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High quality, continuous measurements of CO_2 in Biosphere 2 to assess whole mesocosm carbon cycling

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Abstract

Accurate measurements of atmospheric CO_2 concentrations are performed routinely in a variety of experimental settings including open fields and forests, leaf gas-exchange chambers, phytotrons and specialized growth chambers. However, the accurate monitoring of large scale structurally and biologically complex experimental systems, operating as materially closed systems, is not widely reported. Here we report the design elements, material specifications and other details for high precision monitoring of CO_2 in Biosphere 2, a large scale ecologically diverse experimental facility located in Oracle, AZ. The results are used to illustrate how carbon balance in a temporarily isolated sub-system of the facility is used to assess carbon dynamics under different environmental conditions such as variable atmospheric CO_2 levels, temperature, light, and soil moisture. The analytical system described here should be applicable for any settings in which continuous, high accuracy measurements of CO_2 in a complex system are needed for quantitative research.

Keywords: Biosphere 2; Carbon balance; Carbon dioxide; Flux monitoring; Ecosystem carbon uptake; Respiration

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1. Introduction

High accuracy measurements of CO_2 in the earth's atmosphere provide important insights into the complex processes that set the global balance between terrestrial and oceanic carbon fluxes (Conway et al., 1994). Measurements of CO_2 are made on considerably smaller scales including the atmosphere above crop canopies employed in the free air CO_2 enrichment (FACE) approach (Hartwell, 1992), CO_2 flux over selected areas of forest (Wofsy et al., 1993) and a wide variety of growth chambers (Strain, 1991; Hartwell et al., 1992; Sinclair et al., 1995). Recent reports have addressed the question of high accuracy monitoring of CO_2 in closed, ecologically and structurally complex facilities for the purpose of quantifying CO_2 flux (Wheeler, 1992; Gitelson and Okladnikov, 1994; Jenkins and Wright, 1995; Lawton, 1996). Here we describe a CO_2 monitoring system for the Biosphere 2 facility that can be used for a variety of purposes including studies of carbon cycling within individual mesocosms.

Biosphere 2 is structurally complex and contains large scale synthetic communities (mesocosms) representing desert, rain forest and savanna ecosystems. The large rooting volumes and growing space in Biosphere 2 allow growth of major vegetation forms and functional types, typical of the analog ecosystems on earth (annual grass, perennial grass, shrub, tree, vine; see companion papers in this issue). Biosphere 2 is used as a large gas-exchange chamber to measure net ecosystem exchange of carbon (NEE) in the sealed mesocosms under different CO_2 levels. After correcting for changes in soil CO_2 efflux and plant respiration, estimated from the night-NEE, we show that the whole system carbon assimilation rate increases with increasing levels of atmospheric CO_2. The ability to control the environmental conditions in each mesocosm offers a unique opportunity to study the cycling of CO_2 as a function of atmospheric CO_2 concentration, temperature, rainfall, nutrients, biomass and other factors. In these experiments Biosphere 2 is treated as a large gas-exchange chamber to measure NEE within the whole system and its subsystems.

The current design reflects our experience with the previous CO_2 monitoring system, operated at Biosphere 2 between 1991 and 1994. The first system was based on industrial-type instrumentation, primarily PRIVA sensors (Model APBA-250E; 0–3000 ppmV), with a stated accuracy of $\pm 10\%$ at full scale. This system was calibrated manually every 3 months resulting in significant errors due to instrumental drifts (up to a few hundred ppmV over 3 months). Consequently, the historic record for Biosphere 2 under materially closed conditions remains uncertain. In this paper we describe the design, implementation and performance of the new CO_2 monitoring system recently installed in Biosphere 2. The system, based on a LI-COR gas analyzer, has an automated sample introduction unit allowing high resolution study of the spatial variability within a canopy. It also has an automated calibration and drift correction routine to assure that small differences in carbon flux (e.g. trends in night time respiration) can be unambiguously resolved. Finally, we illustrate an application of the observed data to understanding carbon cycling in the Biosphere 2 rainforest mesocosm.

2. The CO_2 monitoring system

2.1. General design

The CO_2 analytical system was designed to meet three criteria: (1) provide continuous, high resolution CO_2 measurements from each of the mesocosms; (2) contain a multiport sample introduction unit which offers the capability of assessing the spatial variability within a mesocosm (e.g. for studying canopy structure); and (3) include an automated standardization and drift correction protocol. An automated standardization system assures not only the quality of the data but also reduces routine maintenance of these systems.

Two different designs were considered: (1) a central analytical system, with sample lines extending to the mesocosms; and (2) independent units located in each mesocosm or, alternatively, centralization of the standards around multiple analytical units. A single unit, while significantly cheaper, would have limited both the spatial and temporal resolution of sampling within a mesocosm due to the relatively long residence time of air from the sample inlet to the analyzer. Likewise, it would limit the system capability for obtaining readings from all mesocosms simultaneously. Therefore, we preferred the latter option. Independent systems, located in specific mesocosms, minimized the samples travel time due to the proximity of the CO_2 analyzer to the sample inlet, thereby offering greater temporal resolution. Also, shorter sample and standard lines reduced the likelihood of leaks, and simplified plumbing tasks as all bulkhead penetrations were eliminated. All the analyzers were installed in weatherproof boxes (NEMA 3X) in order to shield them from the relatively harsh climatic conditions. In the case of the rainforest mesocosm, a small air conditioner was installed in the cabinet to minimize heat related perturbations of the system.

The conceptual design of the CO_2 monitoring system is based on the design of the LDEO Underway pCO_2 System (LDEO-technical report). The system consists of two components: an IR gas analyzer (IRGA) and a sample introduction unit. The CO_2 analyzers are differential, non-dispersive, infrared gas analyzers (LI-COR model 6262, Lincoln, NB). Measurements are based on the difference in the absorption of infrared radiation between a reference cell and the sample cell. The CO_2 detector is tuned to the 4.26 μm absorption band, and provides excellent rejection of other IR absorbing gases (LI-COR manual 9003-59). The instrumental accuracy of IR gas analyzers is affected by variations in temperature, the air's water content and barometric pressure. The LI-6262 model has built-in correction factors, applied to the linearized channel, to account for variations in temperature, pH_2O and pressure throughout a CO_2 concentration range of 0 to 3000 ppmV (i.e. 0–5 V), thereby allowing precise analysis of wet air. Nonetheless, we chose to dry the air before the analysis. The decision to dry the air, which may seem unjustifiable in view of the built-in corrections of the LI-6262, stems from our resolve to collect both raw and processed data in order to have a complete redundancy in data acquisition. Because the above corrections apply only to the linearized channel and not to the raw data, the decision had two major implications for the system design:

(1) it required frequent, five standard, calibration cycles (see below); and (2) the air needed to be dried because samples are matched against dry standards (including dry N_2 as the reference gas); an apparent CO_2 difference may be seen if water vapor is in the sample stream but absent from the reference side. Such variations are particularly important in environments with high and variable water content as exist in Biosphere 2 where the relative humidity between different mesocosms varies between 40 and 90% and exhibits large diurnal fluctuations. Also, because the raw data are not corrected for differences in flow between the sample and reference gases, which may cause pressure differentials, an optional pressure transducer (LI-6262-03) was added to account for and correct this effect. As we show below, this configuration allows the computation of accurate CO_2 concentrations from the raw data, independently from processed values obtained from the linearized channel. While it may not seem cost-effective, this redundancy saved weeks of data when an intermittent ground-fault contaminated the linearized channel feed.

2.2. Sample introduction

Each mesocosm is sampled at three inlets: the basement, the plant canopy, and at the top near the spaceframe. When the wilderness is in a flow-through mode (i.e. flushing with outside air to manipulate internal CO_2 levels) the basement inlet of the desert analyzer samples the incoming air through the south lung and the rainforest analyzer the outgoing air via an exhaust fan in the rain forest (Fig. 1). Samples are drawn continuously into the analyzer through 1/4 inch Dekoron tubing (type 1300, Dekoron, Aurora, OH) specified because of its non-diffusivity to CO_2. Each of the three lines is flushed by individual 4.5 l/min pumps (KNF Neuberger, Trenton, NJ), so that residence time is on the order of 5 s (Fig. 2). Water traps before the pumps serve to reduce the airs humidity. In order to make flows through the IRGA adjustable, and to avoid pumping into a closed line when the valve is shut, a set of needle valves were connected to shunt lines (Fig. 2). Most of the flow is directed through this shunt, leaving only 40–50 ml/min to be sent to the IRGA. Regulated, pressurized gas cylinders supply flow from the five standards for calibration. The three samples and five standard gases are routed through an 8-port electronic valve (Valco Instruments, Houston, TX). The path for the gas then continues through a normally-closed solenoid, a 20–100 ml/min electronic flowmeter (McMillan, Georgetown, TX), the perma pure dryer (Perma Pure, Toms River, NJ) and a filter (0.45 μm) before entering the IRGA. These ancillary devices function, respectively, to protect the system from power disruptions, to flag the operator when pumps malfunction, and to assure that the IRGA cells are free from debris and water vapor contamination. Since the solenoid will shut off when de-energized, it can prevent losing the contents of a standard gas if a power failure occurs during a calibration run. Note that we use N_2 gas as a 'zero air' standard, reference gas and a dry carrier gas for the Perma Pure Dryer (Fig. 2). The dryer consists of a set of coaxial tubes where wet air passes through the inner tube, made of a semi-permeable material, and there is a counter flow of dry gas in the external tube. Water diffuses through the membrane along the gradient in water vapor pressure between the two gases thereby drying the air sample.

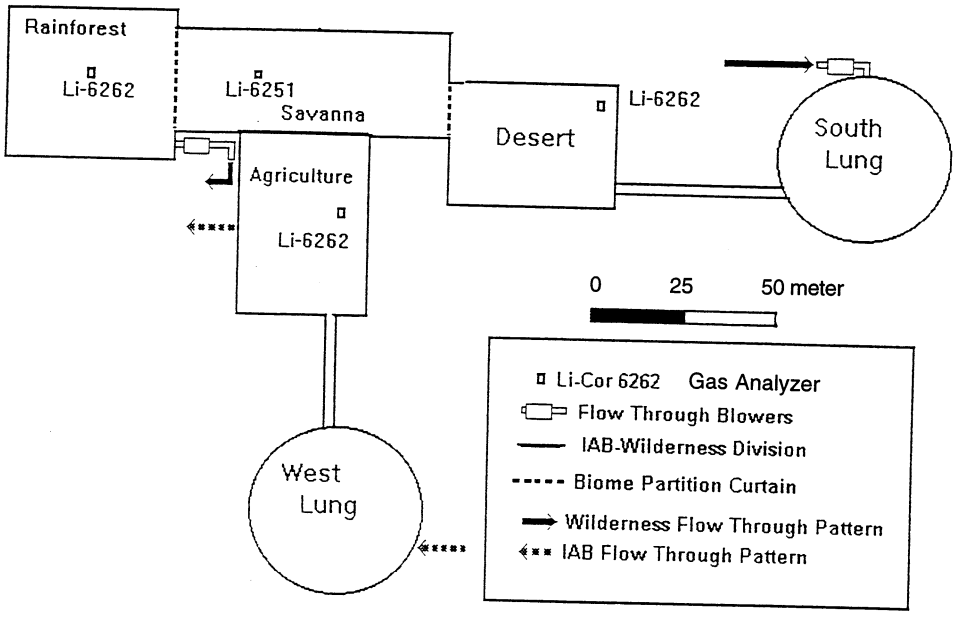

Fig. 1. A schematic floor plan of Biosphere 2 showing the four mesocosms: Desert, DES; savanna, SAV; and rainforest, TRF in the wilderness area and the intensive agriculture mesocosm (IAB). Note the locations of the CO_2 analyzers. The wilderness and agriculture sections are permanently separated while the desert and rainforest mesocosms can be temporarily sealed with plastic curtains (dashed lines). Two separate systems of fans allow independent flushing of the wilderness (through the south lung) and agriculture (through the west lung) sections with outside air as a means of controlling internal CO_2 levels.

2.3. Data acquisition and processing

In the current configuration, three samples and five standards (including a 'zero standard') are routed into the 8-port electronic valve. The measuring sequence, currently ten cycles of air samples (each includes the three sample inlets) followed by a calibration cycle of the five reference gases, is controlled by a BASIC program (available upon request). A reading is taken approximately every 5 min. For each of the eight valve positions the following variables are recorded during a measurement: the time stamp, the valve position, the raw volt signal from the IRGA, the processed value from the raw channel (calculated from the calibration curve as described below); the linearized data (mV and ppm), the IRGA cell temperature, water vapor content, barometric pressure and air flow. Since we sample each port approximately every 5 min, each analyzer produces daily a data matrix of 10 by about 300. This data array has a built-in redundancy allowing data recovery in case of failure.

The raw data are converted to CO_2 concentrations using a third order polynomial curve fit to five reference standards (referred to henceforth as the working

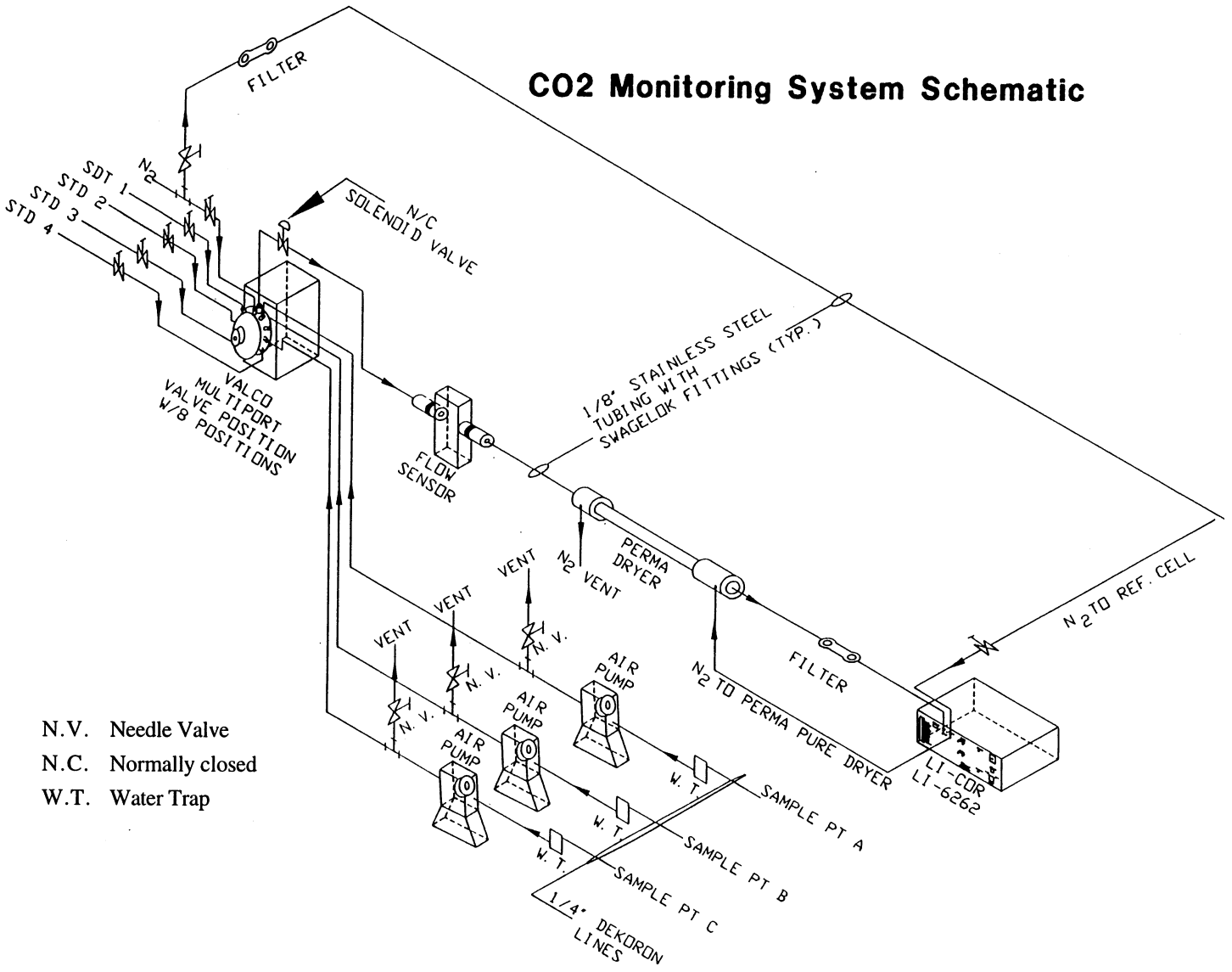
CO2 Monitoring System Schematic
FILTER
SDT 1
STD 2
STD 3
STD 4
N2
N/C SOLENOID VALVE
VALCO MULTIPORT VALVE POSITION W/8 POSITIONS
FLOW SENSOR
1/8" STAINLESS STEEL TUBING WITH SWAGELOK FITTINGS (TYP.)
PERMA DRYER
N2 VENT
VENT
VENT
VENT
N.V.
N.V.
N.V.
N.V.
AIR PUMP
AIR PUMP
AIR PUMP
N2 TO PERMA PURE DRYER
FILTER
N2 TO REF. CELL
LI-COR LI-6262
W.T.
W.T.
W.T.
W.T.
SAMPLE PT A
SAMPLE PT B
SAMPLE PT C
1/4" DEKORON LINES
N.V. Needle Valve
N.C. Normally closed
W.T. Water Trap

Fig. 2.

standards), spanning a concentration range between 0 and 1600 ppm. A calibration curve is obtained approximately every 2.5 h and sample readings are drift corrected using time-weighted, linear interpolation between two subsequent calibration cycles. The drift between calibration cycles is generally <1 ppm. Four NIST traceable standards ($\pm 1\%$) serve as primary standards against which we calibrate our working standards. A more accurate determination of the primary standards concentration, to about $\pm 0.1\%$, was obtained at LDEO by GC and coulometric analysis. The working standards, which are connected to each individual CO_2 analyzer, are inter-calibrated against the primary standards using a bench-top LI-6262 system. This approach has been taken because using secondary standards reduces the operational cost of the systems without significant loss of accuracy.

The long term precision of the instruments is inferred from repeated measurements of working standards. Fig. 3 presents the standards residuals throughout a 20 day period, obtained by subtracting the concentration of working standards, as determined by bench top calibration with the primary standards, from the actual readings of the in-situ analyzers. During this period, the precision of the desert analyzer was 0.15 and 0.35 ppmV (1 S.D.) at the 350 and 1200 ppmV levels, respectively. At the same time, the precision of the TRF analyzer was 0.55 and 0.80 ppmV (1 S.D.) at the 350 and 1200 ppmV levels, respectively. Based on the data we suggest that the analytical precision of CO_2 measurements, obtained from the raw mV data, is better than 0.2% (1 S.D.). This high precision is obtained despite the large diurnal temperature fluctuations inside Biosphere 2. Indeed, the drift corrected processed data suggest a negligible temperature dependence of $>0.01\%$ $°C^{-1}$ over a cell temperature range between 30 and 40°C (note that the built-in corrections of the 6262 models do not apply to the raw mV data). Occasionally, a malfunctioning valve resulted in erroneous readings (due to insufficient flush of the sample cell). Such data points, amounting to less than 1% of the entire data set were rejected from the following statistics.

The accuracy of the instruments can be deduced from the deviation of the residuals from zero; the smaller the deviation the better the accuracy. On average the accuracy was better than 0.5 ppmV in the DES (Fig. 3A) and 1.3 ppmV in the TRF (Fig. 3B), over the entire concentration range (0–1550 ppmV). Evidently, the measurement accuracy is as good as the accuracy by which the concentration of the working standards is determined. Using bench top LI-COR calibration results in analytical accuracy of $\sim 0.3\%$.

Fig. 2. A schematic plan of the CO_2 monitoring system depicting its major components and sample flow: air, sampled at three ports, is drawn continuously into the analyzer through 1/4 inch Dekoron tubing using 4.5 l/min air pumps. Water traps before the pumps serve to reduce the air humidity. Most of the flow is directed through needle valves into shunt lines, leaving only 40–50 ml/min to be sent to the analyzer. The five calibration standards (note that N_2 is used as a 'zero air' standard, reference gas and a dry carrier gas for the Perma Pure Dryer) are supplied from regulated, pressurized gas cylinders. Samples and standard gases are routed through a multiport electronic valve, a normally-closed (N/C) solenoid, a 20–100 ml/min electronic flowmeter, a Perma Pure dryer and a 0.45 μm filter before entering the IRGA. The sampling and calibration sequence is controlled by a BASIC program.

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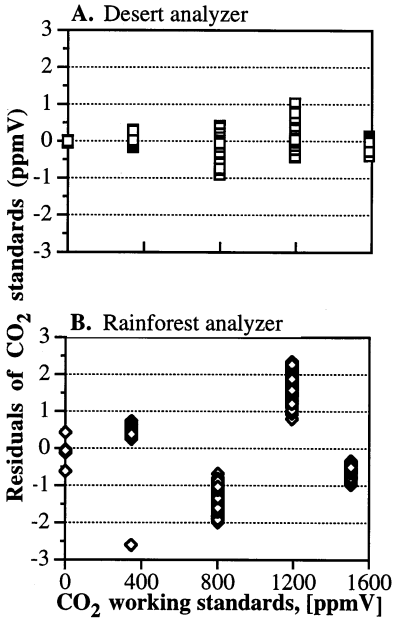

Fig. 3. Residual readings from standard calibrations collected during a 20-day period by the CO_2 analyzers in the desert (A) and rainforest (B). As shown, the precision of both the desert and TRF analyzers is better than 0.2% (1 S.D.) between 0 and 1550 ppmV.

3. Whole mesocosm CO_2 budget

Recent research at Biosphere 2 is focused primarily on plant, soil and ecosystem responses to increased atmospheric CO_2. In these experiments, temporal gradients in atmospheric CO_2 are created by controlled exchange of the elevated CO_2 air inside Biosphere 2 with outside air. In the wilderness area, ambient air, pushed into the south lung, enters the desert mesocosm (DES) then flows northward through the savanna (SAV) and exits from the rainforest mesocosm (TRF; Fig. 1). By changing the flow rate and duration of flush, it is possible to manipulate atmospheric CO_2 levels. Carbon and water mass balance is maintained by continuous measurements of the flow rate, CO_2 concentration and water vapour content of the air entering and exiting the facility. The desired CO_2 level can usually be maintained for more than a week (pending weather conditions), allowing plants to acclimate to the new atmospheric conditions before measurements of plant and soil gas fluxes begin. Following acclimation, mesocosms are temporarily sealed for periods of 24 to 72 h by deployable polyethene curtains. Currently, the plastic dividers allow us to isolate and study the carbon cycling within the two mesocosms of the desert and rainforest in the wilderness area. Changes in atmospheric CO_2 concentrations within a mesocosm, as monitored by the LI-COR CO_2 analyzers,

are used to assess changes in NEE as related to primary productivity and respiration, in response to increasing atmospheric pCO_2. Concurrently, variations in carbon metabolic rates at the foliar and edaphic levels have been studied by extensive measurements of leaf-level gas exchange and closed chamber soil respiration. The advanced climate control system of Biosphere 2 may be used to maintain stable climatic conditions (air and soil temperature, relative humidity) throughout an experiment.

3.1. Methodology

The CO_2 budget within a closed mesocosm can be described as follows:

$$\Delta S_c = A_c + R_s + F_{leak} + F_{conc} \quad (1)$$

where ΔS_c is the observed change in atmospheric of CO_2 inside the closed mesocosm, A_c is the net photosynthetic rate, R_s is the whole system respiration rate which includes both above and underground (autotrophic and heterotrophic) respiration. The integrated photosynthetic flux (A_c) over time is the gross ecosystem productivity (A_c). Negative ΔS_c and A_c signify net carbon uptake by the whole system. The term F_{leak} represents the net CO_2 flux between the rain forest and savanna mesocosms due to air leak through the plastic curtains. The term F_{conc} is the rate of CO_2 uptake by the concrete structure which constitutes a significant sink of CO_2 due to the carbonation reaction with calcium oxides (Severinghaus et al. 1994). The mesocosm respiration includes plants (leaf and wood) and soil (roots and microorganisms) respiration. In principle, as shown in Eq. (1), inferring the ecosystem rates of photosynthesis and respiration from changes in atmospheric CO_2 requires knowledge of the other two, non-biologic fluxes, F_{leak} and F_{conc}. An example, illustrating our approach and the significance of the different terms is given below.

Data collected from the TRF mesocosm during a 24 h closure on January 31, 1996 is shown in Fig. 4. During the preceding night, the facility was in a flow-through mode, maintaining a CO_2 level of ~ 600 ppmV throughout the wilderness area. The TRF mesocosm was isolated from the SAV mesocosm at 08:00 h, shortly after sunrise. The extremely large diurnal cycle of atmospheric CO_2 is driven by the balance between photosynthesis, indicated by the daily CO_2 drawdown, and respiration, shown as the nightly increase in CO_2 (Fig. 4A,B). The large CO_2 amplitude reflects the substantially larger ratio of surface area and biomass to atmospheric volume at Biosphere 2 relative to the earth's biosphere. In contrast, in natural tropical rain forests diurnal CO_2 fluctuations are typically less than 50 ppmV. This problem may be expected in closed, growth chamber experiments. The amplitude of the diurnal CO_2 change depends on light levels, temperature and humidity as well as on the growing biomass and the organic content of the soil. For example, during the day of January 31, 1996, the nightly increase of CO_2 due to respiration exceeded the daily drawdown by net photosynthesis, resulting in a net increase of nearly 400 ppmV in atmospheric CO_2 inside the TRF mesocosm during the 24 h closure (Fig. 4B).

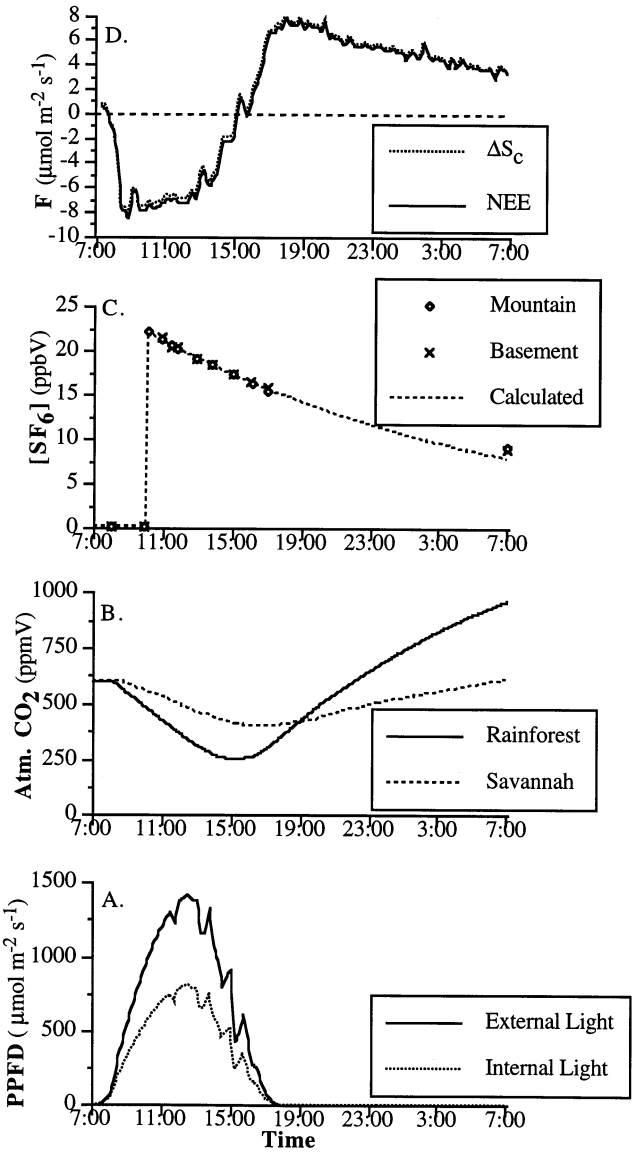

Fig. 4. A continuous record of light, CO_2, SF_6 and NEE data collected in the rainforest mesocosm during a 24-h closure on January 31, 1996. (A) Photosynthetic photon flux density (PPFD) out of, and inside the TRF mesocosm. Note the significant attenuation of light due to the glass and spaceframe cover of Biosphere 2. (B) Atmospheric CO_2 concentrations in the rainforest and savannah mesocosms. Note the significant CO_2 draw-down due to photosynthesis during daytime and the night-time rise due to respiration. (C) A record of SF_6 spike introduced into the rainforest mesocosm (at 10:00 h) showing a decrease due to air exchange with the savannah mesocosm. The initial SF_6 concentration in the savannah mesocosm was at background level. The exponential curve fit is: $[SF_6] = [SF_6] \cdot \exp(-kt)$. (D) Changes in atmospheric CO_2 concentrations (ΔS_c) and the calculated, biologically driven, net ecosystem gas exchange rate (NEE). Note that the two curves are almost identical, suggesting that the contribution of the non-biological terms (F_{leak} and F_{conc}) to the carbon budget is very small.

The net CO_2 flux between the sealed TRF and the SAV mesocosms (F_{leak}) depends both on the air flow through the curtains and the CO_2 gradient between the two chambers. The leak rate was estimated by following the decay of a biologically inert sulfur-hexafluoride (SF_6) spike injected into the closed mesocosm. Air samples were collected from the TRF, SAV and DES mesocosms by syringes every half, to 1 h, and analyzed by GC-ECD calibrated by five gas standards covering the whole concentrations range. The exchange rate during the 24 h closure was 4.9% of the mesocosms air volume per hour (Fig. 4C). Within our sampling resolution the exchange rate was constant throughout the 24 h closure period. Also, the identical results from the basement and top (mountain) levels suggest that the TRF air is well mixed. It is noteworthy that the magnitude of F_{leak} obtained on 16 separate closures (during December 1995–February, 1996) was always below 5% of ΔS_c in both the rainforest and desert mesocosms. Similar results were obtained in other closures, both in the rainforest and desert mesocosms, suggesting that using deployable plastic curtains as proposed by Marino (1994) is a sufficient, inexpensive solution for isolating the mesocosms.

The large concrete structure of Biosphere 2 is a significant sink of CO_2 and therefore should be accounted for in the CO_2 budget (Severinghaus et al., 1994). CO_2 diffuses into the concrete along a concentration gradient created by the reaction of CO_2 with calcium oxides, precipitating calcium carbonate:

$$CO_2(aq) + Ca(OH)_2(s) \rightarrow CaCO_3(s) + H_2O \quad (2)$$

The carbonation rate is diffusion-limited and therefore the flux can be estimated using Fick's first law (Severinghaus et al., 1994). The magnitude of the flux into the concrete depends primarily on the CO_2 concentration of Biosphere 2 air and the diffusivity of CO_2 in the concrete. The atmospheric CO_2 concentrations change by up to 500 ppmV diurnally and by a factor of five to ten seasonally due to biological processes (photosynthesis and respiration). The effect of such diurnal changes on the instantaneous CO_2 flux depends on the diffusion coefficient of CO_2 in the concrete; the time required for any point to respond to a change in surface CO_2 is proportional to the square of its distance from the surface (Z) and inversely related to the diffusion coefficient ($t = Z^2/D$).

From the data of Severinghaus et al. (1994) we estimate a diffusion coefficient of CO_2 in the concrete on the order of 5 to 10 cm^2/h. The effective diffusion coefficient depends largely on the concrete porosity and water content and therefore should be higher in the humid rainforest than in the dry desert mesocosm. The high diffusivity implies that the response time of the CO_2 in the concrete to a change in atmospheric CO_2 is on the order of a few hours and therefore the CO_2 flux into the concrete is sensitive not only to seasonal, but also to diurnal variations in atmospheric CO_2. However, we find that at CO_2 levels below 1000 ppmV the concrete flux (F_{conc}) accounts for only a few percent of the change in atmospheric CO_2 (ΔS_c).

Observed time-dependent changes in atmospheric CO_2 concentrations (ΔS_c) and the calculated, biologically driven, NEE are shown in Fig. 4D. The two curves are almost identical, suggesting that the contribution of the non-biological terms (F_{leak}

and F_{conc}) to the carbon budget (Eq. (1)) is negligible. Such records may be used to assess whole mesocosm metabolic rates. The net ecosystem photosynthetic rate may be estimated from the daily ecosystem gas exchange rate (NEE; Fig. 4D):

$$\text{Day-NEE:} \qquad \Delta S_c - (F_{leak} + F_{conc}) = A_c + R_s \tag{3}$$

The whole mesocosm respiration rate may be obtained from the nightly increase in CO_2:

$$\text{Night-NEE:} \qquad \Delta S_c - (F_{leak} + F_{conc}) = R_n \tag{4}$$

Note that R_n, the night-time respiration, includes both soil efflux and plant respiration but not photorespiration. The latter can be resolved by using soil flux chamber measurements. Also noteworthy is that R_n may change during the course of the day, most likely due to variations in air and soil temperatures. This is suggested from the decreasing trend in R_n: mesocosm respiration decreased from about 7 to about 4 $\mu mol/m^2$ per s during the course of the night (Fig. 4D). Therefore, accurate estimates of net ecosystem photosynthetic rates (A_c) from NEE require knowledge of the diurnal changes in respiration.

4. Biosphere 2: strengths and weaknesses

Needless to say, the large scale, diversity of plants and degree of closure makes this big gas exchange chamber an attractive facility for testing the effects of increasing atmospheric CO_2 on terrestrial ecosystem. Clearly, from an analytical point of view, the quality of the data obtained by the large gas exchange methodology is superior to other methods (e.g. the eddy correlation method). However, the unique and sometimes unnatural conditions of the facility raise questions that need to be addressed before experimental results obtained at Biosphere 2 are broadly useful. Some of the more important issues are:

1. The absence of spatial replication: in the current experiments the CO_2 was alternated between low and high levels to provide some degree of replication. However, in this procedure the problems of temporal heterogeneity remain; i.e. the canopy (e.g. phenological state and LAI) and physical conditions (e.g. light intensity and solar angle) continuously change over the experiment. Also, its utility is limited only to short term experiments.
2. Acclimation: because CO_2 levels at Biosphere 2 are typically higher than ambient levels, the plants are acclimated to high CO_2 levels. Consequently, the plants response to CO_2 was assessed by changing from high to low CO_2 levels, an inverse gradient to the global trend of increasing CO_2. Further, because we could not achieve true ambient CO_2 levels our baseline condition was at 450 ppmV, making the inter-comparison with natural systems and similar experiments rather imprecise due to non-linear effects (Korner, 1995).
3. The unnatural CO_2 cycle of a few hundred ppmV inside the facility: if we are to use the facility for similar research purposes it seems inevitable that we should think of ways for a long term control of CO_2 levels inside the facility as well as for reducing the diurnal CO_2 cycle.

4. Unnatural soil composition and plant community structure: the soil was artificially made from Arizona soil mixed with organic rich material to mimic tropical soil (see companion papers in this issue). The soil profile is not fully developed and its microbial composition is very unique. Further, due to structural constraints, the soil interfaces with the atmosphere both from the upper and bottom sides. The effects of these features on respiration and CO_2 efflux need to be investigated. Further, unlike tropical soils, Biosphere 2 soil is rich in nitrogen which may have important implications for photosynthetic acclimation (Gunderson and Wullschleger, 1994; Pettersson and McDonald, 1994). Likewise, the rain forest mesocosm contains a unique mix of species from a broad range of successional stages making a quantitative comparison between this and other experiments rather difficult.

5. Conclusions

Results obtained in the first experiment during the winter of 1995/6, suggest that carbon assimilation in the tropical rain forest is CO_2 sensitive, at least following a CO_2 exposure of days to weeks (Rosenthal, 1998). This is the first evidence for such a response in a large-scale, diverse tropical ecosystem. The quality of the data collected during the experiment is high, clearly demonstrating the high performance of the new CO_2 monitoring analytical system and the applicability of our methodology. However, the scientific merit of these results depends on our understanding all the phenomena associated with large scale enclosures such as Biosphere 2.

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