was greatest at night, when the microclimate was minimally affected by the chambers. For six of the 12 measurement periods, night NEE<sub>O</sub> was not significantly different to night NEE<sub>E</sub>, and for the other periods the maximum difference was 1.1 μmol m<sup>-2</sup>s<sup>-1</sup>, with an average of 0.72 ± 0.09 μmol m<sup>-2</sup>s<sup>-1</sup>. The comparison was more difficult during the photoperiod, because of differences between the microclimate inside and outside the chambers. During the photoperiod, air temperature (T<sub>air</sub>) and air vapour pressure deficits (VPD) became progressively higher inside the chambers until mid-afternoon. In the morning NEE<sub>O</sub> was higher than NEE<sub>E</sub> by about 26%, consistent with increased temperature inside the chambers. Over the mid-day period and the afternoon, NEE<sub>O</sub> was 8% higher than NEE<sub>E</sub>, regardless of the large differences in microclimate. This study demonstrates both the uses and difficulties associated with attempting to cross validate NEE measurements made in chambers and using eddy covariance. The exercise was most useful at night when the chamber had a minimal effect on microclimate, and when the measurement of NEE is most difficult.

*Keywords:* eddy covariance, net ecosystem exchange, open-top chambers, scrub-oak ecosystem

*Received 12 March 2002; revised version received and accepted 17 May 2002*

## Introduction

The Net ecosystem exchange (NEE) of CO<sub>2</sub> between the biosphere and atmosphere represents the difference between ecosystem carbon uptake and loss, integrated over time periods from seconds to years. Measurements of NEE complement traditional growth analysis, and provide insight into ecosystem productivity and the

dynamics of carbon cycling between the biosphere and atmosphere (Wofsy *et al.*, 1993; Valentini *et al.*, 1996). Forest ecosystems, particularly those in the Northern Hemisphere and tropics, have been identified as important sinks for atmospheric CO<sub>2</sub> (Dixon *et al.*, 1994; Ciais *et al.*, 1995; Denning *et al.*, 1995; Lloyd, 1999; Mahli *et al.*, 1999). Measurements of NEE can be used to parameterize and constrain models estimating the size of this sink (Ruimy *et al.*, 1996). Enclosure methods and eddy covariance are experimental techniques by which NEE can be measured (Baldocchi *et al.*, 1988; Drake *et al.*, 1996).

Correspondence: Sabina Dore, University of Tuscia, Department of Forest Sciences and Resources, via S Camillo De Lellis, 01100 Viterbo, Italy, tel. +39 0761357394, e-mail: dore@unitus.it

To date, validations of enclosures or eddy covariance techniques for measuring NEE have not been made. Simultaneous measurements of NEE from enclosures and eddy covariance could provide a cross-calibration of measurement techniques, and may highlight potential sources of error in either technique. The potential sources of error with the enclosure method include the effects of change in microclimate and increased air pressure (Lund *et al.*, 1999; Van Oijen *et al.*, 1999; Nikalus *et al.*, 2000). The accuracy of eddy covariance measurements is subject to systematic and random errors associated with the atmosphere, surface conditions and instrumentation (Baldocchi *et al.*, 1996; Moncrieff *et al.*, 1996). Comparisons of enclosure and eddy covariance measurements of NEE are difficult and seldom made, primarily because the techniques are used to investigate different questions at different scale of inquiry. Forest ecosystems have often been the focus of eddy covariance studies (Wofsy *et al.*, 1993; Hollinger *et al.*, 1994; Valentini *et al.*, 1996; Valentini *et al.*, 2000), and are not well suited to chamber experiments. Open-top chambers facilitate atmospheric manipulation, and have been widely used to address the effects of atmospheric changes, particularly elevated CO<sub>2</sub> and ozone, on plant physiological processes (Norby *et al.*, 1999). Restrictions on the size of chambers have limited measurements of NEE to ecosystems characterized by low stature vegetation, such as grasslands, where a representative portion of the ecosystem can be enclosed (Ham *et al.*, 1995; Drake *et al.*, 1996; Stocker *et al.*, 1997). By contrast, eddy covariance experiments are not limited to specific ecosystems on the basis of canopy height. The technique is well suited to large-scale studies, over ecosystems as diverse as mature forest or grasslands, where biosphere and atmosphere exchanges of CO<sub>2</sub>, H<sub>2</sub>O and energy are measured over a spatial scale of the order of 1 km (Baldocchi *et al.*, 1996). Restrictions for eddy covariance measurements are associated with surface heterogeneity and complex terrain (Moncrieff *et al.*, 1996).

Where comparisons of ecosystem scale fluxes have been made, it has often been by comparing eddy covariance measurements with estimated fluxes calculated by scaling up component fluxes measured in small enclosures (i.e. soil, stem or leaf fluxes) (Goulden *et al.*, 1996; Lavigne *et al.*, 1997; Law *et al.*, 1999). The lack of directly comparable data presents problems for interpretation. Although Ruimy *et al.* (1995) analysed the response of CO<sub>2</sub> exchange measured using enclosures and eddy covariance to light, the data were not collected simultaneously at the same sites.

In May 1996, a Smithsonian Environmental Research Center project began in the scrub-oak ecosystem of Merritt Island, Florida. The ecosystem was subject to management by prescribed fire and was burnt immediately before the project began. During August 1997 and

throughout 2000, NEE was measured monthly in the chambers for between three and eight days and compared with the continuous eddy covariance measurements being made at the site. In this comparison, three important criteria were met: (i) The chambers were large and replicated, so as to enclose a representative portion of the ecosystem. (ii) Measurements were made simultaneously. (iii) The chambers and eddy covariance station were sited in the same stand.

## Materials and methods

### *The Site*

The study was located within NASA's Kennedy Space Centre on Merritt Island, a barrier island on the east coast of central Florida (28°38'N, 80°42'W). The site was a scrub-oak palmetto community, dominated by sclerophyllous evergreen oaks and the Saw Palmetto (*Serenoa repens* Small). Three oak species, *Quercus myrtifolia* Willd., *Q. geminata* Small. and *Q. chapmanii* Sargent, typically constitute up to 85% of above ground biomass in this ecosystem (Schmalzer & Hinkle, 1992). The substrates were freely draining Pomello (Arenic Haplalumod) and Poala (Spodic quartzipsamment) sands. Both were acidic and low in nutrients (Schmalzer & Hinkle, 1992). The climate was subtropical, warm and humid, with the 100 years average annual precipitation of 131 cm masking high year to year variability. The 100 years average mean maximum and minimum temperatures in July, the hottest month, were 33.3 °C and 21.8 °C, respectively, and 22.3 °C and 9.5 °C in January, the coldest month (Mailander, 1990).

The ecosystem was naturally fire dependent and managed by controlled burns. Two fires, one in August 1995 and one in January 1996, cleared six hectares of land, upon which 16 open top chambers and eight control plots were sited in May 1996, as part of a long-term study into the effects of elevated CO<sub>2</sub> on the ecosystem. The open top chambers were octagonal in plan, enclosing a ground surface area of 9.4 m<sup>2</sup>. The height of the chambers was 1.76 m, creating a chamber volume of 16.5 m<sup>3</sup>. Only the eight chambers exposed to ambient air were used in this study.

For three to eight consecutive days every month, in August 1997 and between April 2000 and July 2001, measurements of NEE were made using the chambers (NEE<sub>O</sub>) and an eddy covariance system (NEE<sub>E</sub>). The eddy station was sited approximately 100 m NW of the closest chamber. In August 1997, the stand leaf area index (LAI) was 0.8, above-ground biomass was 3 t ha<sup>-1</sup> (dry weight), and canopy height was circa. 0.5 m. In 2001 LAI was 2, biomass 8 t ha<sup>-1</sup> and the average height was 0.8 m.

Above-ground biomass was unaffected by the chamber (Dijkstra *et al.*, 2002).

#### Measurement of NEE. 1: chambers

To measure  $NEE_O$ , flat custom designed Lexan lids (Commercial Plastics, Orlando, FL, USA) were fitted to the frustum of each chamber. These lids were removed upon completion of each measurement period. The chambers functioned as an open gas exchange system with a continuous flow of air through them. Air was blown into each chamber at a rate of  $27\text{ m}^3\text{ min}^{-1}$ , with the chamber volume being replaced 1.5 times a minute. Air entered the OTC through four circular ducts each of 20.3 cm diameter, total surface area  $1.23\text{ m}^2$ , and exited through exhausts in the lids with a total exit surface area of  $0.96\text{ m}^2$ . This difference in entrance and exit area, increased chamber pressure and protected against leaks. Two infra-red gas analysers (IRGA) (LI 6262; LI-COR, Lincoln NB) were used to measure both a reference  $\text{CO}_2$  mol fraction, from one of four chamber inlet ducts, and a sample  $\text{CO}_2$  mol fraction inside the chambers, at canopy height. The first IRGA operated in differential mode. The second IRGA continuously measured absolute chamber inlet reference  $\text{CO}_2$  mol fraction and fed this value into the differential analyser, which then corrected the measured differential for changes in background  $\text{CO}_2$  concentration. Both reference and sample air streams were drawn from the chambers at a flow rate of  $8\text{ L/min}$ , fed through a 1.9-L buffer volume, then to the IRGA at a rate of  $1\text{ L/min}$ . To correct for differences in cells, the air flow was switched between the two cells and the respective differential values averaged. Each of the eight ambient chambers was sampled once every 17 min. The flow rate through the chamber was determined at the end of the five-day measurement period from the dilution of a known amount of  $\text{CO}_2$  injected into the blower.

NEE determined using enclosures differs from NEE measured in undisturbed conditions, because of increased chamber pressure. Increased pressure in a chamber will reduce soil  $\text{CO}_2$  efflux (Ham *et al.*, 1995; Fang & Moncrieff, 1998), affecting measurements of NEE (Lund *et al.*, 1999). Higher pressure within the chamber results in artificially high rates of net  $\text{CO}_2$  uptake during the day, and low rates of  $\text{CO}_2$  loss at night. This pressurisation effect can be accounted for, if both the soil  $\text{CO}_2$  efflux ( $R_s$ ) and the suppression of soil efflux ( $p$ ) are known.

From a measured  $\text{CO}_2$  differential ( $\Delta\text{CO}_2$ ), flow rate ( $f$ ), ground surface area ( $A$ ) and suppression of soil  $\text{CO}_2$  flux ( $p$ ),  $NEE_O$  was calculated, as:

$$NEE_O (\mu\text{mol m}^{-2}\text{s}^{-1}) = (\Delta\text{CO}_2 \times f/A) + C$$

The suppressed soil  $\text{CO}_2$  efflux,  $C$  ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ), was determined as:

$$C = R_s * p$$

Soil  $\text{CO}_2$  efflux was measured monthly from June 1999 using a closed dynamic system (LI-COR 6400-09). In addition soil temperature at 10 cm depth and soil water content in the first 15 cm were measured and recorded for each instantaneous chamber NEE measurement. The data were used to build an empirical model (Hanson *et al.*, 1999). Soil  $\text{CO}_2$  efflux was controlled both by soil temperature and soil water content. The model was used to calculate soil  $\text{CO}_2$  efflux for each measurement of  $NEE_O$ ,

$$R_s = (R_b Q^{(T_s/10)})(1 - Cf/100)$$

and

$$R_b = \frac{(kW_s R_{\max})}{(kW_s + R_{\max})}$$

Where,  $R_b$  describes the effect of soil water content on  $R_s$ ;  $Q$  is the change in  $R_s$  for a  $10^\circ\text{C}$  temperature change;  $Cf$  is the percentage in volume of soil coarse fraction;  $k$  is a constant describing the change in  $R_b$  for a given change in  $W_s$ , and  $R_{\max}$  is  $R_b$  when  $W_s$  is 100%. Site-specific parameters determined for the model were,  $Cf=0$ ,  $k=0.42$ ,  $Q=2.37$  and  $R_{\max}=1.2$  ( $r^2=0.77$ ).

A series of experiments quantified the increase in chamber pressure and the reduction of soil  $\text{CO}_2$  efflux that resulted when the lids were placed on the chambers. The suppression of soil respiration was determined comparing soil  $\text{CO}_2$  efflux measured on each plot inside the chamber before and after the lids were installed. The suppression factor ( $p$ ) changed in time, ranging from 0.2 to 0.6 and was correlated to soil water content (SWC) ranging from 3 to 8%, following the relationship  $p=0.43 * \ln(\text{SWC}) - 0.24$  ( $P=0.001$ ,  $r^2=0.84$ ), this relationship was used to predict  $p$  at each  $NEE_O$  measurement.

The quality of the data was found to be dependent on wind speed. In nights with low wind speed, the  $\text{CO}_2$  concentration built up heterogeneously in time and space, making flux measurements with an open system difficult. From experiments based on the dilution of a constant flow of  $\text{N}_2\text{O}$  into the chambers, we determined that only wind speeds higher than  $5\text{ ms}^{-1}$  caused outside air to enter the chambers affecting the measurements (data not shown). For these reasons only data with wind speed below  $5\text{ ms}^{-1}$  and night data with wind speed above  $1\text{ m/s}$  were considered valid. On average only 5% ( $\pm 1.3$ ) of the data were rejected because of a wind speed above the threshold.

#### Measurement of NEE. 2: Eddy Covariance

The eddy covariance technique was used to evaluate flux densities of  $\text{CO}_2$  ( $NEE_E$ ), water vapour and sensible heat between the vegetation and the atmosphere. Turbulent

fluctuations were determined from the difference between instantaneous and mean scalar quantities (Aubinet *et al.*, 2000). The scalar concentrations were determined with a closed path IRGA (LI-COR 6262, USA); the wind velocity was measured with a three-dimensional sonic anemometer (R3, Gill Instruments, Lymington, UK), positioned 3.5 m above the soil. Simultaneous measurements of soil heat flux were made with two plates (REBS model HFT-3, Bellevue, WA, USA) buried five centimetres below the soil surface. Net radiation was measured above the vegetation with a net radiometer (Rebs, Bellevue, WA, USA). To prevent over-pressure and water condensation in the sample chamber, air was drawn into the analyser at 9 L/min (Moncrieff *et al.*, 1997). The air inlet tube was protected by a Gelman filter and positioned 10 cm from the anemometer sensors. The tube (4 mm internal diameter and 9 m long) attenuated temperature fluctuations and generated turbulent flow (Leuning & Judd, 1996). The canopy was less than one metre high, therefore the storage of CO<sub>2</sub> was calculated from the difference in CO<sub>2</sub> concentration in time at the measurement height (Greco & Baldocchi, 1996). Data were collected and calculated fluxes were averaged over 30 min intervals. Correction for co-ordinate rotation was applied (Aubinet *et al.*, 2000). The time lag between the anemometer and IRGA signals was calculated by maximising their covariance at 30 min intervals (Baldocchi *et al.*, 1988; Leuning & Judd, 1996). Corrections for damping of fluctuations in gas concentration due to the tube, sensor separation and sampling frequency were less than 15% and were applied to 30 min data, as a function of horizontal wind speed (Aubinet *et al.*, 2000). Night-time data were plotted against friction velocity  $u^*$  to determine if low wind speeds would affect the measurements of carbon fluxes. Below  $u^* = 0.15 \text{ ms}^{-1}$ , NEE data were not considered reliable. Of the total data set 27% ( $\pm 2.7$ ) was discarded because of a  $u^*$  below the threshold.

Above a one metre tall canopy, the 3.5 m measurement height was enough to measure in the internal boundary layer (Monteith & Unsworth, 1990) and to avoid disturbances associated with canopy roughness (Kaimal & Finnegan, 1994). Instrument height also maximised the footprint of the measurements. One concern was that CO<sub>2</sub> emissions from the chambers maintained at elevated atmospheric CO<sub>2</sub> concentrations and located 100 m from the eddy flux instrumentation, would contaminate the eddy flux measurements. This was not a problem because firstly, only 4% of the daytime and 6% of the night wind direction came from the direction of the open-top chambers. Secondly, simulating the area generating 70% of the fluxes for each individual data (Schmid, 1997), the typical dimension was *c.* 100 m during the day and 140 m during the night, due to increased atmospheric

stability. The area of major contribution to the measured fluxes (Schmid, 1997) was between 15 m and 30 m from the tower.

#### *Micrometeorological measurements*

Air temperature, soil temperature, PPF and SWC were measured simultaneously inside and outside the chambers. Air temperature was recorded at 2.5, 1.5, 1, 0.75, 0.5 m, in the centre of one chamber and outside, using shielded, cross-calibrated copper/constantan thermocouples (Omega, CT, USA). Soil temperature ( $T_s$ ) was measured at a depth of 0.01, 0.1 and 0.5 m. Photosynthetic photon flux density (PPFD) was recorded at canopy height in the centre of one chamber and at a height of three metres outside, using cross-calibrated quantum sensors (LI-COR 190S, Lincoln, NB, USA). Soil water content (SWC) was measured in each of the eight chambers and in eight unchambered plots using water content reflectometers integrating over the first 15 cm (CS615, Campbell Scientific, UT, USA). Air vapour pressure deficit (VPD) inside and outside the chambers was calculated using water concentration and air temperature (0.5 m), measured inside and outside the chamber, respectively.

#### *Data Analysis and Comparison*

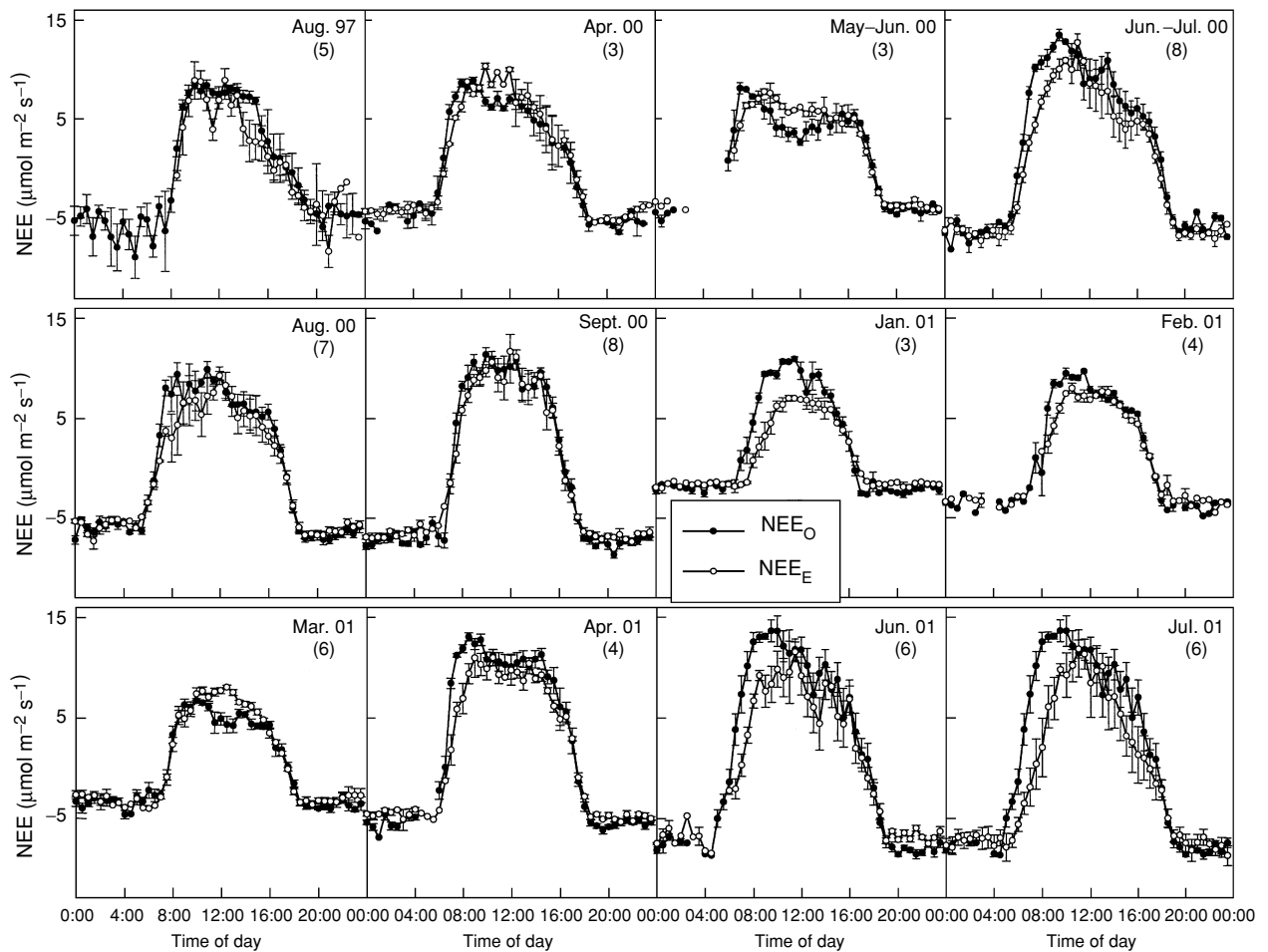
For both measurement techniques, CO<sub>2</sub> uptake by the ecosystem was represented by a positive flux and CO<sub>2</sub> loss by a negative flux. Data comparisons were made for each of the measurement periods averaging carbon fluxes and environmental variables (PPFD,  $T_{\text{air}}$ ,  $T_s$ , VPD, SWC) measured at the same time of day. Secondly by comparing NEE made at a common PPF and  $T_{\text{air}}$ .

The effect of chamber on night NEE,  $T_{\text{air}}$ ,  $T_{\text{soil}}$ , VPD and SWC was analysed using a two tailed student's *t*-test. For statistical analysis of NEE the mean of NEE<sub>O</sub> for the chambers was compared with the simultaneously measured NEE<sub>E</sub>.

## **Results**

For the night and afternoon, NEE<sub>O</sub> was less than 4% different from NEE<sub>E</sub> (Figs 1 and 7). However, NEE<sub>O</sub> was 26% higher than NEE<sub>E</sub> during the morning. Occasionally, clear decreases in NEE were observed inside the chambers over the middle part of the day, compared with less pronounced decreases outside (spring 2000, 2001).

The microclimate within the chamber differed from the climate outside particularly with respect to PPF,  $T_{\text{air}}$  and VPD (Fig. 2a, b, c). During the photoperiod the chamber reduced PPF between 20% and 30%. The average daytime difference in  $T_{\text{air}}$  was  $4 (\pm 0.2) ^\circ\text{C}$ . The temperature difference was greatest during sunny days and



**Fig. 1** Daily trend of  $NEE_E$  (open symbols) and  $NEE_O$  (closed symbols) during twelve measurement periods (August, 1997 and between April, 2000 and July, 2001). Symbols shown are the mean ( $\pm 1$  SE) of measurements made at the same time of day over 3–8 consecutive days (shown in parentheses). Night  $NEE$  data were eliminated when wind and turbulence were lower than, 1 m/s and 0.15 m/s, respectively. Day  $NEE_O$  values were eliminated when wind speed was  $> 5$  m/s, and during rain. Negative numbers represent carbon leaving the ecosystem, positive numbers carbon uptake by the ecosystem.

in spring, with a maximum observed value of *c.* 13 °C (Fig. 2b). The VPD was higher inside the chambers, particularly during the spring (Fig. 2c). The average day-time difference in VPD was 0.7 ( $\pm 0.05$ ) kPa. Differences in  $T_{air}$  and VPD were larger in the afternoon (Fig. 3).

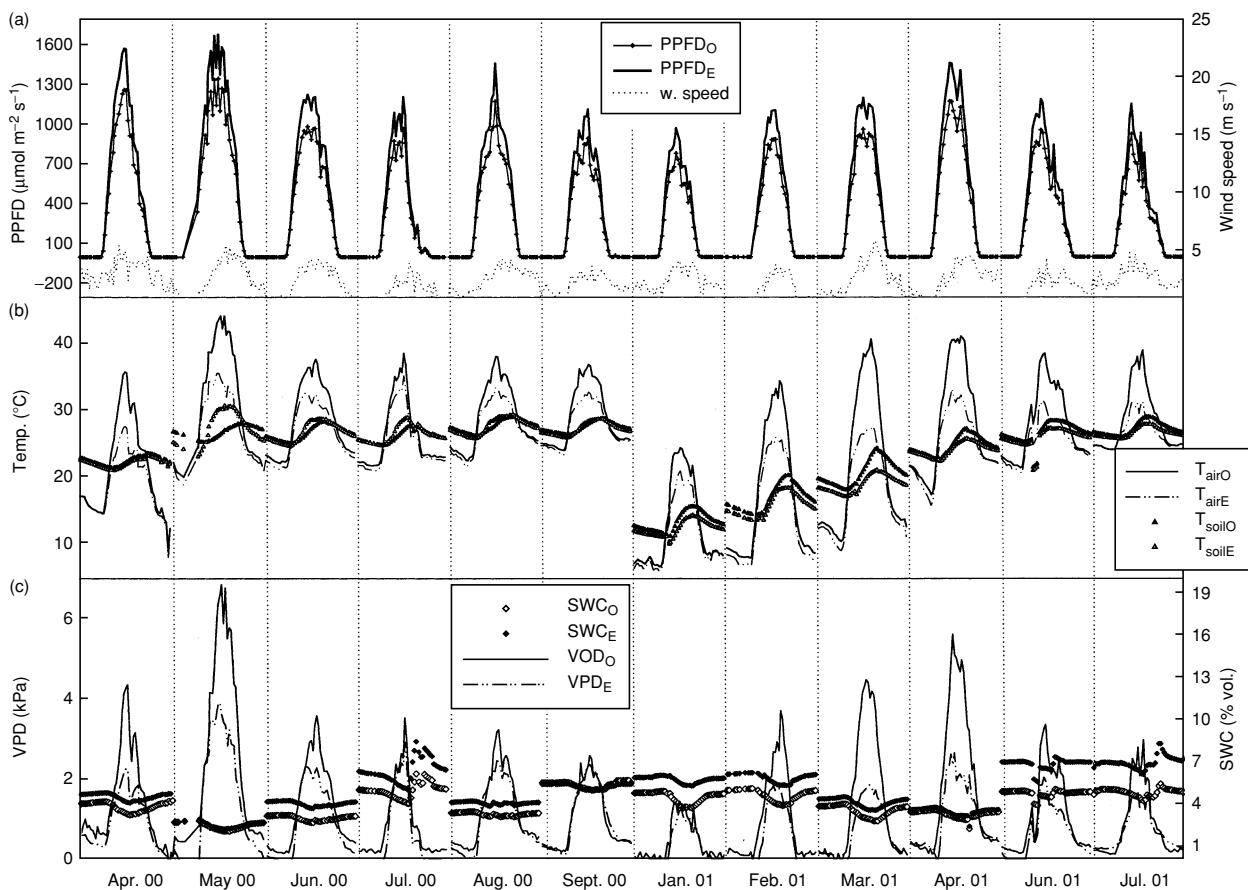
At night the chamber effect on soil, air temperature and VPD was minimal (Fig. 2a, b, c and 3). Night time average differences in soil and air temperature were both 0.6 ( $\pm 0.009$  and  $\pm 0.12$ , respectively) °C, VPD was on average 0.12 ( $\pm 0.04$ ) kPa higher and SWC 0.9 ( $\pm 0.2$ )% higher.

Many of the observed differences in  $NEE$  were consistent with the differences in microclimate. For example  $NEE_O$  was higher than  $NEE_E$  during the morning, or over the mid-day period, when temperature was higher inside the chambers. However, frequently  $NEE_O$  and  $NEE_E$  were in good agreement regardless of differences in microclimate. For example  $NEE_O$  was not always

higher in the morning (August, 1997; April, 2000; September, 2000; March, 2001), and was generally the same in the afternoon. In May 2000 and in March 2001, the decreases in  $NEE_O$  were not explained by a decrease in PPFD or  $T_{air}$  (Fig. 2a, b) and were likely indicative of increased stomatal limitation of photosynthesis. Both periods were characterised by high VPD, with higher values, up to 6 kPa, recorded inside the chambers.

Maximum  $NEE$  ( $NEE_M$ ) was similar for both techniques, except in January, and April–June 2001, when it was 3.5–4  $\mu\text{mol m}^{-2}\text{s}^{-1}$  higher inside the chamber (Fig. 4). The largest difference in  $NEE_M$  was in July, both years. Night respiration and its seasonal variation was not affected by the measurement technique (average differences of less than 1  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ).

At low PPFD the response of  $NEE$  to PPFD differed between measurement techniques: the maximum apparent quantum yield ( $\phi$ ) was always higher in the



**Fig. 2** Mean diurnal pattern in PPFD and wind speed (a), air and soil temperature (respectively 0.5 m and 0.1 m) (b), soil water content and VPD (c), during twelve measurement periods, inside (O) and outside (E) the chambers. Data are the average of the measurements made at the same time of day, over 3–8 consecutive days.

chambers, with an average  $\phi$  of 0.068 ( $\pm 0.007$ ), compared to a  $\phi$  for eddy covariance of 0.035 ( $\pm 0.002$ ). The depression of mid-day  $NEE_O$  was reflected in the response of  $NEE_O$  to PPFD, where  $NEE_O$  decreased at high PPFD, when temperature and VPD inside the chamber were high (Fig. 5). At all PPFD levels,  $T_{\text{air}}$  was always higher inside the chambers.

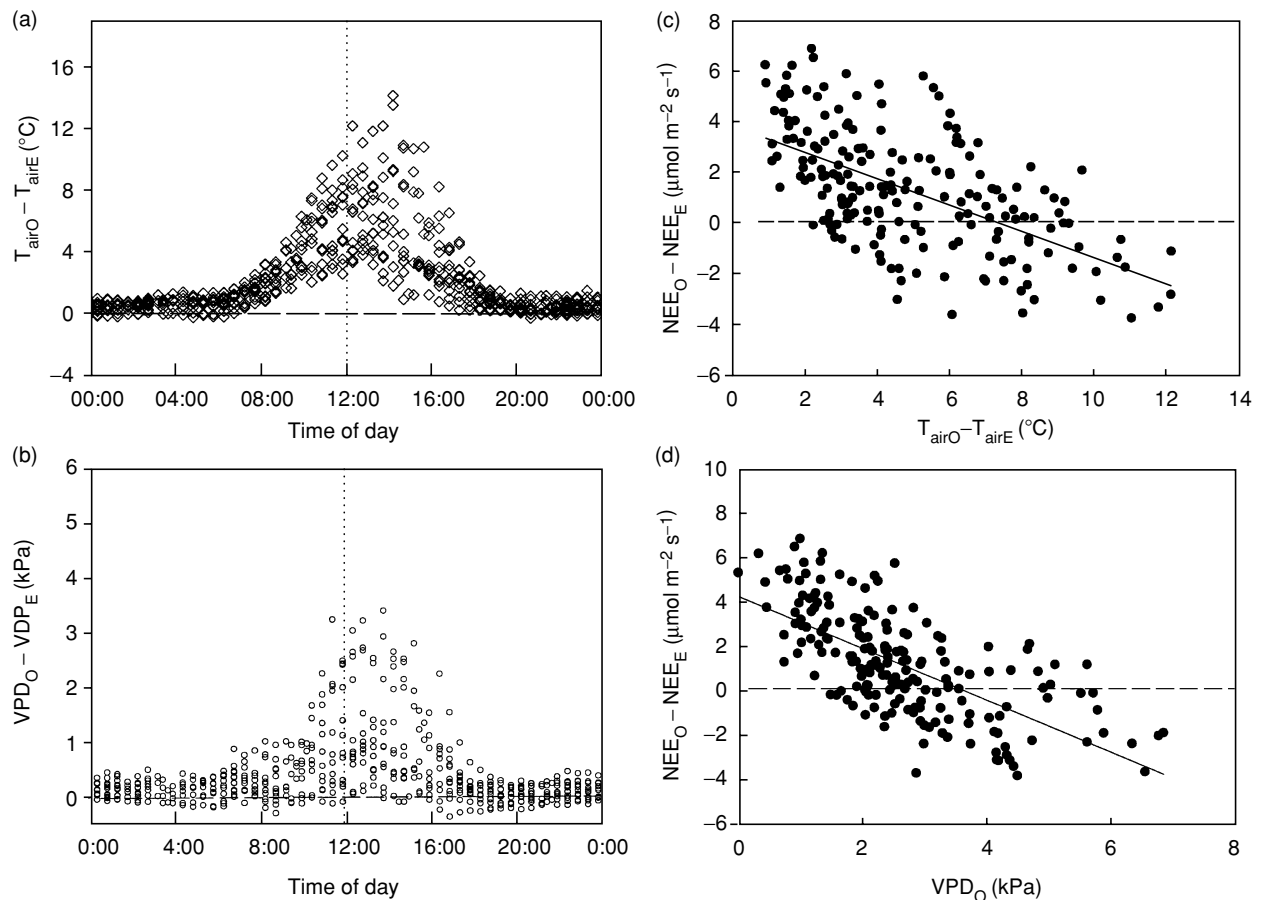
At high temperatures,  $NEE_O$  was not stimulated (e.g. April, 2001) or even decreased (e.g. May, 2000) by increased  $T_{\text{air}}$  inside the chambers. Even if at a common  $T_{\text{air}}$  PPFD was lower inside the chambers, at light saturation  $NEE_O$  and  $NEE_E$  measured at the same  $T_{\text{air}}$  were the same (Fig. 6).

Differences between  $NEE_O$  and  $NEE_E$  were partially dependent on the increase in  $T_{\text{air}}$  (Fig. 3c,  $r^2 = 0.35$ ,  $P < 0.01$ ) and absolute VPD inside the chambers (Fig. 3d,  $r^2 = 0.45$ ,  $P < 0.01$ ). Heterogeneity in the fetch measured by the eddy covariance system could explain a variability in the agreement between the two techniques, however, the NEE difference was not dependent on wind direction ( $r^2 = 0.06$ ,  $P < 0.01$ , data not shown).

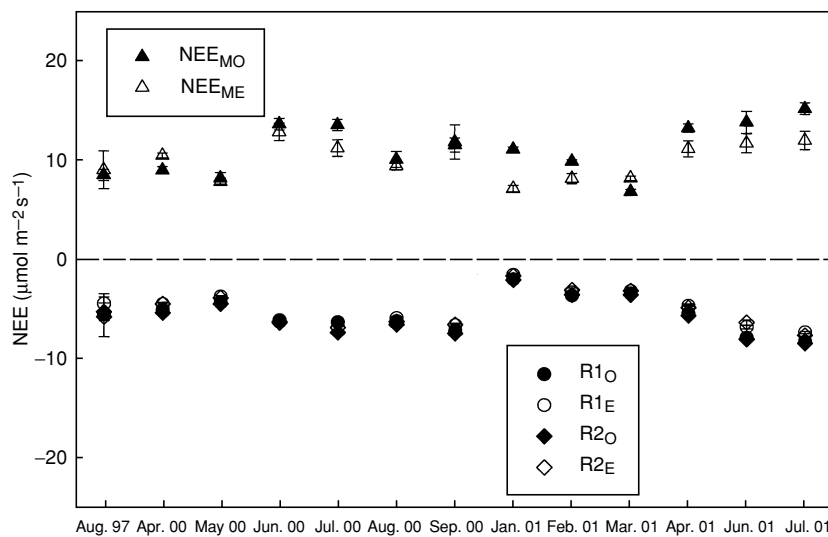
Plotting all 30 minute averages of  $NEE_O$  against  $NEE_E$ , shows that  $NEE_O$  is 10% higher than  $NEE_E$  (intercept  $-0.4$ ,  $r^2 = 0.93$ ), over the 24 h period. During the night  $NEE_O$  is only 4% higher, during the morning 26% and during the afternoon 2% lower (Fig. 7).

## Discussion

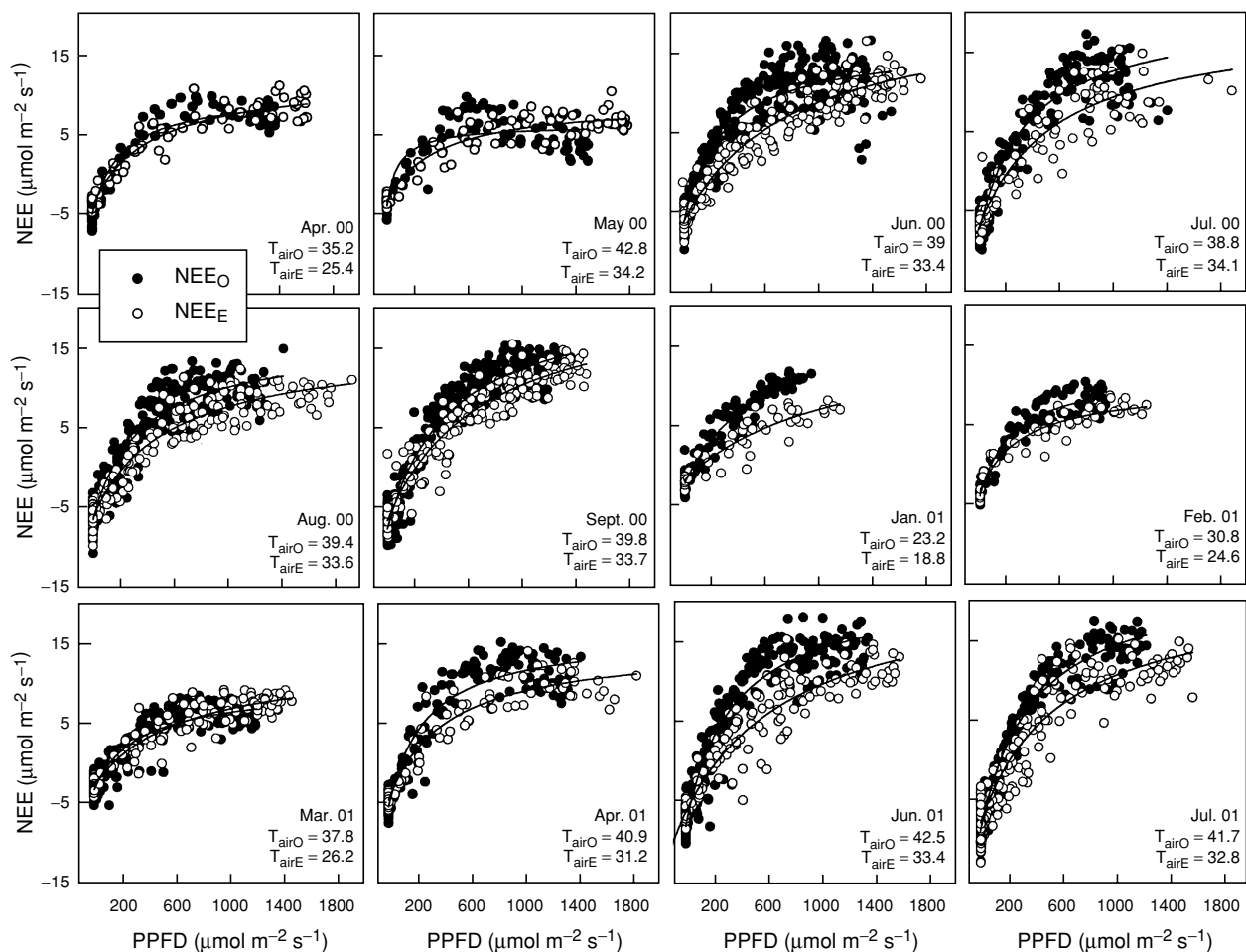
This study compared NEE, measured simultaneously using chambers ( $NEE_O$ ) and eddy covariance ( $NEE_E$ ), in the same scrub-oak palmetto ecosystem, in an attempt to cross-validate the two techniques. For measurements made over 15 months, the 24 h diurnal cycles were characterised by: (i) night respiration measurements that were unaffected by measurement technique; (ii) morning  $NEE_O$  higher than  $NEE_E$ ; (iii) a mid-day and afternoon period in which the differences between  $NEE_O$  and  $NEE_E$  were reduced. These findings will be discussed with respect to the effects of the chambers on the microclimate, and their complex interactions with NEE.



**Fig. 3** The 24 h distribution of temperature difference ( $T_{\text{airO}} - T_{\text{airE}}$ ) (a) and VPD difference ( $\text{VPD}_O - \text{VPD}_E$ ) (b). Differences are calculated from the 30-min averages of all measurement periods. Also shown is the response of the NEE difference ( $\text{NEE}_O - \text{NEE}_E$ ) for a change in the temperature difference ( $T_{\text{airO}} - T_{\text{airE}}$ ) (c) or in VPD inside the chamber (d). Data are limited to  $\text{PPFD} > 500 \mu\text{mol m}^{-2} \text{s}^{-1}$ .



**Fig. 4** A comparison of maximum NEE and night ecosystem respiration measured by eddy covariance and chambers in thirteen measurement periods between 1997 and 2000. Subscript O indicates measurements made inside the chambers, subscript E by eddy covariance. The maximum NEE ( $\text{NEE}_{\text{MO}}$ ,  $\text{NEE}_{\text{ME}}$ ) represents the maximum observed values of the 30-min average NEE. Night ecosystem respiration was calculated as the average value over the measurement period ( $\text{R2}_O$ ,  $\text{R2}_E$ ), and as intercept of the light response curve ( $\text{R1}_O$ ,  $\text{R1}_E$ ) (Ruimy *et al.*, 1995).



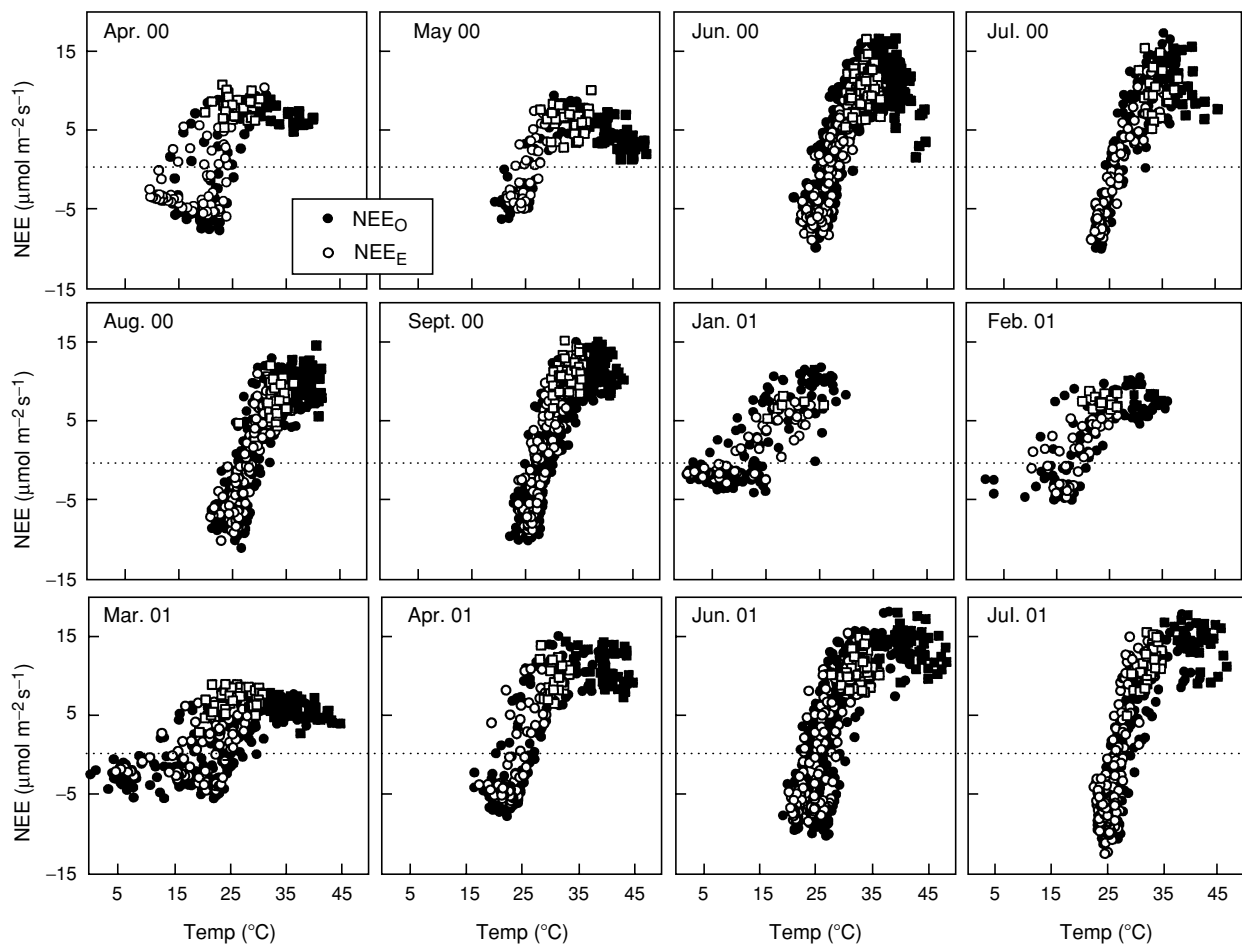
**Fig. 5** Relationships between instantaneous  $NEE_E$  (open symbols) and  $NEE_O$  (solid symbols) and PPFD. For  $NEE_O$  open symbols represent the mean ( $\pm 1$  SE) of measurements made in eight replicate chambers. A non-rectangular hyperbola has been fitted to the response of NEE to PPFD for each data set (solid line) (Ruimy *et al.*, 1995). For each measurement period, air temperature for PPFD  $> 1000 \mu\text{mol m}^{-2}\text{s}^{-1}$ , inside ( $T_{airO}$ ) and outside ( $T_{airE}$ ) the chambers, is also shown.

At night  $NEE_E$  and  $NEE_O$  were the same, as was their seasonal variation. The similarity in measured fluxes was consistent with a similarity in microclimate, which was minimally affected by the chambers at night. Because of problems in determining night-time fluxes using eddy covariance when the atmospheric turbulence is reduced (Fan *et al.*, 1995; Grace *et al.*, 1996), chamber measurements are viewed as an important tool to complement measurements. (Goulden 1996; Law *et al.*, 1999; Falge *et al.*, 2001). But, in this study, low wind speeds at night, leading to large heterogeneous fluctuations in  $\text{CO}_2$  concentration, limited both measurement techniques. However, the ability to measure NEE using chambers at night can be increased with improvements in the system design, such as drawing air from high above the canopy where  $\text{CO}_2$  concentration is less variable, or using buffer volumes that would dampen out  $\text{CO}_2$  fluctuations.

For measurements made during the day, the value of the comparison was minimised by important and interacting effects of the chamber on the microclimate. During the morning  $NEE_O$  was typically higher than  $NEE_E$ . Several possible mechanisms could be responsible for this response, and attributing this phenomenon to a particular process was not possible.

In the morning, increased  $T_{air}$  inside the chamber could increase photosynthesis, even at low light. For data collected when PPFD was between 200 and  $400 \mu\text{mol m}^{-2}\text{s}^{-1}$ , the difference between  $T_{airO}$  and  $T_{airE}$  was around  $2^\circ\text{C}$ , being highest in January 2001 ( $5^\circ\text{C}$ ) and lowest in February 2001 ( $0.43^\circ\text{C}$ ). Not only did the difference between  $T_{airO}$  and  $T_{airE}$  change over the seasons, but also did its effect on NEE, because of a different initial slope of the relationship between NEE and  $T_{air}$ . If, for each measurement period, the average increase in  $T_{air}$





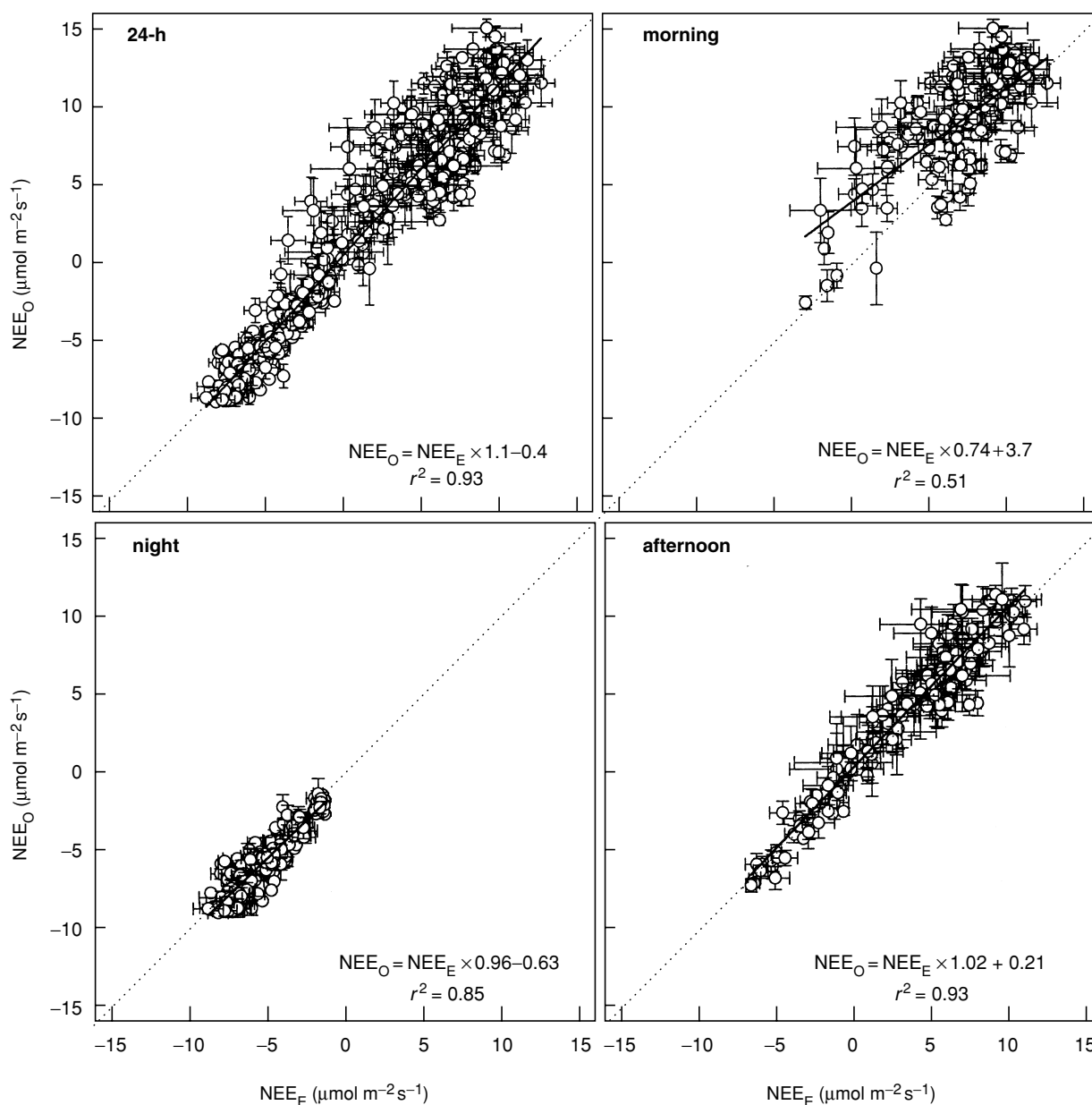
**Fig. 6** Relationship between instantaneous  $NEE_E$  (open symbols) and  $NEE_O$  (solid symbols) and  $T_{air}$ , measured outside and inside the chambers, respectively. For  $NEE_O$  closed symbols represent the mean ( $\pm 1$  SE) of measurements made in eight replicate chambers. Square symbols represent light saturated values ( $PPFD > 1000 \mu\text{mol m}^{-2}\text{s}^{-1}$ ).

(PPFD between 200 and  $400 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) was calculated and from this the corresponding increase in NEE, in 9 of 12 measurement periods the calculated NEE difference was higher than the measured NEE difference. This suggested that increased  $T_{air}$  could account for the increase in  $NEE_O$  during the morning.

This finding does not exclude the involvement of other mechanisms, for example dew formation and in general the different energy and water fluxes, or the increased proportion of diffuse light inside the chambers. (Denmead, 1991; Tenhunen *et al.*, 1990; Hollinger *et al.*, 1994; Fan *et al.*, 1999; Granier *et al.*, 2000).

In the afternoon, the increase of the differences in VPD and  $T_{air}$  (Fig. 3a, b) shows a change in chamber microclimate with possible counteracting effects on NEE. Over the mid-day period and during the afternoon the differences between  $NEE_O$  and  $NEE_E$  were reduced, even though  $T_{air}$  was higher inside the chambers (Figs. 2a and 3a). This was because the response of NEE to  $T_{air}$  was

similar for both measurement techniques and had a light saturated NEE with a broad temperature optimum (Fig. 6). For example, in March 2001, the maximum  $NEE_O$  of  $c. 6 \mu\text{mol m}^{-2}\text{s}^{-1}$  corresponds to a temperature ranging from 20 to  $40^\circ\text{C}$ . Each measurement period, at low light ( $200\text{--}400 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) the difference in temperature was small, but the response of NEE to temperature was very high. However, at saturated light ( $> 1000 \mu\text{mol m}^{-2}\text{s}^{-1}$ ), a large  $T_{air}$  difference had no clear effect on NEE (Fig. 6). This broad temperature optimum could be due to a higher  $Q_{10}$  for respiration processes or it may reflect a limitation on photosynthesis. The afternoon increases in VPD inside the chambers (Fig. 3b) could limit the carbon uptake via stomata closure, counteracting any positive effects of the chambers on microclimate. Temperatures above the optimum level could also cause a decrease in carbon uptake. The limitation of VPD on  $NEE_O$  is clearly shown by the depression of mid-day  $NEE_O$  in April, May, 2000 and March, 2001 (Figs 1, 3 and 4).



**Fig. 7** Relationship between 30-min daily average of  $NEE_O$  and  $NEE_E$  of all the measurement periods ( $\pm 1$  SE) for all data collected (24 hours); data between 7:00 and 12:30 (*morning*); between 12:30 and 19:00 (*afternoon*) and when PPFD is below  $10 \mu\text{mol m}^{-2} \text{s}^{-1}$  (*night*). The parameters obtained fitting the data with a linear relationship are also shown.

For the light, at each light level,  $T_{\text{air}}$  inside the chambers was higher than outside. More useful was the comparison of the response of NEE to temperature, which showed that the relationship was similar for the two techniques, particularly when temperature was the only driving factor, during night-time and at light saturation (Fig. 6). The similar NEE responses to temperature inside and outside the chambers, showed that when similar temperature conditions are met, similar fluxes are measured.

The effect of the chambers on temperature may reflect the various interacting environmental factors.

The aim of this study was to provide a cross validation of NEE measured using chambers and eddy covariance. This study was unique in that three important criteria enabling the two measurements of NEE to be directly compared were fulfilled. (i) The large replicated open-top chambers enclosed a representative portion of the ecosystem. (ii) Measurements were made simultaneously.

(iii) Measurements were made in the same stand. The importance of the comparison was greatest at night, when microclimate differences were minimised. Under these conditions the two techniques measured the same NEE. It is at night when low wind speed and turbulence make the eddy covariance less reliable, that the chambers may provide a way to gap fill eddy covariance datasets. The value of this study was lower during the day, when interacting microclimate differences confound the comparison of the techniques.

### Acknowledgements

We thank Hans Anderson and Giovanni Manca for their skilled technical assistance. This work was performed while the S.D. held a National Research Council Research Associateship award at NASA/Kennedy Space Center.

### References

- Aubinet M, Grelle A, Ibrom A *et al.* (2000) Estimates of the annual net carbon and water exchange of forests: The EUROFLUX Methodology. *Advances in Ecological Research*, **30**, 113–175.
- Baldocchi DD, Hicks BB, Meyers TP (1988) Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology*, **69**, 1331–1340.
- Baldocchi D, Valentini R, Running S *et al.* (1996) Strategies for measuring and modelling carbon dioxide and water vapour fluxes over terrestrial ecosystems. *Global Change Biology*, **2**, 159–169.
- Ciais P, Tans PP, Trolier M *et al.* (1995) A large northern hemisphere terrestrial CO<sub>2</sub> sink indicated by 13C/12C ratio of atmospheric CO<sub>2</sub>. *Science*, **269**, 1096–1102.
- Denmead OT (1991) Sources and sinks of greenhouse gases in the soil–plant environment. *Vegetatio*, **91**, 73–86.
- Denning AS, Fung IY, Randall D (1995) Latitudinal gradient of atmospheric CO<sub>2</sub> due to seasonal changes with land biota. *Nature*, **376**, 240–243.
- Dijkstra P, Hymus GJ, Colavito D *et al.* (2002) Elevated atmospheric CO<sub>2</sub> stimulates shoot growth in a Florida scrub oak ecosystem. *Global Change Biology*, **8**, 90–103.
- Dixon RK, Brown S, Houghton RA *et al.* (1994) Carbon pools and flux of global forest ecosystems. *Science*, **263**, 185–190.
- Drake BG, Muehe MS, Peresta G *et al.* (1996) Acclimation of photosynthesis, respiration and ecosystem carbon flux of a wetland on Chesapeake Bay, Maryland, to elevated atmospheric CO<sub>2</sub> concentration. *Plant and Soil*, **187**, 111–118.
- Falge E, Baldocchi D, Olson R *et al.* (2001) Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agricultural and Forest Meteorology*, **107**, 43–69.
- Fan SM, Goulden ML, Munger JW *et al.* (1995) Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: a growing season of whole-ecosystem exchange measurements by eddy correlation. *Oecologia*, **102**, 443–452.
- Fang C, Moncrieff JB (1998) An open-top chamber for measuring soil respiration and the influence of pressure difference on CO<sub>2</sub> efflux measurement. *Functional Ecology*, **12**, 319–325.
- Goulden ML, Munger JW, Fan S-M *et al.* (1996) Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Global Change Biology*, **2**, 169–182.
- Grace J, Mahli Y, Lloyd J *et al.* (1996) The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. *Global Change Biology*, **2**, 209–217.
- Granier A, Ceschia E, Damesin C *et al.* (2000) The carbon balance of a young Beech forest. *Functional Ecology*, **14**, 312–325.
- Greco S, Baldocchi DD (1996) Seasonal variations of CO<sub>2</sub> and water vapour exchange rates over a temperate deciduous forest. *Global Change Biology*, **2**, 183–198.
- Ham JM, Owensby CE, Coyne PI *et al.* (1995) Fluxes of CO<sub>2</sub> and water vapour from a prairie ecosystem exposed to ambient and elevated CO<sub>2</sub>. *Agricultural and Forest Meteorology*, **77**, 73–93.
- Hanson PJ, Wullschlegler SD, Bohlman SA *et al.* (1993) Seasonal and topographic patterns of forest floor CO<sub>2</sub> efflux from upland oak forest. *Tree Physiology*, **13**, 1–15.
- Hollinger DY, Kelliher FM, Byers JN *et al.* (1994) Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology*, **75**, 134–150.
- Kaimal JC, Finnegan JJ (1994) *Atmospheric Boundary Layer Flows. Their Structure and Measurement*. Oxford University Press, Oxford.
- Lavigne MB, Ryan MG, Anderson DE *et al.* (1997) Comparing nocturnal eddy covariance measurements to estimates of ecosystems respiration made by scaling chambers measurements at six coniferous boreal sites. *Journal of Geophysical Research*, **102**, 28977–28985.
- Law BE, Ryan MG, Anthoni M (1999) Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biology*, **5**, 169–182.
- Leuning R, Judd JM (1996) The relative merits of open and closed-path analysers for measurements of eddy fluxes. *Global Change Biology*, **2**, 241–253.
- LI-COR (1996) *LI-6262 CO<sub>2</sub>/H<sub>2</sub>O Analyser Operating and Service Manual*. Publication Number 9003–59.
- Lloyd J (1999) The CO<sub>2</sub> dependence of photosynthesis, plant growth responses to elevated CO<sub>2</sub> concentrations and their interaction with soil nutrient status, II. Temperate and boreal forest productivity and the combined effects of increasing CO<sub>2</sub> concentration and increased nitrogen deposition at a global scale. *Functional Ecology*, **13**, 439–459.
- Lund CP, Riley WJ, Pierce LL *et al.* (1999) The effects of chamber pressurisation on soil-surface CO<sub>2</sub> flux and the implications for NEE measurements under elevated CO<sub>2</sub>. *Global Change Biology*, **5**, 269–281.
- Mahli Y, Baldocchi DD, Jarvis PG (1999) The carbon balance of tropical, temperate and boreal forests. *Plant, Cell and Environment*, **22**, 715–740.
- Mailander JL (1990) *Climate of the Kennedy Space Center and vicinity*. NASA Technical Memorandum. 103498 Florida.
- Moncrieff JB, Mahli Y, Leuning R (1996) The propagation of errors in long-term measurements of land atmosphere fluxes of carbon and water. *Global Change Biology*, **2**, 231–241.
- Moncrieff JB, Massheder JM, de Bruin H *et al.* (1997) A system to measure surface fluxes of momentum, sensible heat, water vapour and carbon dioxide. *Journal of Hydrology*, **188**, 589–611.

- Monteith JL, Unsworth MH (1990) *Principles of Environmental Physics*. Edward Arnold, London.
- Niklaus PA, Stocker R, Koerner CH *et al.* (2000) CO<sub>2</sub> flux estimates tend to overestimate ecosystem C sequestration at elevated CO<sub>2</sub>. *Functional Ecology*, **14**, 546–559.
- Norby RJ, Wullschlegel SD, Gunderson CA *et al.* (1999) Tree responses to rising CO<sub>2</sub> in field experiments: implications for the future forest. *Plant, Cell and Environment.*, **22**, 683–714.
- Ruimy A, Jarvis PG, Baldocchi DD *et al.* (1995) CO<sub>2</sub> fluxes over plant canopies and solar radiation: a review. *Advances in Ecological Research*, **26**, 1–68.
- Ruimy A, Kergoat L, Field CB *et al.* (1996) The use of CO<sub>2</sub> flux measurements in models of the terrestrial carbon budget. *Global Change Biology*, **2**, 287–296.
- Schmalzer PA, Hinkle CR (1992) Species composition and structure of Oak-Palmetto scrub vegetation. *Castanea*, **57**, 220–251.
- Schmid HP (1997) Experimental design for flux measurements: matching the scale of the observations to the scale of the flux. *Agricultural and Forest Meteorology*, **87**, 179–200.
- Stocker R, Leadley PW, Körner C (1997) Carbon and water fluxes in a calcareous grassland under elevated CO<sub>2</sub>. *Functional Ecology*, **11**, 222–230.
- Tenhunen JD, Sala Serra A, Harley PC *et al.* (1990) Factors influencing carbon fixation and water use by Mediterranean Sclerophyll shrubs during summer drought. *Oecologia*, **82**, 381–393.
- Valentini R, de Angelis P, Matteucci G *et al.* (1996) Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. *Global Change Biology*, **2**, 199–208.
- Valentini R, Matteucci G, Dolman AJ *et al.* (2000) Respiration as the main determinant of European forest Carbon balance. *Nature*, **404**, 864.
- Van Oijen M, Schapendonk AHCM, Jansen MJH *et al.* (1999) Do open-top chambers overestimate the effects of rising CO<sub>2</sub> on plants? An analysis using spring wheat. *Global Change Biology*, **5**, 411–421.
- Wofsy SC, Goulden ML, Munger JW *et al.* (1993) Net exchange of CO<sub>2</sub> in a mid-latitude temperate forest. *Science*, **260**, 1314–1317.