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Carbon dioxide efflux from a 550 m^3 soil across a range of soil temperatures

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Abstract

Because of scaling problems point measurements of soil CO_2 efflux on a small volume of soil may not necessarily reflect an overall community response. The aim of this study was to test this hypothesis in the Biosphere 2 facility and achieve the following broad goals: (1) investigate soil net CO_2 exchange–temperature relationship at the community level; (2) compare soil net CO_2 exchange at the community level to the traditional sample point estimates of CO_2 efflux scaled up to the community level; (3) evaluate the usefulness of a facility such as Biosphere 2 for conducting community level experiments for studying response to a climatic perturbation under controlled environmental conditions. A 550 m^3 volume of soil with 282, 15 cm tree stumps was enclosed at the Biosphere 2 Center and warmed from 10 to 25 °C over a period of 34 days. Net CO_2 exchange from this community was measured at various points on the soil surface with 78.5 cm^2 chambers and for the whole community using each of the three bays at Biosphere 2 Center as a closed system. Soil CO_2 efflux rates obtained by point measurements showed tremendous variability from location to location. At the community level and with point measurements, net CO_2 exchange increased exponentially with increasing soil temperatures. Q_{10} values from both the point and community level measurements ranged from 1.7 to 2.5. Scaling of point measurements by soil surface area and time overestimated community rates by 36% revealing some of the limitations of point measurements. This experiment demonstrates how Biosphere 2 facility could be used to study behavior of individual components and measure responses at the community level and test our capacity to scale point in time and space measures of community processes to the community level.

Keywords: Community level soil respiration; Scaling; Soil warming; Environment-controlled facility

1. Introduction

The annual global flux of CO_2 from soils to the atmosphere is estimated to average between 68 and

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77 Pg C per year (Raich and Schlesinger, 1992). This is 25% of the total annual flux of CO_2 exchange for terrestrial and marine sources (Post, 1990). Thus, soil respiration is a major flux pathway in the global carbon cycle, second only to gross primary productivity (Houghton and Woodwell, 1989).

It is now predicted that global temperatures will be 1–6 °C warmer by the year 2100 (IPCC, 2001). An increase in global air temperature should lead to a corresponding increase in soil CO_2 efflux assuming other factors such as soil moisture, litter quality, organic matter are not limiting (Boone et al., 1998; Trumbore et al., 1995; Kirschbaum, 1995; Winkler et al., 1996; Raich and Schlesinger, 1992; Schimel et al., 1994; Grace and Rayment, 2000). Because of the large amounts of carbon present in soils the release of even small amounts of CO_2, as a result of increasing soil temperatures, could be quite significant (Kirschbaum, 2000). This could exacerbate greenhouse-warming of the earth's atmosphere (Woodwell, 1995; Rustad et al., 2000).

Although the soil CO_2 efflux–temperature relationship has been extensively studied, our understanding is still quite limited due to the large variability typically observed using point measures of soil CO_2 efflux rates. Observed variability can be attributed to both measurement methodology and the inherent spatial heterogeneity of soil. Soils are extremely variable. Soil CO_2 efflux could vary spatially within and between soil types due to differences in soil temperature, soil moisture, microbial population size and composition, and nutrient levels (Seto and Yanagiya, 1983; Howard and Howard, 1993).

Several technologies have been used for soil warming experiments; however, there are limitations to the degree, area, and depth a soil can be warmed. Quite often only a small area of soil is warmed to a depth of a few centimeters in a small range of temperature around the normal soil temperature (Peterjohn et al., 1993). Warming a large area or volume of soil to a significant depth has been technically difficult. Biosphere 2 laboratories permits a system for achieving whole profile warming and wide ranges in soil temperature that can be sustained for long periods of time.

Most techniques used to measure soil CO_2 efflux in the field or laboratory, require sampling of an isolated volume of air from a small section of the soil enclosed within a chamber. However, this could potentially introduce error due to pressure difference between the chamber air and that of the ambient air (Lund et al., 1999). Moreover, extracting and transferring soil cores from the field to the laboratory for incubation studies could alter soil macro-structure and/or the microbial populations that could affect soil respiration. At Biosphere 2 labs we avoid such methodological problems by warming the entire 500 m^3 soil mass and making non-invasive measurement of belowground CO_2 efflux for the whole 550 m^2 of soil area.

Most of the common problems associated with soil warming studies such as inability to heat large areas of soil, disturbance of the soil profile, achieving large temperature differentials, and confounding effects of soil temperature and moisture, can be overcome at the Biosphere 2 laboratory with relative ease. Here we present a pilot study that examines the effect of increasing soil temperatures on belowground CO_2 efflux of a coppiced eastern cottonwood (*Populus deltoides* Bartr.) forest system. This study had the following objectives:

(1) investigate soil CO_2 efflux–temperature relationship at the community level;
(2) compare soil CO_2 efflux at the community level to the traditional sample point estimates scaled up to the community level;
(3) evaluate the usefulness of a facility such as Biosphere 2 for conducting large community level experiments for studying response to a climatic perturbation under controlled environmental conditions and our ability to scale point measurements to the community level.

2. Methods

2.1. Study site

This pilot study was conducted in the Intensive Forestry Biome (IFB) at the Biosphere 2 Center located in Oracle, AZ, USA (32.5°37.13′N; 110°47.05′W; 1200 m a.s.l.). The IFB covers an area of approximately 2000 m^2, has an air volume of 38,000 m^3, and a soil volume of roughly 2000 m^3. The IFB is partitioned into three areas called bays that are separated by a lightweight 0.30 mm thick transparent polyvinylchloride (PVC) curtain. The bays are referred to as East, Center, and West bays based on their relative placement. Each

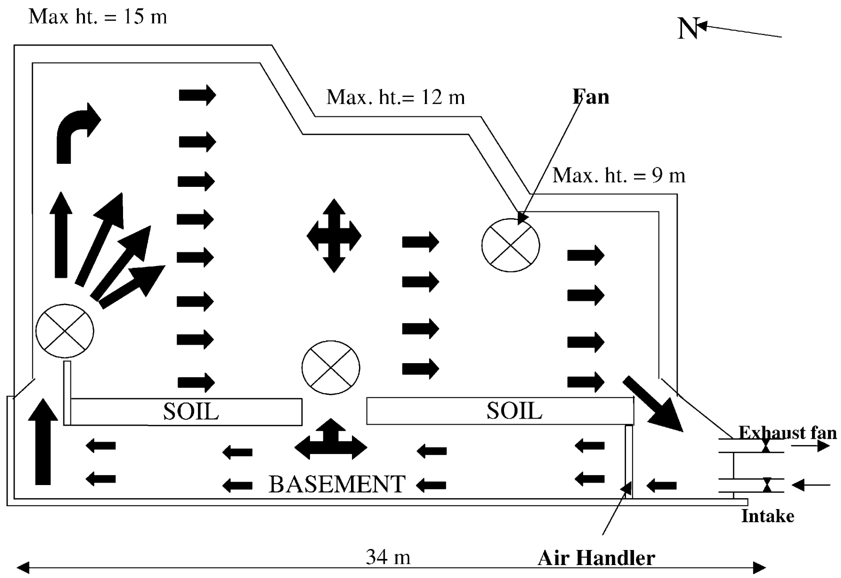

Fig. 1. A schematic diagram showing a longitudinal section of a bay in the IFB at the Biosphere 2 Center. Arrows depict direction of airflow within each bay.

bay measures 41 m × 18 m in a north–south orientation, has an approximate soil surface area of 550 m^2, soil volume of 550 m^3, air volume of 11,700 m^3 and average height available for plant growth of 14 m (Fig. 1). Atmospheric CO_2, air and soil temperature, soil water and humidity levels can be independently manipulated and measured within each bay. Details of the structure, layout, and control of environmental parameters are described elsewhere (Dempster, 1999; Zabel et al., 1999; Griffin et al., 2002).

2.2. Soil

The soil bed is approximately 1 m deep and rests on a concrete floor constructed over a basement (Fig. 1). For further details on construction see Marino and Odum (1999). The soil was constructed from a mixture of base soil (60%) and organic matter (40%). The textural classification of the soil is silt loam (Gee and Bauder, 1986) with an average of 27.8% sand, 54.4% silt, and 17% clay content. The soil has been evolving for more than 8 years with crops of various kinds and the pedogenic processes that give rise to diagnostic properties have been in operation. However, they have not yet progressed to the point of stratification and structure to merit classification (Johnson, pers. commun.). Currently, soil bulk density ranges from 1.2 to 1.3 g cm^{-3}, soil organic carbon from 2.2 to 2.5%, and carbon:nitrogen (C:N) ratio is 9.9. Results of the pre-experiment soil nutritional analysis are given in

Table 1
Soil extractable elements averaged over 1 m depth of soil in the East, Center, and West bays of the IFBs of the Biosphere 2 Center[a]

Bays	Ca (g kg^{-1})	Mg (g kg^{-1})	K (g kg^{-1})	SOM[b] (g kg^{-1})	P (mg kg^{-1})	Cu (mg kg^{-1})	Mn (mg kg^{-1})	Zn (mg kg^{-1})	Fe (mg kg^{-1})	Bo (mg kg^{-1})	NO_3 (mg kg^{-1})
East	2.9	0.45	0.70	30	161	6.5	9	4.4	56.3	1.7	38
Center	2.5	0.38	0.63	27	140	5.2	6.7	3.4	50	1.6	47
West	2.6	0.42	0.70	28	152	5	8	3.6	54	1.9	38

[a] Each value is an average of nine observations (three locations within the bay and at three depths).
[b] Soil organic matter.

Table 1. More details about original soil composition and development over the past few years can be found in Torbert and Johnson (2001).

2.3. Plant material

Two hundred and eighty two cuttings of eastern cottonwoods (*P. deltoides* Bartr.) of similar genotype (S7C8) originating from an east Texas source were planted in the IFB in May 1998. The trees were subjected to chilling temperatures at the end of the growing season, forced into dormancy, and then coppiced by cutting the trees back to 30 cm above the soil. For the subsequent growing season (1999) the trees were allowed to grow from the stump and pruned such that only one leader was maintained for each tree. At the end of the year the trees were again coppiced. The present study was conducted the following year in the IFB during February–March 2000. During this study there was no aboveground tree biomass. However, the live tree stumps with 2-year-old root systems were still present in the soil.

2.4. Environmental parameters

The environmental parameters measured inside each bay were air temperature, soil temperature, volumetric soil water content, and photosynthetic photon flux density (PPFD). All environmental parameters were measured every 15 s, averaged and stored every 15 min in data-loggers (Campbell-CR10×, Campbell Scientific, Logan, UT, USA). Each bay was divided into four quarters where all environmental parameters were measured at approximately the center of each quarter. Volumetric soil water content was measured at the 20–50 and 50–80 cm depth ranges using CSI 615 water content reflectometer probes (Campbell Scientific, Logan, UT, USA). Measured volumetric water content was obtained as the integrated value for each 30 cm length of the probe. Volumetric soil water content was also periodically measured at the surface (0–30 cm) with a similar probe. Soil temperature was measured at 20, 50, and 80 cm depth with thermocouples; however, surface soil temperature at a depth of 10 cm was measured at only two locations in each bay. Air temperature and PPFD were measured at the same four locations in each bay at 3, 6, and 9 m from the ground. In addition, air temperature was also measured at a height of 15 m in one central location in each bay.

3. Experimental protocol

3.1. Temperature regime

The soil CO_2 efflux study was conducted between 9 February and 12 March, 2000. The soil was warmed by circulating warm air from an external source to the bays using large air handlers situated in the basement of each bay. Air was circulated both below the concrete bed on which the soil rests and directly above the soil layer (Fig. 1). Therefore, warming of the soil was achieved both via direct contact with the soil and possibly by conduction through the concrete layer supporting the soil mass.

Air temperature was maintained constant until the soil temperature at all depths was within 1.0 °C. The time required for the soil to warm to a uniform temperature varied considerably because of the substantial soil volume that had to undergo warming. Therefore, the daily soil temperature trend over the course of the study exhibited a continuous gradually increasing relationship as opposed to a strict discrete step function. Air temperatures used in this study resulted in an average hourly soil temperature ranging 10.8–24.0, 11.5–23.0 and 11.0–23.0 °C for the East, Center, and West bays, respectively (Fig. 2). The average daily soil temperature differences between the bays were less than 1.0 °C (data not shown). Similarly, soil temperature within the soil profile did not vary substantially from one depth to another (Fig. 2). Therefore, all statistical analyses were performed using average soil profile temperature.

3.2. Atmospheric CO_2 manipulation and monitoring

The bays were operated in a ‘‘closed’’ mode isolated from the outside air. Each day the air volume of each bay was purged for 2 h in the morning (06:00–08:00 h) and at dusk (18:00–20:00 h) with outside ambient air flushed with a pair of large fans (capacity of 127 $m^3\ min^{-1}$ each) (see Fig. 1). Each 2 h flush resulted in a 1.25 air volume exchange and was necessary to prevent a large buildup of CO_2. Such a buildup would have decreased the diffusion gradient

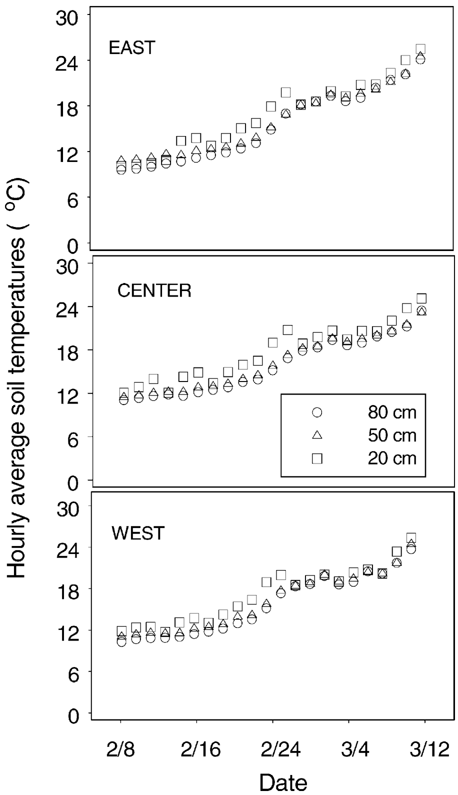

Fig. 2. Hourly average soil temperatures at the 20, 50, and 80 cm soil depth for the East, Center, and West bays in the IFB at the Biosphere 2 Center over the entire study period. For purposes of clarity all hourly observations are not shown.

and thus influence soil CO_2 efflux rate. Air within the bay was constantly circulated by three large air handlers located in the basement of each bay and four other fans located in each bay. Pressure differences between soil depths and the atmosphere were measured using a sensitive differential pressure meter and was found to be less than 2 Pa. This excluded the possibility of a large CO_2 efflux as a result of pressure differences. Leaks between bays and to the outside were determined before and after the experiment using a trace gas, sulfahexaflururide (SF_6). Concentration of CO_2 in each bay was then corrected based on the leak rate obtained from SF_6 calculations.

3.3. Soil moisture

Drip irrigation was used to water the trees in the three bays. The drip nozzles of the irrigation system were located 0.61 m apart and discharged 2.27 l/h per emitter resulting in a uniform average soil volumetric water content of 0.31 $m^3\ m^{-3}$ across bays. Drip nozzles were located at a distance of 30 cm from the foot of every tree stump and from the soil moisture probes. Average soil profile volumetric water content ranged from 0.29 to 0.33, 0.29–0.34, and 0.29–0.34 $m^3\ m^{-3}$ in the East, Center, and West bays, respectively. Water draining through the soil profile was automatically collected and exported out of the bays.

4. Measurements

4.1. Point measurements of soil CO_2 efflux rate (R_p)

Point measurements of soil CO_2 efflux (R_p) were obtained using a portable infrared gas analyzer (model Li-Cor 6200, Li-Cor, Lincoln, NE, USA) equipped with a Li-Cor 6000-09 respiration chamber. Measurements were made at 10 randomly selected locations in each bay, five were in the wet, and five in the dry zone. The wet zones were those that were within the surface influenced by the drip irrigation. Measurements were made periodically at the same locations during the study period, spanning different soil temperatures. Measurements were made both in the mid-morning and afternoon so as to account for differences due to time of the day.

4.2. Community level measurement of net CO_2 exchange rate (R_w)

Estimation of net CO_2 exchange at the community level utilized the sampling of the CO_2 concentration in air in a given bay at periodic intervals. A measurement was taken every 10 s using an infrared gas analyzer (model Li-Cor 6262, Li-Cor, Lincoln, NE, USA). Since, there were no tree stems present, the CO_2 buildup in each bay originated solely from the soil and the coppiced root system. These values were averaged and stored in data-loggers every 15 min. Carbon dioxide concentration of air samples taken at different points within each bay showed very little variance indicating that the air mass was well mixed.

Community net CO_2 exchange rate for a bay was determined by fitting a linear regression equation to the atmospheric CO_2 data as a function of time between two consecutive flushes. Separate regressions were developed for each 12 h period (daytime 06:00–18:00 and nighttime 20:00–06:00). Observations consisted of the 15 min average CO_2 measurements obtained between the flushes, yielding 40–48 observations per regression. The slope of the regression equation was adjusted for bay volume and area, yielding community net CO_2 exchange rate (R_w) in μmol CO_2 m^{-2} s^{-1} for each day and night period. Total daily community net CO_2 exchange rate (R_{day}) was calculated by multiplying R_w by the total amount of time that CO_2 efflux occurred and by bay soil surface area. R_{day} is the sum for two consecutive periods (day and night) expressed as daily CO_2 efflux for the community in mol CO_2 bay^{-1} per day or more correctly mol CO_2 bay^{-1} per 20 h period.

It should be noted that in the above two measurements a distinction has been made between CO_2 efflux measured by point measurements, which is a direct measure of soil CO_2 efflux and that measured at the community level which is actually net CO_2 exchange.

4.3. Modeling soil CO_2 efflux as a function of temperature

The soil CO_2 efflux (R_p) and net CO_2 exchange rate (R_w) and temperature relationship was modeled using a modified version of the Arrhenius function (Lloyd and Taylor, 1994) and is defined as

$$R = R_{10}\exp\left[\left(\frac{b_0 + b_1T + b_2T^2}{R}\right)\left(\frac{1}{T_{10}} - \frac{1}{T}\right)\right]$$

or

$$R = R_{10}\exp\left[\left(\frac{b_0 + b_1T + b_2T^2}{8.314}\right)\left(\frac{1}{283.15} - \frac{1}{T}\right)\right] \quad (1)$$

where R is the soil CO_2 efflux or net CO_2 exchange rate in μmol m^{-2} s^{-1}; R_{10} the soil CO_2 efflux rate at 10 °C (μmol m^{-2} s^{-1}); T the average soil profile temperature (K); b_0, b_1, and b_2 the parameters of the quadratic equation relating activation energy (E_0) and T; R the ideal gas constant (8.314 J mol^{-1} K^{-1}); T_{10} the average soil profile temperature (K) at 10 °C. The parameters b_0, b_1, b_2, and R_{10} were estimated.

The temperature coefficient Q_{10} (Salisbury and Ross, 1985), which denotes a change in the rate of a reaction with a 10 °C increase was calculated using

$$Q_{10} = \left(\frac{k_2}{k_1}\right)^{10/(T_2 - T_1)} \quad (2)$$

where k_1 is the CO_2 efflux rate at the lower measurement temperature T_1 and k_2 the CO_2 efflux rate at the higher measurement temperature T_2.

4.4. Scaling of point estimates (R_p) to daily community net CO_2 exchange rate (R_{pday})

Point estimates of soil CO_2 efflux were scaled to the community level by first fitting Eq. (1) to the point estimate data. Then soil CO_2 efflux rates were estimated by substituting average soil profile temperature into the fitted model. Estimated soil CO_2 efflux rates were then averaged by bay for each day for the wet and dry locations to obtain R_{pavg}. Daily community net CO_2 exchange rate estimates (R_{pday}) was calculated by

$$ER_{pday} = R_{pavg}At \quad (3)$$

where ER_{pday} is the daily community net CO_2 exchange rate estimates (mol bay^{-1} per day) for either the wet or dry zone, R_{pavg} the daily average rate of estimated soil CO_2 efflux (μmol m^{-2} s^{-1}) for either the dry or wet zone, A the total soil surface area (m^2) of the bay (A is the area for either the wet or dry zones for the entire bay. The surface area of the wet zones were estimated by multiplying the average area one drip nozzle could distribute water by the total number of nozzles in each bay.) and t the total time CO_2 efflux occurred (s). R_{pday} was estimated as the sum of ER_{pday} for the wet and dry zones.

4.5. Statistical analysis

The soil CO_2 efflux model (function 1) was fit to both the community net CO_2 exchange rate (R_w) and point measured CO_2 efflux rates (R_p) using nonlinear techniques (Proc NLIN, SAS, 1988). Results were evaluated using fit statistics such as sum of squares, absolute bias and the correlation coefficient between the observed and predicted values.

Daily community net CO_2 exchange rate estimates (R_{pday}) obtained by scaling point measurements of soil

CO_2 efflux rates were evaluated on the basis of how much they deviated from the direct measurement of daily total community net CO_2 exchange rate (R_{day}) using the following evaluation statistics:

$$\text{Bias} = \frac{1}{n}\sum(R_{pday} - R_{day})$$

$$\text{Percent bias} = \frac{100}{n}\sum\frac{R_{pday} - R_{day}}{R_{day}}$$

$$\text{Absolute deviation} = \frac{1}{n}\sum|R_{pday} - R_{day}|$$

$$\text{Absolute percent deviation} = \frac{100}{n}\sum\frac{|R_{pday} - R_{day}|}{R_{day}}$$

$$\text{Accuracy} = \frac{1}{n}\sum(R_{pday} - R_{day})^2$$

The ability of this facility to effectively serve as a controlled environment useful for experimental manipulation was tested by evaluating the uniformity of environmental parameters across the bays. This was accomplished by testing for and estimating differences between the bays for the specified environmental conditions. The experiment was replicated three times by subjecting the three bays to the same temperature simultaneously. Mean differences in environmental parameters such as soil temperature and moisture, and atmospheric CO_2 concentration of the bays were estimated using Tukey's option with simultaneous 95% confidence limits in the analysis of variance. Each day of the study period was considered as a block and the analysis was performed as a randomized block design with three treatments (bays). Rate of CO_2 efflux among bays was tested using analysis of variance and F-tests. All statistical analyses were conducted using SAS (SAS, 1988).

5. Results

5.1. CO_2 concentration

Each day the CO_2 concentration in each bay increased linearly by an average of 150 μmol CO_2 mol^{-1} in a 10 h period between two consecutive flushes (Fig. 3). Actual CO_2 concentrations ranged from a minimum of 380 to a maximum of 645 μmol CO_2 mol^{-1} during the study period. Daily mean difference (95% confidence interval) in bay CO_2 concentration between the Center and East was 36.93 μmol CO_2 mol^{-1} (32.28–41.6),

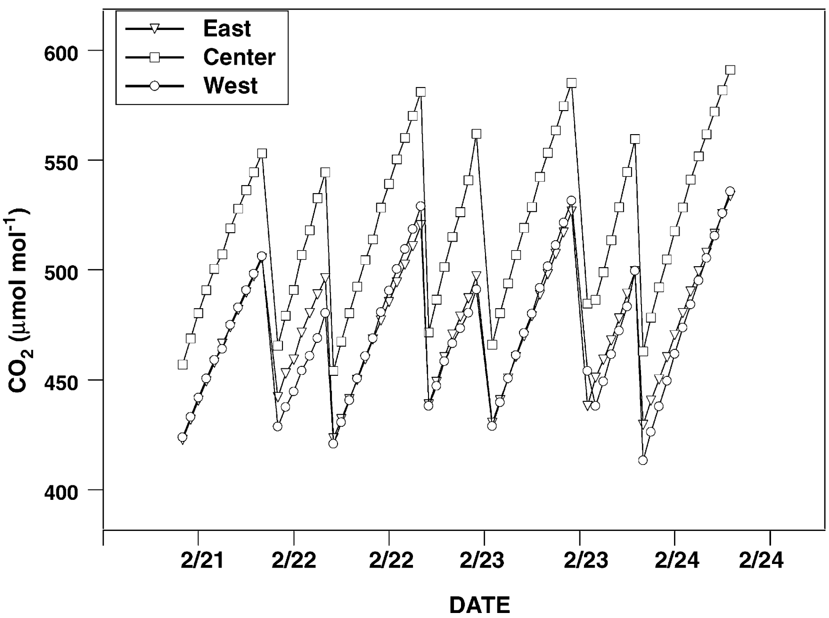

Fig. 3. Typical atmospheric CO_2 (μmol CO_2 mol^{-1} air) concentration in the East, Center, West bays in the IFB at the Biosphere 2 Center for a subset of 4 days during the study period. Each upward progression of observations represents either day or nighttime values.

between West and East was 1.51 μmol CO_2 mol^{-1} (−3.15 to 6.16) and between West and Center was 35.43 μmol CO_2 mol^{-1} (30.77–40.08). The confidence interval indicates that the average CO_2 concentration in the Center bay was significantly different from that in the West and East bays. There were no significant differences in the CO_2 concentration between the East and West bays.

5.2. Point measurement of soil CO_2 efflux (R_p)

Increasing soil temperature resulted in an increase in soil CO_2 efflux in both the wet and dry zones, in all three bays (Fig. 4). Mean soil CO_2 efflux rates in the wet zones were significantly higher than in the dry zones in all three bays. Maximum soil CO_2 efflux rates for the whole study in all bays ranged from 7.2 to 8.4 in the wet zone and from 4.8 to 5.8 μmol m^{-2} s^{-1} in the dry zone. For the dry zones CO_2 efflux rates in the West bay were significantly higher than those measured in the East or Center bays (data not shown). Soil CO_2 efflux rates of the wet zones were not significantly different between bays. Response curves fit to point measurements using function 1 are shown in Fig. 4. Parameter estimates and the fit statistics obtained by fitting R_p data to function 1 are shown in Table 2. Overall, the function fit the data quite well. Fit statistics revealed that the fit was slightly better for the dry than for the wet locations. This is reflected in the lower mean square error and absolute bias fit statistics, though not as much in the coefficient of correlation (Table 2). R_{10} rates in the East and West bays were also higher by a factor of 3 μmol m^{-2} s^{-1} in the wet compared to the dry zones.

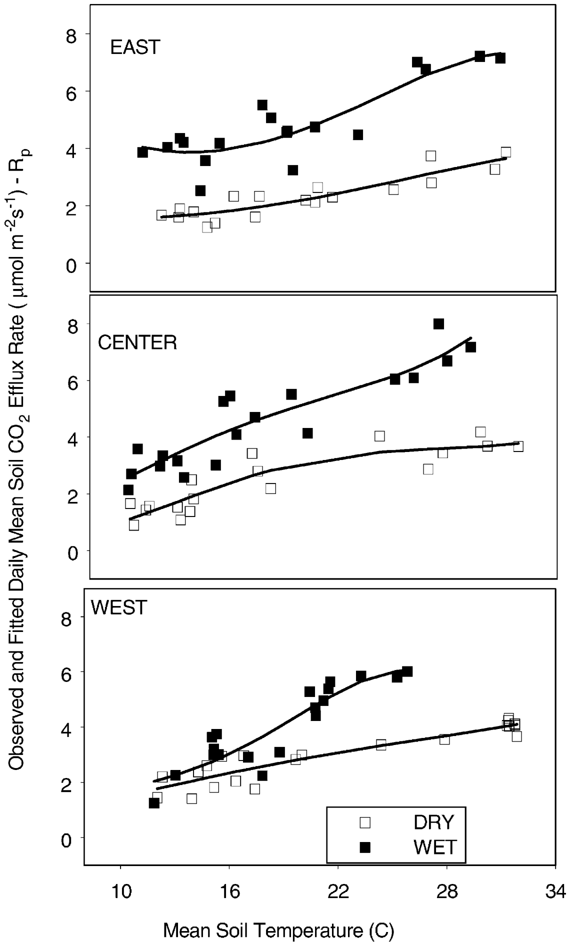

Fig. 4. Observed and predicted daily mean soil CO_2 efflux rates, R_p (μmol m^{-2} s^{-1}) obtained by point measurements for the East, Center, West bays in the IFB at the Biosphere 2 Center. Open symbols denote measurements made in the dry zones and closed symbols denote measurements made in the wet zones. Solid lines represent the predicted rates obtained by fitting function 1 to the point measurement data.

5.3. Community net CO_2 exchange rates (R_w)

The effect of increasing soil temperature on mean daily community net CO_2 exchange rate (R_w) and the response curve fit to the data using function 1, for the entire study period is shown in Fig. 5. With the exception of some scatter at lower temperatures, all the three bays showed a similar pattern in the response of community net CO_2 exchange rate to increasing temperature. Graphical representations of the observed and predicted R_w indicated a good fit of function 1. There were no significant differences in the rate of net CO_2 exchange between the bays. Parameter estimates and the fit statistics obtained by fitting function 1 to the mean daily rates of community net CO_2 exchange are shown in Table 3. R_{10} rates were well within expected range. Mean sums of squares and absolute bias values were quite low and demonstrate the goodness of fit between the observed and the predicted. The high correlation

Table 2
Parameters estimated by fitting function 1 to daily mean soil CO_2 efflux rate data obtained by point measurements (R_p) for dry and wet zones in the East, Center, and West bays in the IFB of the Biosphere 2 Center (fit statistics for the data are also presented)

Location	Parameters					Fit statistics	
	b_0[a]	b_1[a]	b_2[a]	R_{10}[a]	M.S.E.[b]	Absolute bias	CORR[c]
Dry							
East	4 512 715	−29117.9	47.38	0.97	0.09	4.11	0.93
Center	18 833 661	−121624	197.1	0.69	0.09	4.14	0.97
West	13 486 642	−85503.9	135.9	0.84	0.38	8.77	0.85
Wet							
East	99 164 618	−678719	1162	4.68	0.21	5.28	0.95
Center	30 109 857	−197195	323.7	1.80	0.51	9.24	0.92
West	49 916 015	−337207	570.24	2.84	0.41	8.49	0.88

[a] Estimated parameters of the quadratic function in model 1. R_{10} refers to the respiration rate (μmol m^{-2} s^{-1}) at a temperature of 10 °C.
[b] Mean square error between the predicted and observed.
[c] Correlation coefficient between the predicted and observed.

coefficients obtained also confirm the goodness of fit of the model.

5.4. Evaluation of point estimators against R_{day}

Point (R_p) soil CO_2 efflux rates were scaled to provide daily total soil CO_2 efflux for the community (R_{pday}) and compared against actual daily community values (R_{day}). R_{day} values determined over the study period averaged 79, 95, and 86 mol CO_2 bay^{-1} per day for the East, Center, and West bays, respectively. Scaled point estimates (R_{pday}) values averaged 125, 143, and 140 mol CO_2 bay^{-1} per day for the East, Center, and West bays, respectively. When compared to R_{day}, R_{pday} overestimated the daily totals by approximately 35.3% in all three bays (Fig. 6). The evaluation criteria for R_{pday} was based on its magnitude of deviation from R_{day}, the lower is the evaluation statistics the better is the estimate. On a percentage basis both the percent bias and the percent absolute deviation were greater than 60% for all three bays (Table 4).

5.5. Q_{10} values

Q_{10} values were calculated from both the community and point measurement CO_2 efflux rates. Mean community Q_{10} value of the East bay was significantly higher than that obtained for the Center or West bay (Table 5). Q_{10} values obtained from point measurement CO_2 efflux rate were slightly lower than that obtained from the community net CO_2 exchange rate. No significant differences were obtained in the point measurement Q_{10} values between bays either in the wet or dry zones.

Table 3
Parameters estimated by fitting function 1 to daily mean community net CO_2 exchange rate (R_w) data obtained for the East, Center, and West bays in the IFB of the Biosphere 2 Center (fit statistics for the data are also presented)

Location (bay)	Parameters					Fit statistics	
	b_0[a]	b_1[a]	b_2[a]	R_{10}[a]	M.S.E.[b]	Absolute bias	CORR[c]
East	33 979 754	−231 951	396.6	0.967	0.046	4.28	0.98
Center	36 609 196	−247 740	419.7	1.242	0.029	6.33	0.93
West	10 513 910	−702 235	117.9	1.078	0.021	4.11	0.98

[a] Estimated parameters of the quadratic function in model 1. R_{10} refers to the respiration rate (μmol m^{-2} s^{-1}) at a temperature of 10 °C.
[b] Mean square error between the predicted and observed.
[c] Correlation coefficient between the predicted and observed.

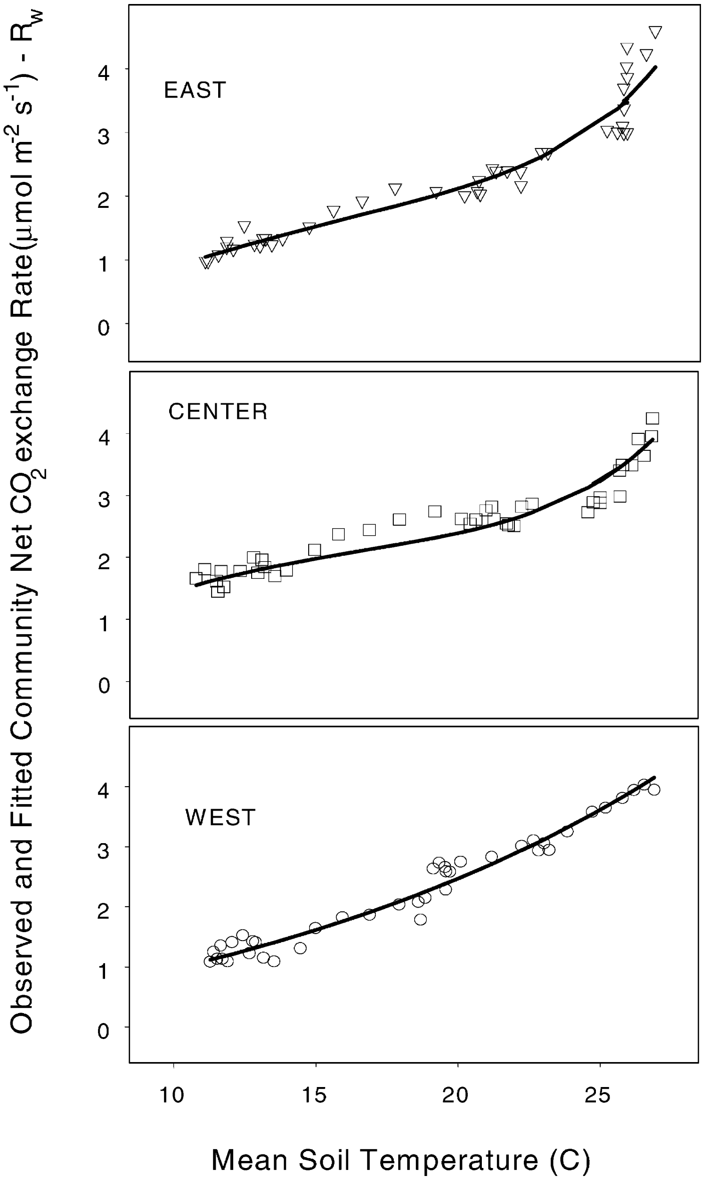

Fig. 5. Observed and predicted mean daily community net CO_2 exchange rate, R_w (µmol m^{-2} s^{-1}) for the East, Center, and West bays in the IFB at the Biosphere 2 Center. Symbols represent the observed rate and the solid line the predicted rate obtained by fitting function 1 to the data.

6. Discussion

Results from this study showed a weak exponential increase in soil respiration in response to an increase in temperature for the whole enclosed community. The average community net CO_2 exchange rate of 2.38 µmol m^{-2} s^{-1} and average community Q_{10} value of 2.26 are consistent with previous research (Peterjohn et al., 1994; Van Cleve et al., 1990; Rustad and Fernandez, 1998; Simmons et al., 1995; Billings et al., 1998; Russell and Voroney, 1998; Raich and Schlesinger, 1992).

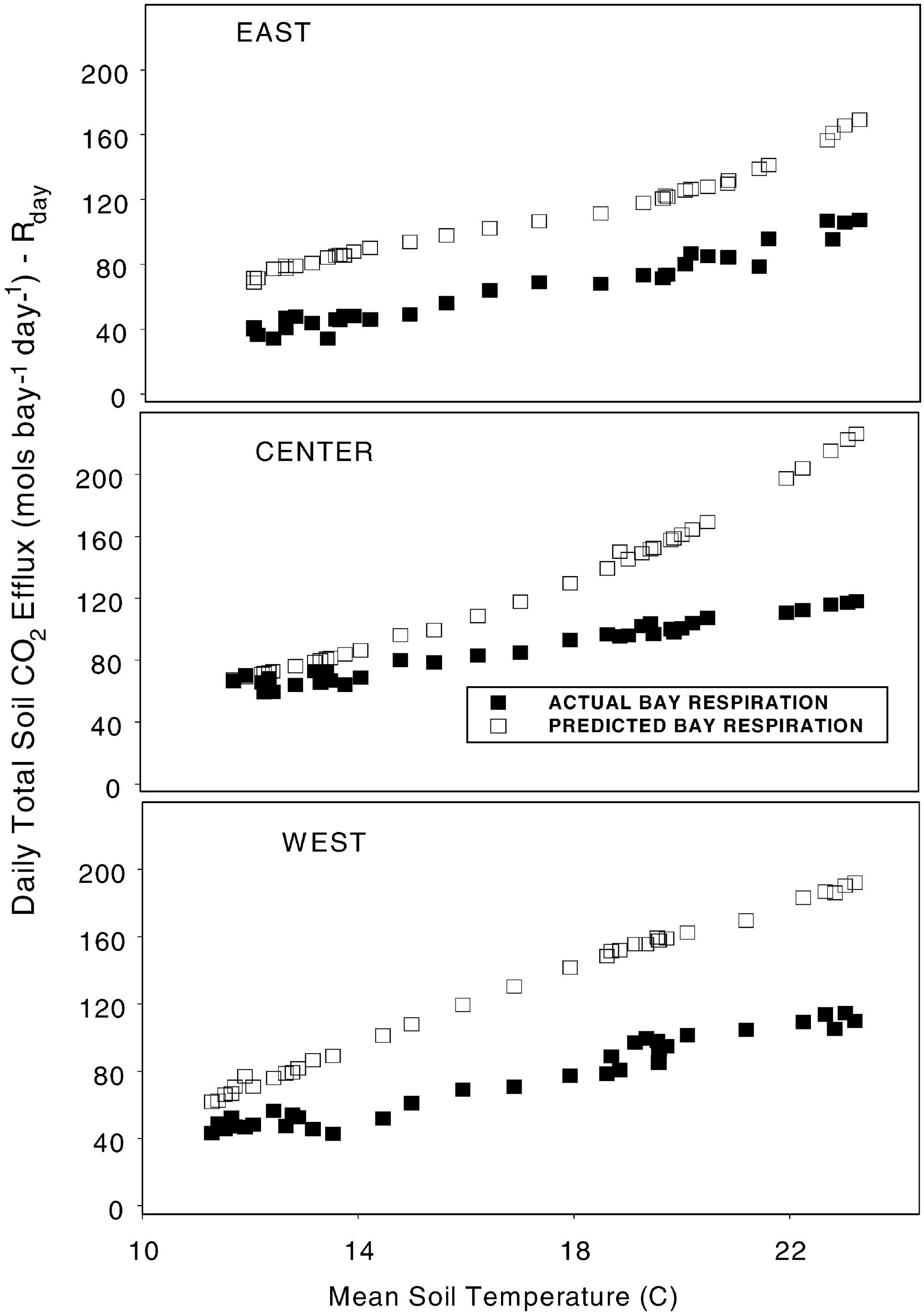

Fig. 6. Daily total belowground CO_2 efflux (mol bay^{-1} per day) for the East, Center, and West bays in the IFB at the Biosphere 2 Center. The closed symbols denote the actual value at the community level (R_{day}) and the open symbols denote R_{pday} (estimated values of R_{day} obtained by scaling up point measurements (R_p) data).

Table 4
Evaluation statistics comparing estimates of mean daily total community CO_2 efflux obtained by scaling up point measurement estimates (R_{pday}) to actual mean daily total community net CO_2 exchange (R_{day}) obtained from the entire community as a whole, for the East, Center, and West bays of the IFB at the Biosphere 2 Center

Evaluation statistics	East	Center	West
Bias	45.98	70.33	53.74
Bias (%)	66.52	67.63	62.61
Absolute deviation	45.98	71.64	53.74
Absolute deviation (%)	66.52	69.58	62.61
Accuracy	2196.8	7103.9	3443.9

Table 5
Mean Q_{10} values for soil respiration rates (standard error) derived from community level estimates (R_{day}) and from point measurements (R_p) for the dry and wet locations in the East, Center, and West Bays of the IFB in the Biosphere 2 Center (units for Q_{10} values are μmol m^{-2} s^{-1})[a]

Bay	Mean Q_{10}		
	Whole system	Point measurements	
		Dry	Wet
East	2.54 a (0.069)	1.84 a (0.143)	1.96 a (0.100)
Center	2.11 b (0.051)	1.86 a (0.142)	2.02 a (0.096)
West	2.15 b (0.050)	1.74 a (0.123)	1.91 a (0.157)

[a] Means in a column followed by the same letter are not significantly different from each other.

The community net CO_2 exchange rate observed in this study was a combination of root and microbial CO_2 efflux, arising from a coppiced forest system that was emerging from winter dormancy. Although there was no aboveground biomass, the living root biomass would have also contributed to the observed community net CO_2 exchange. However, it is difficult to assert what proportion of the whole is attributed to the roots. According to recent reports (Hanson et al., 1993, 2000) root respiration can amount to 40–50% of total soil CO_2 efflux. However, other studies have reported that root contribution was the lowest during the dormant season (Rochette and Flanagan, 1997; Edwards, 1991), but increased dramatically through spring and summer (May–June) (Edwards et al., 1977). Therefore, the pattern of soil CO_2 efflux observed here would most likely follow the pattern of respiration of soils undergoing a similar transition in nature (i.e. emerging from dormancy). Thus, some of the increase that we attribute to an increase in soil temperature could actually be due to increased root activity as the roots emerge out of dormancy and increased microbial activity.

By operating this facility in a 'closed' mode we were able to arrive at estimates of daily total community net CO_2 exchange (R_{day}). Estimates obtained by scaling point measurements (R_p) indicate that R_{pday} overestimated R_{day} by nearly 36%. The magnitude of the difference between point measurement derived estimates and the true bay values underlines a problem that is faced in a number of physiological measurements. Most of the current physiological measurements are taken on sections of soil in the ground or laboratory, or individual organs of a plant. There occurs not only variability among the various measurements but also the response could potentially vary depending on whether the perturbation is on the entire system, or on an isolated component (Griffin et al., 2002). In addition, scaling from point measurements magnifies the error observed at the point locations. This could pose serious problems when such parameters are used in models for large-scale predictions.

Scaling of point measurements in this study was simple and overestimated the community net CO_2 exchange rate on average by 36%. Several factors such as root distribution, uneven organic matter and nutrient distribution, and the limited number of point measurements taken could be responsible for the observed variability and possible overestimation of point measurements. Soil CO_2 efflux rates from point measurements were higher and more variable in the wet zones. Others have also reported similar findings (Rochette et al., 1991; Borken et al., 1999; Wildung et al., 1975). Rochette et al. (1991) reported that spatial variability could occur at a scale smaller than 15 cm, probably due to non-homogenous distribution of soil organic matter and roots. Observed variability could also be attributed to inherent problems associated with chamber techniques. Hungtington et al. (1998) reported an increased respiration rate when using chamber techniques, most probably due to pressure problems induced as a result of closure (Lund et al., 1999). These problems are usually observed when using point measurements thus making scaling difficult. Increasing the number of observations would reduce the overall variability; however, statistically

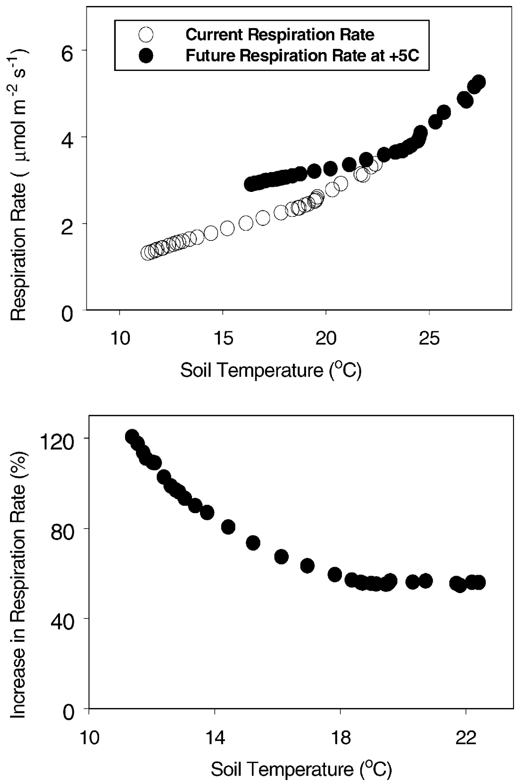

Fig. 7. Soil respiration rate estimated using function 1 for (a) a 5 °C increase in soil temperature and (b) the percent increase in soil respiration rate as a result that increase in soil temperature.

the number of point measurements that would be required from a 550 m^2 area to obtain a low coefficient of variation would be quite high, making sampling of large areas an arduous task. An overestimation of the community net CO_2 exchange by 36% translates to an additional 15 kg of carbon from a 550 m^3 volume of soil over a 33-day period or 165 kg per year. This suggests that extrapolation from point measurements to a global scale could have misleading conclusions. We can also conclude that small-scale variation in soil physical properties such as moisture has dramatic effects on soil CO_2 efflux and, therefore, needs to be considered in prediction equations.

To put the results of this study in the context of global climate change, the community net CO_2 exchange parameterized form of function 1 was used to calculate soil CO_2 efflux for a 5 °C increase in temperature. This resulted in an average increase of 62.3% in the efflux of CO_2 (Fig. 7a). We also observed that this percent increase in CO_2 efflux was higher at lower temperatures and lower at higher temperatures (Fig. 7b). This would suggest that an increase in temperature of soils at higher latitudes or at night, would result in a larger percent increase in soil CO_2 efflux. Since, global warming appears to be more pronounced at night (Easterling et al., 1997; Alward et al., 1999), the above conclusion could have dramatic effects on soil CO_2 efflux, and therefore the global carbon cycle.

The Biosphere 2 Center offers some unique features and several advantages that allowed us to conduct this experiment at the community level. Previously, soil warming experiments have been conducted using electrical heat-resistance ground cables (Peterjohn et al., 1993, 1994; Lukewille and Wright, 1997; McHale et al., 1998; Bergh and Linder, 1999; Rustad and Fernandez, 1998; Grime et al., 2000), passive heating greenhouses (Kennedy, 1995; Shaver et al., 1998), field chambers (Tingey et al., 1996; Jonasson et al., 1996; Jones et al., 1998; Welker et al., 1999), overhead infrared lamps (Bridgham et al., 1999), suspended electric heaters (Harte et al., 1995), and large screens (Luxmoore et al., 1998). Most of these methods are restrictive in terms of the total soil surface area, volume, and depth over which temperature can be manipulated. Also, most methods are able to manipulate soil temperature to within ±5 °C of ambient. In the present study, soil warming was achieved by actively warming the air mass, similar to the expected mechanism under global warming scenarios, with very good results. Despite the large soil volume and surface area we were able to successfully warm the entire soil area over a range of approximately 15 °C. Techniques used for measuring soil CO_2 efflux range from static chamber methods with soda lime (Edwards, 1982; Wildung et al., 1975; Seto and Yanagiya, 1983; Winkler et al., 1996), to open or closed flow through chamber methods utilizing gas chromatography (Billings et al., 1998) or infrared gas analysis (Howard and Howard, 1993; Kelting et al., 1998; McGinn et al., 1998; Boone et al., 1998; Grogan and Chapin, 2000). Other methods have used calculations based on soil air CO_2 concentrations and diffusivity constants (DeJong and Schappert, 1972), to micrometeorological techniques based on eddy covariance and concentration gradients (Valentini et al., 2000), to isotope techniques (Trumbore et al., 1995; Townsend et al., 1997).

However, with the exception of eddy covariance all other methods are either invasive, causing some disruption of the soil material or highly labor intensive. In the present system all sampling can be done in a non-invasive method with no disturbance to the soil. More importantly, measurements could be achieved for the whole community rather than for sections of soil, thereby not limiting our scope of inference. Important information can be obtained by point measurements using chamber techniques. However, the number of measurements that need to be taken to obtain a low coefficient of variation could be quite large and presents logistic difficulties.

Although the soil in this facility is only 1 m deep, initially artificially composited, and rich in organic matter, it has stabilized over time due to several years of crop rotations and management. It now has a C:N ratio of 9.9 indicating that the soil is reaching equilibrium (Stevenson, 1994). Average nutrient contents were quite similar across the bays and sufficient for plant growth. Results revealed that the Center bay exhibited higher CO_2 concentrations (Fig. 3). There are several possible explanations for this phenomenon. It is possible that the West and East bays may have leaked to the Center bay. Leak tests were done at a fixed temperature (20 °C) and not at the range of temperatures used in the experiment. These tests showed that leaks occurred at the rate of 2%/h from the Center to the West and East bays. CO_2 concentrations in the bays were corrected based on this static leak test. Therefore, it is possible, though unlikely, that leaks could have occurred in the reverse direction, from the West and East into the Center bay at other temperatures. It is also possible that the higher concentration of soil nitrogen observed in the Center bay may have been responsible for a higher microbial metabolic activity that resulted in a higher soil CO_2 efflux. Another explanation is that the amount of root biomass was higher in the Center bay. It was assumed that the amount of root biomass was similar among bays since they had the same number of trees or root stumps with similar stem diameters in the beginning of the experiment. Mean (standard deviation) root stump diameters taken at the beginning of the study were 43.4 (6.86), 45.37 (8.04), and 44.3 mm (9.86) for the East, Center, and West bay, respectively. No significant difference was observed in the stem diameters between the bays (data not shown). Based on established allometric regressions this would suggest that unequal amount of root biomass between bays was unlikely. Excavation of soil to perform detailed root analysis would have been informative; clearly, further tests will be needed to ascertain the cause of the higher soil CO_2 efflux rate observed in the Center bay. However, the most likely reason for the higher CO_2 concentrations is probably that the Center has a slightly larger soil surface area (585.6 m^2) as opposed to the 546.4 and 543.8 m^2 of the East and West bays, respectively.

7. Conclusions

There is evidence that respiratory responses of plant tissues may not exhibit simple temperature functions when integrated at the community scales (Gifford, 1994). Belowground CO_2 is a function of several interrelated factors, including organic matter decomposition, microbial activity, water availability, root respiration, soil type, standing crop, and season. Similarly, soils consist of different components with each exhibiting a different Q_{10} value (Boone et al., 1998). Temperature sensitivity of a soil depends on various factors, such as soil moisture, microbial activity, etc. However, to successfully model such a complex system by examining each individual component within a theoretical framework may prove to be a daunting task. To undertake such a task one has to measure and quantify the contribution of each component, model each component, scale all components to the whole and validate the result and study the interactions. Such a breakdown will become essential if we were to endorse increased soil carbon storage as a means of slowing the rate of atmospheric CO_2 increase. However, this would involve soil manipulations, and our ability to understand and model the behavior of each component of the soil will become extremely critical. The Biosphere 2 facility provides the necessary infrastructure to follow such an approach. Not only can we study behavior of individual components, but we can also validate models at the community level.

Small-scale warming facilities with short vegetation or only litter may be constructed for specific investigation; however, our objective was to demonstrate the utility of this facility in research at the community level. Assessment of community responses to global change requires much more information at that scale. We anticipate that results from various community level manipulations will be used in models to provide a synthesis of the combined effects of changing water, CO_2, and temperature conditions on a community. The Biosphere 2 system has several advantages over other systems for community level research. It is more suitable to address mass balance issues because it can be operated as a closed system and CO_2 fluxes can be measured on the community. Also, we have greater control of environmental parameters over the entire community that allows us to study responses to small perturbations. Hence, we conclude that this facility should prove very useful in the study of whole communities under changing environments.

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