105

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REGRESSION MODELS FOR CALCULATING GAS FLUXES MEASURED WITH A CLOSED CHAMBER

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Abstract

Portable closed chambers provide a valuable tool for measuring crop photosynthesis and evapotranspiration. Typically, the rates of change of CO_2 and water vapor concentration are assumed to be constant in the short time required to make the closed-chamber measurement, and a linear regression model is used to estimate the CO_2 and H_2O fluxes. However, due to the physical and physiological effects the measurement system has on the measured process, assuming a constant rate and using a linear model may underestimate the flux. Our objective was to provide a model that estimates the CO_2 and H_2O exchange rates at the time of chamber closure. We compared the linear regression model with a quadratic regression model using field measurements from two studies. Generally, 60 to 100% of all chamber measurement data sets were significantly nonlinear, causing the quadratic model to yield fluxes 10 to 40% greater than those calculated with the linear regression model. The frequency and degree of nonlinearity were related to the measured rate and chamber volume. Closed-chamber data should be tested for nonlinearity and an appropriate model used to calculate flux. The quadratic model provides users of well-mixed closed chambers an alternative to a simple linear model for data sets with significant nonlinearity.

Chamber techniques can quantify the rates of many biological gas exchange processes. Although the terminology varies, gas exchange measurement systems may be classified into three main types: (i) closed, non-steady state; (ii) closed, steady state (null balance); and (iii) open (flow through or dynamic). The advantages, limitations, assumptions, and computation of exchange rates differ greatly among these designs (Livingston and Hutchinson, 1995). We limit our discussion to the closed, non-steady-state system.

Photosynthesis (as carbon dioxide exchange rate, CER) and evapotranspiration (ET) measurements have been made at the canopy scale with closed chambers (up to 9 m^3 volume and 2.0 to 3.0 m^2 area) (Reicosky and Peters, 1977; Meyer et al., 1987; Daley et al., 1984; Reicosky, 1990). Depletion of CO_2 concentration or an increase in H_2O vapor are recorded while the chamber is closed for a short time (60–80 s). Soil respiration rates are measured similarly, except that CO_2 concentration increases with time. Rates were calculated by performing a linear regression of gas concentration (converted to mass basis and corrected for temperature and pressure) with time and then multiplying the resulting slope by the ratio of chamber volume to chamber area. Reicosky et al. (1990) labeled this technique the concentration regression (CR) method.

Reicosky et al. (1990) found that selecting a linear model based on high coefficient of determination (r^2) values may underestimate gas exchange rates. They discussed several techniques to estimate gas exchange at time zero (t_0), before the potential effects of the altered chamber environment become significant. Wagner and Reicosky (1992) showed that plots of closed-chamber CO_2 and H_2O concentrations vs. time appeared linear, and that a linear model accounted for much of the variability ($r^2 > 0.970$); however, further analysis suggested that gas concentration data often are nonlinear. Canopy gas exchange rates calculated using linear regression underestimated CO_2 and H_2O flux by 10% on average for corn (*Zea mays* L.), based on the modified rate regression (MRR) technique. A reliable method of estimating the CER and ET rates at the instant of chamber closure required further study.

Several factors affect the complex processes of canopy CER and ET (Acock, 1991; Gutschick, 1991; Norman and Arkebauer, 1991). However, in the 60 s required to make a closed-chamber measurement, several of these variables remain constant and do not contribute to the nonlinearity found in some data sets. Those parameters that remain constant include canopy architecture; light penetration; leaf N, age, and area; plant water status; and solar irradiance. Of course, care must be exercised in making measurements on partly cloudy days to ensure constant radiation for each measurement.

Gas concentration changes are the most obvious factors causing nonlinearity in closed-chamber measurements. The CO_2 and H_2O vapor concentrations necessarily change during the 60 s of measurement, since monitoring these changes is the basis for the closed-chamber technique. Using a closed system with syringe sampling, Akers and Green (1987) found the CER of tall fescue (*Festuca arundinacea* Schreb.) sampled at closure and after 60 s was significantly greater than that obtained from gas samples taken at 60 and 120 s. They observed an even larger rate when using an open-chamber technique.

A simple model for photosynthesis or transpiration can be based on Fick's law of diffusion, which states that the flux is proportional to the gradient and inversely proportional to the resistance; i.e., for photosynthesis:

$$\text{flux} = \frac{C_a - C_i}{r} \quad [1]$$

where C_a is the ambient CO_2 concentration (μmol m^{-3}), C_i is the intercellular CO_2 concentration (μmol m^{-3}),

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Abbreviations: CER, carbon dioxide exchange rate; CR, concentration regression; ET, evapotranspiration; H_0, null hypothesis; H_a, alternative hypothesis; QR, quadratic regression; r^2, coefficient of determination; R^2, coefficient of multiple determination; t, time; t_0, time zero.

and r is the resistance (s m^{-1}). It is intuitive that, in a non-steady-state closed-chamber system, the concentration difference driving the flux (the numerator in Eq. [1]) diminishes over the course of a closed-chamber measurement, thus reducing the flux. Resistance r is the sum of the boundary layer and stomatal resistance. Except under optimal plant water conditions, stomatal resistance is considered the major component of r. Thus, the change in gas concentration, along with the temperature increases occurring in the closed system, may affect the stomatal aperture, resulting in lower flux. Air and leaf temperature increases as large as 2 to 4°C in the 60-s closed-chamber measurements have been recorded (Daley et al., 1984; Wagner and Reicosky, 1992). Although care is taken, conditions of field canopy measurements sometimes preclude making a perfect chamber-to-soil seal, so leakage may also contribute to nonlinearity observed in some data sets.

Our objective was to provide a tool to estimate the CER and ET rate at the time of chamber closure. Numerous field measurements displayed nonlinear gas concentration data. A quadratic regression model was used to estimate the CER and ET rates when the data were significantly nonlinear, but this model does not explain the physical and physiological mechanisms that are creating the nonlinearity. The simple diffusion model described by Eq. [1] was presented to explain our results in a qualitative sense. We emphasize the need to check closed-chamber data for nonlinearity and to choose the appropriate model using statistical procedures.

Materials and Methods

The chamber system used was described previously (Reicosky et al., 1990; Reicosky, 1990). Two portable chambers were constructed by covering metal frames with clear plastic (Lexan, General Electric,[1] Pittsfield, MA). Four large squirrel-cage fans (each delivering 0.22 m^3 s^{-1}) were spaced uniformly near the bottom of the chambers, with air flow directed diagonally upward. Each chamber covered 2.67 m^2 of soil. The volume of the large chamber was 8.15 m^3, and the height was 3.70 m. The small chamber was used for small plants and for soil respiration measurements. Its height was 1.22 m, and volume was 3.25 m^3. The selected chamber was mounted on a forklift mechanism attached to a farm tractor.

An infrared gas analyzer (IRGA) (BINOS-Model 4b.2, Leybold-Heraeus, Hanau, Germany) monitored the CO_2 and H_2O concentrations of a gas sample continuously drawn from an aspirated cylinder near the top of the chamber. An inline 35 L min^{-1} pump circulated a gas sample from the chamber to the analyzer to minimize lag time (mean sample lag time = 8 s). Small pumps in the analyzer housing extracted a 1.5 L min^{-1} subsample. The analyzer operated in the differential mode (range of ± 50 μmol CO_2 mol^{-1} and $\pm 10\,000$ μmol H_2O mol^{-1}). The sample was analyzed with respect to a 0.065-m^3 ambient air reference tank that buffered short-term fluctuations and allowed reference gases to follow diurnal changes. All data were collected at 2-s intervals for 60 to 80 s.

Carbon dioxide exchange and ET rates were calculated using the linear concentration regression (CR) method and a multiple linear (quadratic) regression (QR). The CR method (Reicosky et al., 1990) assumes a linear change in gas concentration during chamber deployment. The gas concentration data were converted to a mass basis (corrected for temperature and pressure) prior to the regression analysis. The slope of the linear regression is multiplied by the chamber volume divided by chamber area and a time factor to convert the results to hourly units. Gas exchange rates were calculated from 15 data points (n = 15) collected at 2-s intervals, after the appropriate lag times. Results of CR with n = 25 were calculated, but are not reported because this procedure resulted in greater underestimation of gas exchange rates than CR with n = 15. For example, using soybean [*Glycine max* (L.) Merr.] measurements made in 1987, CR with n = 25 provided an estimate of CER that was 15% smaller on average than with n = 15.

The QR model extends the linear model to account for nonlinearity in the data. We added an observer-effect term to account for the combined influence of one or more physical and physiological changes occurring in the closed system that resulted in nonlinear gas exchange data. The quadratic model for CO_2 exchange used was:

$$[CO_2] = \text{linear process} + \text{observer effect} \qquad [2]$$
$$= a + bt \qquad + ct^2$$

This model is the sum of the logical parts; i.e., $a + bt$, the linear process of interest, and ct^2, the observer effect created by the chamber presence. Photosynthesis is a linear process only if the conditions driving the process remain constant. We assume that, with no chamber present and with constant environmental conditions, the flux is essentially constant (i.e., a linear process) in the small time step required to make a measurement. If the flux remained constant with the crop canopy enclosed, the linear model would be adequate. However, the presence of the chamber distorts the linear process we wish to measure, and so the second-order term is added to the model (Eq. [2]). The form of the quadratic equation was determined empirically. Other quadratic terms may fit the data equally well, but will not change the end result significantly. Differentiating Eq. [2] with respect to time yields:

$$CER_{QR} = d([CO_2])/d(t) = b + 2ct \qquad [3]$$

Setting t = 0 yields CER at t_0, before the observer effect diminishes the rate. The quadratic regression CO_2 exchange rate (CER_{QR}), then, is derived from the slope of the linear gas exchange process that we assumed would occur with no chamber present (b in Eq. [2]), as follows:

$$CER_{QR} = b \times (V/A) \times t_f \qquad [4]$$

where V is the chamber volume, A is the chamber area, and the time factor t_f converts to hours. In practice, parameters a, b, and c in Eq. [2] were derived from parameter estimates of a least squares multiple linear regression with one dependent variable [CO_2] and two independent variables (t and t^2). For H_2O vapor increase or CO_2 increase (i.e., soil respiration), the sign of the observer effect term (c in Eq. [2]) is negative.

The coefficient of multiple determination, R^2, and a standard F-test were used to indicate the utility of the QR model. A one-tailed Student's t-test was done to test the null hypothesis:

$$H_0: \qquad c = 0 \qquad [5]$$

The alternative hypothesis was:

$$H_a: \qquad c < 0 \text{ or } H_a: c > 0 \qquad [6]$$

for increasing or decreasing gas concentrations, respectively. A t-value in the rejection region at the 95% confidence level

[1] Mention of a trademark name or a proprietary product does not constitute a guarantee or warranty of the product by USDA, and does not imply its approval to the exclusion of other products that may be suitable.

Table 1. Study 1 comparison of quadratic regression (QR) and the linear concentration regression (CR) for CO_2 exchange rate (CER) in soybean and corn. The CER measurements >0.2 g CO_2 m^{-2} h^{-1} were averaged over 3 yr (1985–1987).

	Soybean			Corn		
	Positive CER >0.2 g CO_2 m^{-2} h^{-1}	Significant runs, CER_{QR}†	Avg. diff., CER_{CR} and CER_{QR}‡	Positive CER >0.2 g CO_2 m^{-2} h^{-1}	Significant runs, CER_{QR}†	Avg. diff., CER_{CR} and CER_{QR}‡
	no.	no. (%)	%	no.	no. (%)	%
Large chamber	83	55 (66)	30	992	623 (63)	14
Small chamber	811	646 (80)	24	104	100 (96)	15

† Number of positive CER measurements where QR model tests indicated significant nonlinearity at the 0.05 probability level.
‡ Average difference between CR and QR models for those instances where QR model tests indicated significant nonlinearity.

indicated significant nonlinearity that would likely cause the CR model to underestimate the flux. A one-tailed t-test was selected because the effect of the chamber's presence should never enhance the rate estimated with the CR model. The criteria established to replace the CR model with the QR model were: the quadratic term (observer effect) was significant at the 95% confidence level, the QR model resulted in an increase in the R^2, and the QR model F-test was significant.

Results of the QR model were compared with the CR model when standard statistical tests indicated significant nonlinearity in the data. The models were evaluated for numerous closed-chamber measurements from two field studies between 1987 and 1991 to compare the models over a wide range of measurement conditions, different crops, and different chamber volumes. Data were collected with the large, ventilated, closed chamber described above; however, the regression models presented may be suitable to other variations of the closed-chamber design, or for different target gases. We calculated the frequency (expressed as a percentage of all data sets) with which the QR model selection criteria were met and then estimated the average difference in the rate calculated with the CR and QR models for those cases. Only significantly nonlinear measurements were included in the average, because the differences between the CR and QR model results were meaningless if the QR model selection criteria were not satisfied. Including only those CER measurements > 0.2 g CO_2 m^{-2} h^{-1} prevented the average differences from being unduly influenced by the very high percentage differences possible due to random error at very low rates.

The improvement in accuracy provided with the QR model was demonstrated with numerous chamber measurements for two chamber volumes and two crops in two field studies. Photosynthesis measurements were made in Study 1 in a 3-yr tillage–irrigation experiment on irrigated and nonirrigated plots of corn and soybean. Several hundred measurements were made (Tables 1 and 2) at various stages of crop growth. Evapotranspiration measurements were available for the 1987 growing season only. Most soybean measurements were made with the small chamber, and most corn measurements were made with the large chamber.

Study 2 measurements were made on 9 and 10 Apr. 1989 on irrigated and nonirrigated spring wheat (*Triticum durum* Desf.) at the Maricopa Agricultural Center (MAC IV) experiment farm near Phoenix, AZ. The diurnal measurements made 90 d after planting (Reicosky et al., 1994) included 65 irrigated wheat measurements and 65 nonirrigated wheat measurements (Table 3). Crop height was 0.97 m, the density was 140 plants m^{-2}, and the green leaf area index was 4.9 (Dugas et al., 1991).

Results and Discussion

Figure 1 displays a typical large-chamber measurement on irrigated corn [Day of Year 209, 1122 h daylight time]. The ET calculated with the CR method was 0.40 mm h^{-1} ($r^2 = 0.997$). The data appear quite linear; however, the ET calculated with the QR method was 12% higher, or 0.45 mm h^{-1} ($R^2 = 0.999$, $t = -9.914$, and $F = 20229$). The CER calculated with the CR method was 5.3 g CO_2 m^{-2} h^{-1} ($r^2 = 0.993$). The result of the QR method was 8% higher or 5.7 g CO_2 m^{-2} h^{-1} ($R^2 = 0.998$, $t = 3.847$, and $F = 6656$).

Model comparisons for Study 1 soybean and corn CER measurements are summarized in Table 1. The table shows the number of CER measurements > 0.2 g CO_2 m^{-2} h^{-1}, the number and percentage of runs that were significantly nonlinear, and the average difference between the QR and CR model. In Study 1, 78% of soybean CER measurements displayed significant nonlinearity using criteria established for the QR model. Overall, about 64% of the corn CER measurements were nonlinear, but significant nonlinearity was demonstrated in 96% of small-chamber measurements, emphasizing the greater importance of selecting an appropriate model for small chamber volumes and relatively high rates of gas concentration change. The average difference in the CER_{CR} and CER_{QR} was much lower for corn than for soybean (14 vs. 24%, respectively). There may be a difference related in part to the species, but we should note that the majority of the corn CER measurements in Study 1 were made with the large chamber, while the

Table 2. Study 1 comparison of quadratic regression (QR) and the linear concentration regression (CR) for evapotranspiration (ET) in soybean and corn (1987).

	Soybean			Corn		
	ET samples	Significant runs, ET_{QR}†	Avg. diff., ET_{CR} and ET_{QR}‡	ET samples	Significant runs, ET_{QR}†	Avg. diff., ET_{CR} and ET_{QR}‡
	no.	no. (%)	%	no.	no. (%)	%
Large chamber	132	106 (80)	13	280	217 (78)	11
Small chamber	530	513 (97)	20	25	25 (100)	24

† Number of positive ET measurements where QR model tests indicated significant nonlinearity at the 0.05 probability level.
‡ Average difference between CR and QR models for those instances where QR model tests indicated significant nonlinearity.

Table 3. Study 2 comparison of quadratic regression where n = 15 (QR15) with the linear concentration regression (CR) for CO_2 exchange rate (CER) and evaporation (ET) measurements in wheat.

	CER			ET		
	Positive CER >0.2 g CO_2 m^{-2} h^{-1}	Significant runs, CER_{QR15}†	Avg. diff., CER_{CR} and CER_{QR15}‡	ET samples	Significant runs, ET_{QR15}†	Avg. diff., ET_{CR} and ET_{QR15}‡
	no.	no. (%)	%	no.	no. (%)	%
Irrigated	51	41 (80)	43	64	64 (100)	63
Nonirrigated	37	29 (78)	45	65	64 (98)	47

† Number of positive measurements where QR model tests indicated significant nonlinearity at the 0.05 probability level.
‡ Average difference between CR and QR for those instances where QR model tests indicated significant nonlinearity.

majority of soybean CER measurements were made with the small chamber. Nonlinearity occurred more frequently for the small chamber than the large chamber. This would be expected if the nonlinearity is due mainly to the decrease in concentration gradient for the enclosed plants.

The relationship between CER_{QR} and CER_{CR} for a subset of the Study 1 soybean measurements (1987 only) was summarized in Fig. 2. We plotted only those instances with significant nonlinearity in the concentration data. Of more than 300 measurements, only 8 were obvious outliers, probably due to random error.

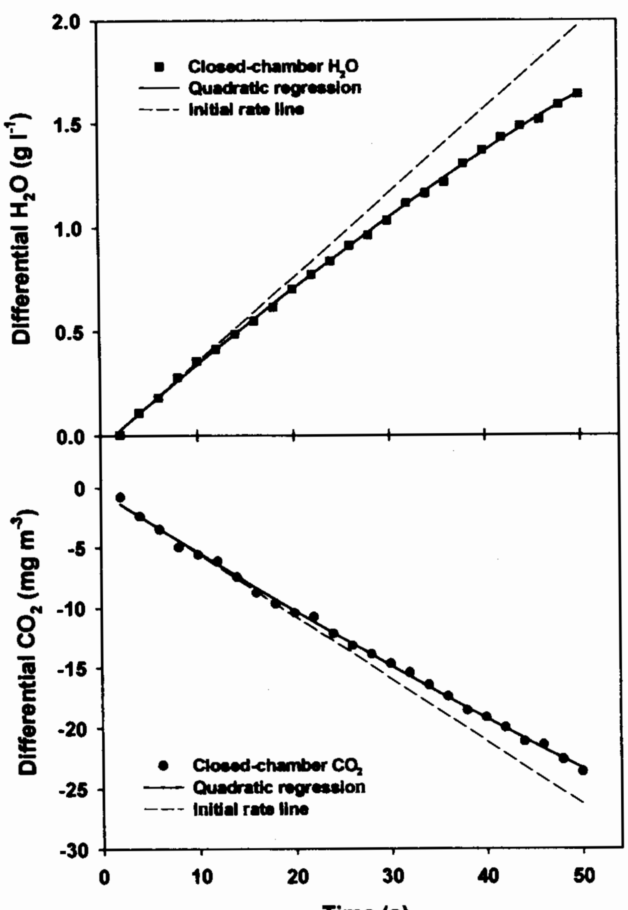

Fig. 1. Typical closed-chamber corn data set displays water vapor increase and CO_2 decrease in the large chamber. Symbols represent the differential gas analyzer output of the actual field canopy measurements. Solid line: quadratic regression curve; dashed line: initial slope (rate at t_0) of the quadratic curve. Both CO_2 and H_2O are measured differentially. Time = 0 is after initial canopy mixing and gas lag time adjustments.

Figure 3a displays CER_{CR} vs. CER_{QR} for all Study 1 CER–corn measurements (1987 only), while Fig. 3b shows only those measurements with significant nonlinearity. Most of the measurements fall on or above the 1:1 line. Several of the measurements included in Fig. 3a that fall above the 1:1 line (indicating that the CR method may be underestimating the CER) are not significantly nonlinear at the 95% confidence level and, therefore, are not plotted in Fig. 3b. More measurements displayed in Fig. 3a would be included in Fig. 3b if the model selection criteria confidence level were lowered. However, points below the 1:1 line in Fig. 3a will not pass model selection criteria (i.e., one-tailed t-test), ensuring that the QR model was not selected when CER_{QR} was less than CER_{CR}.

Table 2 summarizes the model comparisons for ET measurements on soybean and corn made in 1987 (Study 1); 94% of soybean measurements were nonlinear and the QR model results were 19% greater on average than with the CR model. The average difference between the models was larger for the small chamber, and the data were nonlinear more frequently for small-chamber measurements. About 80% of the corn ET measurements were significantly nonlinear, resulting in an average 13% difference between the CR and QR models. All the small-chamber measurements on corn were significantly

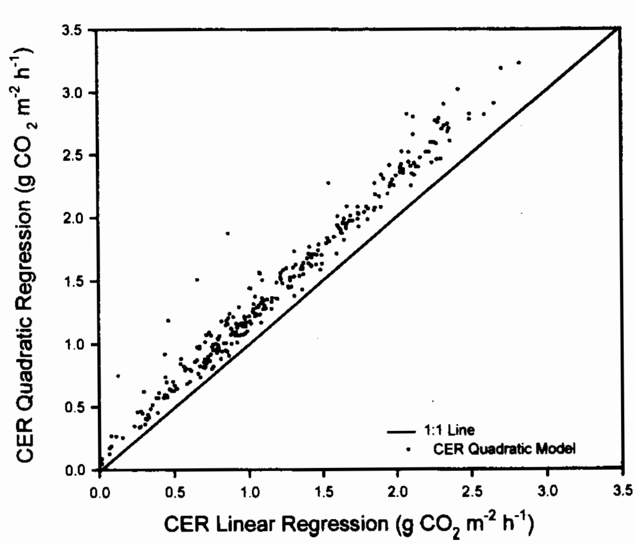

Fig. 2. Carbon exchange rate measurements for Study 1 soybean (1987 only). Instances with significant nonlinearity: n = 324.

nonlinear, and the average difference between the CR and QR model was about twice that calculated for the large chamber, reinforcing the importance of chamber volume. These data point to the importance of appropriate model selection for ET measurements.

In Study 2, gas concentration data were collected for just enough time to permit linear regression with 15 data points, so a quadratic regression with 15 data points (ET_{QR15}) was used. These measurements were made with the small chamber, which was largely filled with fully developed wheat plants under extreme evaporative demand that resulted in high ET and CER. Under these conditions, the QR model with $n = 15$ indicated significant nonlinearity for 80 and 78% of irrigated and nonirrigated CER wheat measurements, respectively, resulting in an average difference between the CR and QR models of about 44% (Table 3). For ET, 100% of irrigated and 98% of nonirrigated measurements were nonlinear, resulting in an average difference between the CR and QR models of 63% for irrigated and 47% for nonirrigated treatments. The combination of high rates and small chamber volume in Study 2 emphasized the limitations of the CR method and demonstrated the importance of selecting an appropriate model to overcome the inherent nonlinearity of the closed-chamber technique.

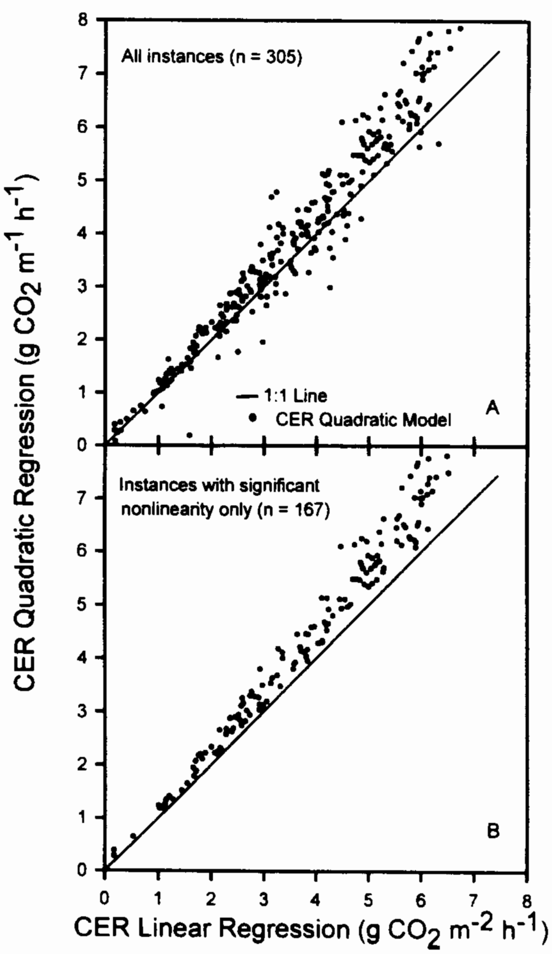

Fig. 3. Carbon exchange rate measurements for Study 1 corn (1987 only).

Conclusions

The closed-chamber technique provides a portable means of making CER and ET measurements at the crop-canopy level. The CR linear model, typically used for calculating fluxes from closed-chamber data, may be sufficient in some instances; however, numerous measurements indicated conclusively that closed-chamber gas concentration data should be tested for nonlinearity and the appropriate model selected. The QR model presented here estimates the flux at the instant of chamber closure.

The frequency of significant nonlinearity in the data sets varied from 60 to 100%. The average difference between the CR and QR models usually varied between 10 and 30%, but was as high as 63% for ET measurements in irrigated wheat. Nonlinearity in the data sets was related to the chamber volume and gas exchange rate, suggesting that altered gas concentration gradients are affecting the diffusion processes during the 60 s of measurement. The QR model presents a consistent mathematical framework to obtain the flux at the instant of chamber closure when data are nonlinear. Criteria outlined for selection of the QR model are increase in R^2, significant F-value, and a one-tailed Student's t-test indicating a significant observer effect term. The model accounts for the observer effect, regardless of the complex physical and physiological mechanisms creating the nonlinearity. The same model can be used for both increasing or decreasing gas concentrations. This empirical model provides a necessary tool to estimate the measured rate at the time of chamber closure; however, future work may require developing a model based on the complex physical and physiological mechanisms involved. Until such a model is developed and tested, the accuracy of the closed-chamber technique flux measurements may be substantially improved by selecting the QR model, when appropriate, to prevent potential underestimation of the rates by simple linear regression.

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