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A Multiple Chamber, Semicontinuous, Crop Carbon Dioxide Exchange System: Design, Calibration, and Data Interpretation

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Abstract. Long-term, whole-crop CO_2 exchange measurements can be used to study factors affecting crop growth. These factors include daily carbon gain, cumulative carbon gain, and carbon use efficiency, which cannot be determined from short-term measurements. We describe a system that measures semicontinuously crop CO_2 exchange in 10 chambers over a period of weeks or months. Exchange of CO_2 in every chamber can be measured at 5 min intervals. The system was designed to be placed inside a growth chamber, with additional environmental control provided by the individual gas exchange chambers. The system was calibrated by generating CO_2 from $NaHCO_3$ inside the chambers, which indicated that accuracy of the measurements was good (102% and 98% recovery for two separate photosynthesis systems). Since the systems measure net photosynthesis (P_{net}, positive) and dark respiration (R_{dark}, negative), the data can be used to estimate gross photosynthesis, daily carbon gain, cumulative carbon gain, and carbon use efficiency. Continuous whole-crop measurements are a valuable tool that complements leaf photosynthesis measurements. Multiple chambers allow for replication and comparison among several environmental or cultural treatments that may affect crop growth. Example data from a 2 week study with petunia (*Petunia ×hybrida* Hort. Vilm.-Andr.) are presented to illustrate some of the capabilities of this system.

Photosynthesis is the primary process for plant biomass production and has been studied extensively. Since most commercially available equipment has been designed for leaf measurements, leaf photosynthesis has been studied in more detail than canopy photosynthesis. Unfortunately, leaf photosynthesis measurements often are poorly correlated with dry matter production and yield (Elmore, 1980; Evans, 1993). Reasons for this poor correlation include the following: 1) the section of the leaf that is measured may not be representative of the entire leaf, 2) the measured leaf may not be representative of the entire canopy, 3) diurnal changes in photosynthesis, 4) changes in leaf CO_2 exchange during development, and perhaps most importantly 5) respiratory CO_2 efflux of roots and shoots is not measured. Another disadvantage of commercial leaf photosynthesis equipment is that only one leaf can be measured at a time.

Whole canopy measurements bypass the problem of finding a representative leaf and have been used successfully (e.g., Wells, 1991). In a literature review, Zelitch (1982) showed that there is generally a good correlation between canopy photosynthesis throughout the growing season and yield. This correlation would be expected to improve as measurements are taken more frequently. However, most canopy chambers are designed to take short-term measurements on one canopy at a time. There have been several new designs of whole-canopy gas exchange systems over the last few years. Andriolo et al. (1996) described a system for hourly measurements of carbon, water, and nitrate uptake by hydroponically grown plants, but this system has the limitation that it only measures one canopy. This also is the case for several other whole-plant or canopy gas exchange systems (Baille et al., 1996; Bugbee, 1992; Dutton et al., 1988; Long et al., 1996; Mitchell, 1992). A whole-plant, open, gas exchange system with two gas exchange chambers was described by Miller et al. (1996), but this system has the limitation that the gas exchange chambers do not have environmental control and are designed for short-term measurements. A system that can measure CO_2 exchange rates of multiple crops throughout their entire development does not have these limitations and should provide a rigorous test of long-term treatment effects compared to control plants. Poni et al. (1997) and Wünsche and Palmer (1997) describe multiple-chamber systems for continuous measurement of canopy gas exchange under field conditions. Field systems have the advantage that photosynthesis can be determined under conditions that resemble a natural environment. However, field systems normally do not allow for precise environmental control, limiting the type of research that can performed.

Growth chamber-based systems, on the other hand, allow for simple control of environmental conditions (CO_2, temperature, light, and relative humidity), facilitating study of environmental effects on photosynthesis and respiration. Growth chamber measurements also eliminate natural and unpredictable fluctuations in environmental conditions, simplifying data interpretation. This facilitates the study of changes in canopy CO_2 exchange during the growth cycle of a crop. A growth-chamber-based, multichamber, plant-growth system with precise environmental control (temperature and CO_2 concentration) has been described (Akers et al., 1985), and was later adapted for short-term (minutes to hours) CO_2 exchange measurements (Knight et al., 1988).

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Although a variety of whole-plant CO_2 exchange systems have been described, none of these systems allow for long term (weeks or months) measurements of CO_2 exchange under controlled environmental conditions. In this paper, we describe a system that semicontinuously measures CO_2 exchange of multiple crops enclosed in transparent acrylic CO_2 exchange chambers. The system can be placed in a greenhouse or growth chamber. With this system, it is possible to measure 10 crops at 5 min intervals (30 s per chamber). The ability to monitor semicontinuously multiple crops allows for comparison between environmental conditions or other treatments and determination of several parameters that cannot be collected with traditional CO_2 exchange methods.

Materials and Methods

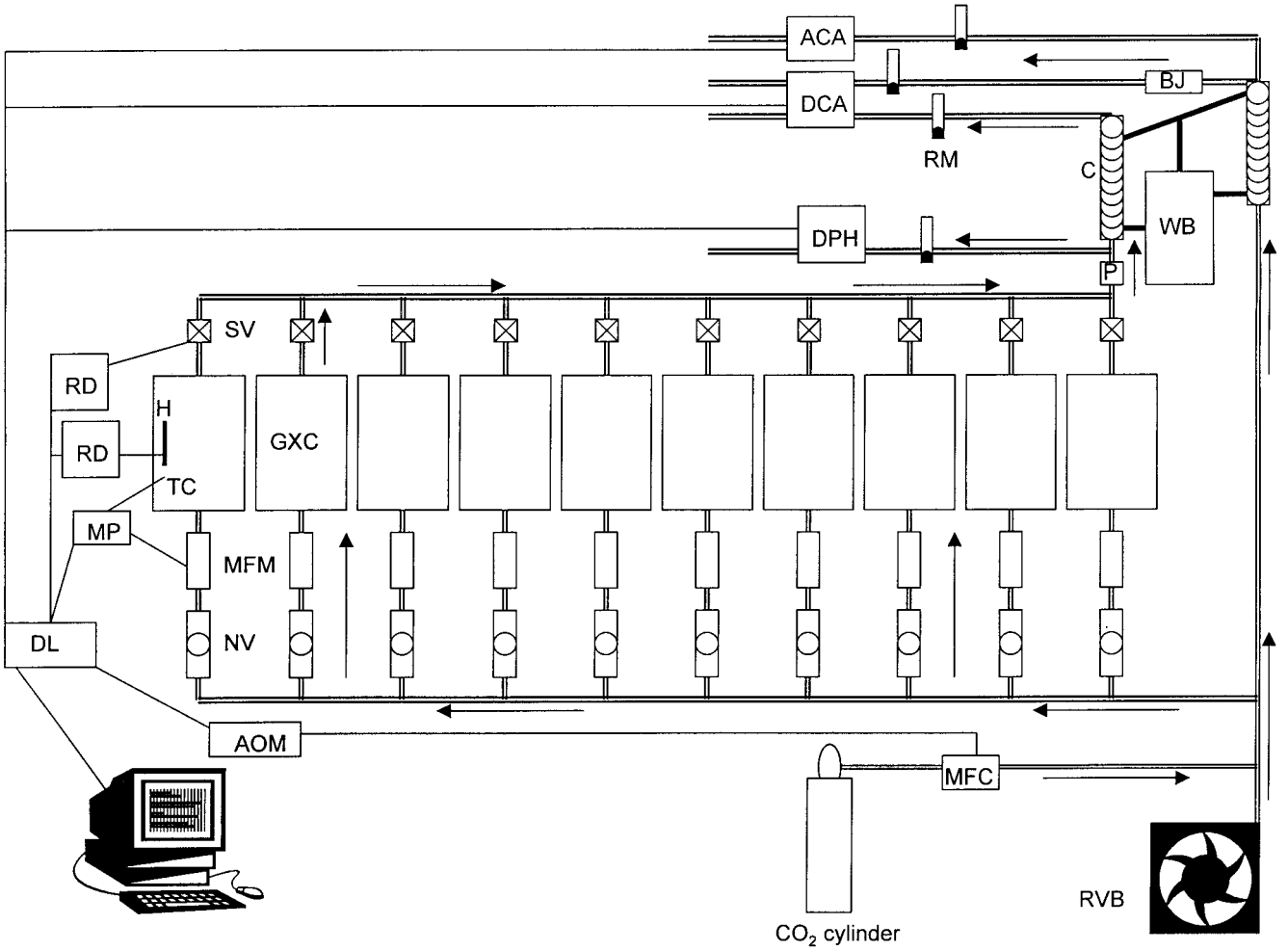
Carbon dioxide exchange measurements

Two slightly different, 10-chamber, open, gas exchange systems have been built at Utah State University and The University of Georgia. The basic operating principles are the same as those of single chamber measurements (Bugbee, 1992; Field et al., 1991; Mitchell, 1992). A rotary vane blower (Sutorbilt, Gardner Denver Machinery, Quincy, Ill.) provides air to a manifold, where the air stream is split into 10 separate tubes (Fig. 1). The CO_2 concentration of the air is measured with an infrared gas analyzer in absolute mode (IRGA, SBA-1, PP-systems, Haverhill, Mass.).

Air flow (10 to 20 $L \cdot min^{-1}$) through the individual tubes is measured with mass flow meters (model 820; Sierra Instruments, Monterey, Calif.) connected to a multiplexer and datalogger (AM25T and CR10T, Campbell Scientific, Logan, Utah). The outlets of the mass flow meters are connected to the gas exchange chambers with flexible plastic tubing (Bev-a-Line IV, 6.4 mm i.d., Cole-Palmer, Vernon Hills, Ill.). Mass flow meters have significant advantages over volumetric flow meters for use in gas exchange measurements, because mass flow meters automatically correct flow rate for changes in temperature and pressure, which can cause significant errors when volumetric flow meters are used.

The gas exchange chambers are made out of 5 mm thick sheets of cast acrylic plastic (Lucite, DuPont, Wilmington, Del.; 0.47 m long × 0.36 m wide × 0.61 m high, 101 dm^3 volume) with 6 mm acrylic rods in the corners for additional support. Lucite uniformly transmits 92% of light from 400 to 700 nm. Air inside the chamber is mixed continuously with fans (V624L, Micronel, Vista, Calif.; 500 $L \cdot min^{-1}$). Since the system is designed as an

Fig. 1. Diagrammatic representation of a multiple chamber system for semicontinuous CO_2 exchange measurements of crops or canopies. Double lines indicate tubing for air flow, thick lines indicate water lines, and thin lines indicate electrical and electronic connections. Arrows indicate the direction of the air flow. For clarity, the heater and thermocouple are shown in only one of the gas exchange chambers. A detailed view of the gas exchange chambers is illustrated in Fig. 2. ACA (absolute CO_2 analyzer), AOM (analog output module), BJ (buffer jar), C (condensor), DCA (differential CO_2 analyzer), DL (datalogger), DPH (dew point hygrometer), GXC (gas exchange chamber), H (heater), MFC (mass flow controller), MFM (mass flow meter), MP (multiplexer), NV (needle valve), P (pump), RM (rotometer), RVB (rotary vane blower), SV (solenoid valve), WB (water bath), RD (relay driver), and TC (thermocouple).



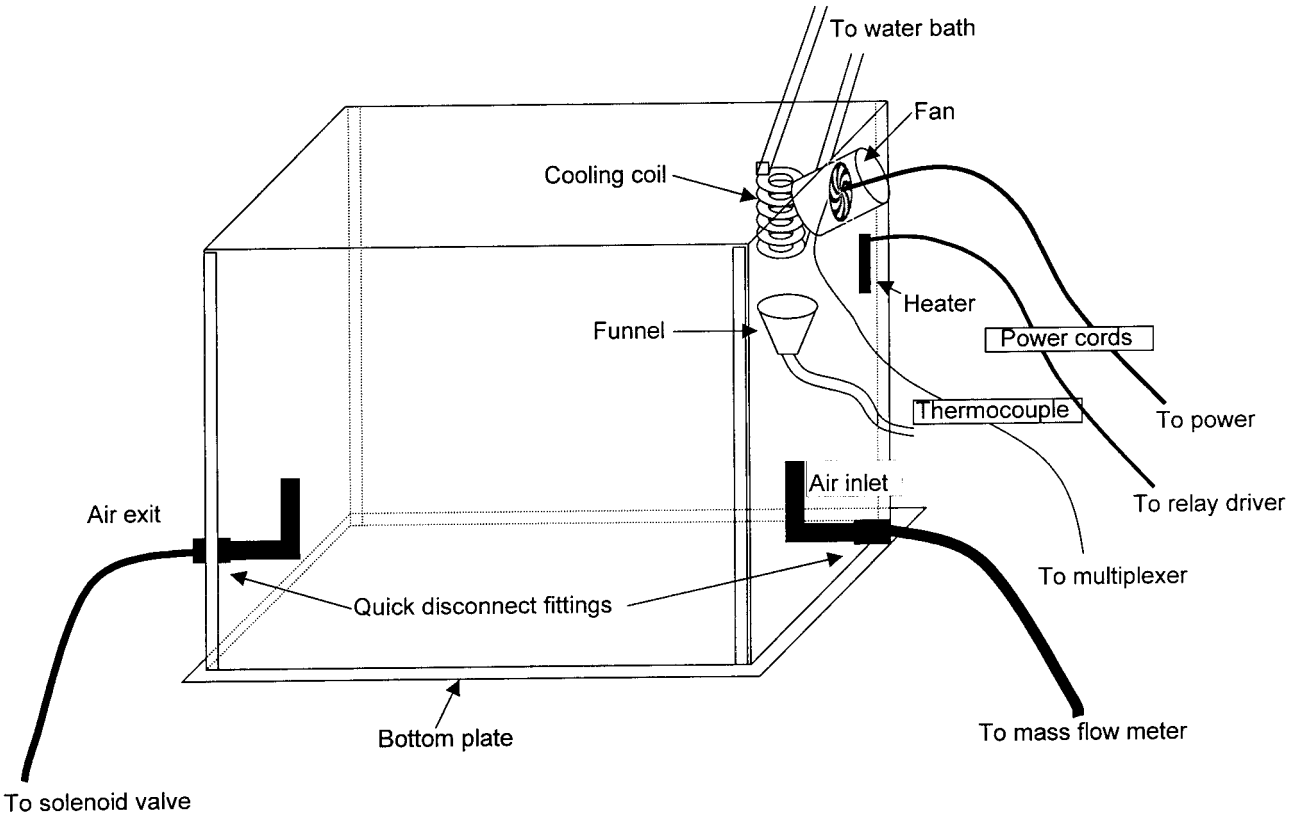
open gas-exchange system, the chambers do not need to be airtight. Thus, the chambers are simply placed on top of a base plate (Fig. 2), which makes it easy to place plants inside the chambers.

Tubing (3.2 mm i.d.) is attached to an outlet of the chamber and the tubing from all chambers goes to a manifold. Airflow through the individual tubes is controlled by opening or closing two-way solenoid valves with a solenoid driver (SDM-CD16, Campbell Scientific, Logan, Utah), controlled by the datalogger. Only one solenoid valve is opened at one time, so air from each chamber is sampled individually. The relay drivers can control a maximum of 16 solenoid valves, so the system can be expanded to include more chambers without a significant change in design.

A pump (MAA-P122, Gast, Benton Harbor, Mich.) draws air from the gas exchange chamber through the manifold and blows it to a dew point hygrometer (Dew-10, General Eastern, Woburn, Mass.) and through a condenser to a differential infrared gas analyzer (IRGA; LI-6251, LI-COR, Lincoln, Nebr.). The condenser is necessary to remove most of the water from the air, preventing interference between water vapor and CO_2 in the gas analyzer (Bugbee, 1992). All IRGAs are also sensitive to atmospheric pressure, which is affected by elevation. Calibration of the IRGA automatically corrects for the effects of elevation, but not for daily pressure changes. These can alter the calibration by ±1% and can be corrected for with an optional pressure sensor (LI-6262-03, LI-COR, Lincoln, Nebr.). Other IRGAs are available that automatically correct for water vapor and changes in atmospheric pressure.

When switching from measuring one chamber to another, the tubing is purged for 15 s to remove the air from the previous chamber. The differential IRGA is used to measure the difference in CO_2 concentration between the air entering and exiting the gas exchange chamber (ΔCO_2, $\mu mol \cdot mol^{-1}$). Net photosynthesis (P_{net}) and respiration during the dark period (R_{dark}, $\mu mol \cdot s^{-1}$) of the plants in the chambers is calculated by multiplying ΔCO_2 and mass flow of the air through the chambers ($mol \cdot s^{-1}$).

Fig. 2. Diagram of a CO_2 exchange chamber. The air in the chamber is mixed with a fan to assure uniform conditions. The heater, thermocouple, and cooling coil are used to control temperature and humidity in the chamber. Condensate is collected with a funnel and drained out of the chamber.



Environmental control

The small, transparent chambers can be placed inside a larger growth chamber and the environmental controls of the large growth chamber can be used to control the environment inside the gas exchange chambers. If different conditions are desired within the separate gas exchange chambers, it is possible to control the environment in every chamber individually.

Controlling CO_2 concentration. The CO_2 level in each chamber is controlled primarily by adding CO_2 to the prechamber air stream so that the CO_2 concentration of the air inside the chambers is depleted to the desired CO_2 level. A rapidly growing crop can reduce the CO_2 concentration by ≈100 $\mu mol \cdot mol^{-1}$, so that when ambient CO_2 concentrations are desired, the prechamber air has to be enriched to ≈470 $\mu mol \cdot mol^{-1}$ during the light period. The amount of CO_2 that is added to the prechamber air stream is regulated with a mass flow controller, which is controlled by the datalogger and an analog output module (SDM-AO4, Campbell Scientific, Logan, Utah). When the chambers have different photosynthetic rates, the air flow through the individual chambers can be adjusted with needle valves to maintain the same CO_2 concentration in each chamber.

Controlling humidity. Cooling coils provide independent humidity control for each chamber. To accomplish this, a 50 cm long coil of either copper or stainless steel tubing is placed in front of the fan (Fig. 2). The humidity is controlled by adjusting the temperature of chilled water through this coil. The dew point of

the air in the chamber is measured with the dew point hygrometer and normally is within 1 °C of the temperature of the coil. Relative humidity thus depends on the coil and air temperature inside the chambers. A small funnel below the coil collects and drains the condensed water. Since the solubility of CO_2 and HCO_3^- in pure water is low, this does not have a measurable effect on the gas exchange measurements (Bugbee, 1992).

Controlling temperature. Temperature control is accomplished by adding a small (50 to 100 W) electric resistance heater near the fan at the top of the chamber. The datalogger cycles this heater on and off as needed to achieve the desired temperature, which is measured by a shielded aspirated thermocouple. Short term temperature (15 min) fluctuations of 1 °C are typical, with daily averages within 0.2 °C of the set point. These heaters can increase the temperature inside a gas exchange chamber by up to 12 °C above the temperature of an unheated chamber.

Controlling photosynthetic photon flux (ppf). For most studies, it is imperative that *PPF* levels are similar among all gas exchange chambers. Since the light distribution inside growth chambers is normally not perfectly uniform, light levels may have to be adjusted by shading individual chambers with a neutral density shade material to achieve identical *PPF* levels inside the gas exchange chambers.

System calibration, error sources, and response time

Calibration. Although several designs for canopy gas exchange have been published (Baille et al., 1996; Bugbee, 1992; Corelli-Grapadelli and Magnanini, 1993, Dutton et al., 1988; Long et al., 1996; Mitchell, 1992; Poni et al., 1997, Wünsche and Palmer 1997), none of these papers address techniques for integrated system calibration. Calibration of the individual components does not ensure overall system accuracy, because of possible calculation errors or leaks. We tested system performance in two ways. First, gas exchange was measured in empty chambers, to ensure that measured CO_2 exchange was zero. Although this test is used commonly, it does not detect certain calibration or programming errors and does not guarantee system accuracy under conditions when the CO_2 exchange rate is not zero. Second, a calibration test was performed by placing a known amount of $NaHCO_3$ in a chamber and adding dilute acid to it at a slow rate. In the resulting reaction, 1 mole of CO_2 is evolved from each mole of $NaHCO_3$. These tests showed that the accuracy of the systems at Utah State University and The University of Georgia were 102.0% ± 6.0% and 98.4% ± 2.8% (mean ± SD), respectively.

The difference in accuracy between the two systems may be due partially to flow meter calibration. Preliminary tests indicated calibration problems with the mass flow meters from two manufacturers (model 820; Sierra Instruments, Monterey, Calif. and model GFM37, Aalborg Instruments, Monsey, N.Y.). After the mass flow meters were received from the manufacturer, they were connected in series to detect differences in calibration of the meters. Differences of up to 6% were found in flow meters of both brands, while specifications indicate an accuracy of 1.5% of full scale. This problem persisted even after the flow meters were returned repeatedly for factory recalibration, suggesting that the calibration may shift during shipment. Finally, we connected all flow meters in series and adjusted them to the average value. The $NaHCO_3$ calibration (see above) indicated that system accuracy is acceptable, implying that flow meter calibration was adequate.

Error sources. A potential error source is leaks in the system, which can cause errors in two ways. Leaks between the flow meters and the acrylic chambers cause an overestimation of CO_2 exchange, because the mass flow of air into the chambers is overestimated. Secondly, leaks can cause errors if outside air leaks into the tubing, thereby changing the CO_2 concentration. Leaks are inevitable, because the air that is blown into the chambers (10 to 20 $L \cdot min^{-1}$) needs to exit again, and only a small fraction (<1 $L \cdot min^{-1}$) is used for H_2O and CO_2 analysis. To minimize errors due to leaks, it is important to maintain positive pressure in most of the system, thus preventing outside air from leaking into the system. However, the pump that draws the air from the solenoid valves creates a partial vacuum between the gas exchange chambers and the pump, so it is crucial that all connections in the part of the system between the gas exchange chambers and pump are airtight.

To minimize noise due to fluctuations in the CO_2 concentration of the air blown into the system, a buffer jar is included in the tubing that directs prechamber air to the differential IRGA. The buffer jar ensures that it takes both pre- and postchamber air the same amount of time to reach the differential IRGA. The flow rate of the prechamber air to the differential IRGA is much less than the flow rate of the air through the gas exchange chambers. Therefore, the volume of the buffer jar needs to be determined based on the flow rate through the jar, the flow rate through the gas exchange chambers, and the volume of the gas exchange chambers. Measurements of empty chambers were used to confirm the appropriate size of the buffer jar.

Calibration drift of the IRGA measuring the ΔCO_2 also can cause error in the measurements. The LI-6251 IRGA has a stable span calibration and small zero drift. However, if ΔCO_2 is small, the zero drift can introduce significant errors. If necessary, this error can be corrected by measuring an empty chamber and subtracting the ΔCO_2 measured in this chamber from the ΔCO_2 in the other chambers. Since the relay drivers can control 16 solenoid valves, an additional chamber can be added to the system for this purpose.

Response time. Although photosynthesis responds quickly to changing environmental conditions (e.g., *PPF* and temperature), short-term changes in photosynthesis are measured with a delay (i.e., a 50% increase in P_{net} does not cause an immediate 50% increase in ΔCO_2). How fast this occurs depends on the response time of the system (τ) and the time (t) since the change in P_{net} occurred:

$$\% \text{ change measured} = 100 \times (1 - e^{-t/\tau}) \qquad \text{[Eq. 1]}$$

where τ is the volume of the gas exchange chamber divided by the flow rate through the chamber. If a sudden change in P_{net} occurs, 63% of that change will be evident in the measurements after a period τ, 95% after 3τ and 99% after 5τ. If a fast response is required, a smaller chamber can be used or the flow rate can be increased. With a flow rate of 10 to 20 $L \cdot min^{-1}$ and a chamber volume of 101 L, τ varies from 5 to 10 minutes.

Data interpretation

The described system measures net CO_2 exchange rates (P_{net}, R_{dark}) directly and several other parameters can be calculated from these data. Since R_{dark} is measured as the CO_2 exchange rate of the crop, it is expressed as a negative value (CO_2 efflux from the plants). Average gross photosynthesis during the light period ($P_{gross,avg}$) can be estimated as the difference between the daily averages of P_{net} ($P_{net,avg}$) and R_{dark} ($R_{dark,avg}$), assuming that respiration is similar in the light and dark. This is an estimate of the CO_2-fixation rate of the crop.

Previous studies have also assumed that respiration occurs at

the same rate in the light and the dark (Amthor, 1989; McCree, 1982; Monje and Bugbee, 1998), but this assumption has not been confirmed rigorously. Current evidence suggests that the rate of dark respiration in leaves in the light is less than in the dark. Villar et al. (1994) present data suggesting that dark respiration in the light may be only 55% of R_{dark} in the leaves of two woody species. In the light, TCA cycle activity may be lower and energy produced in photophosphorylation could be used to offset both nitrate reduction and maintenance costs in chloroplasts. However, leaf respiration accounts for only a fraction of total plant respiration because of respiration in stems and roots. Measurements in our laboratory indicate the root respiration increases about 30% during the light period, probably because of the increased carbohydrate supply (Monje and Bugbee, 1996). We thus assume that whole plant respiration is the same in the light as in the dark.

Crop carbon accumulation [daily carbon gain (DCG) or cumulative carbon gain (CCG)] depends both on the amount of CO_2 fixed by the canopy, and on how much CO_2 is lost by respiration:

$$DCG = (P_{net,avg} \times t_{light}) + (R_{dark,avg} \times t_{dark}) \quad \text{[Eq. 2]}$$

where t_{light} and t_{dark} are the duration of the light and dark period (s), respectively. Cumulative carbon gain over time can be calculated as the sum of the DCGs or the integral of all P_{net} and R_{dark} measurements. Daily carbon gain is similar to crop growth rate (in moles C per day), while CCG is the total amount of carbon accumulated by the plants since the start of the experiment. We have found a close correlation ($r^2 > 0.98$) between CCG and plant dry weight at the end of experiments (van Iersel and Bugbee, 1997, van Iersel, 1999a), indicating that these measurements are indeed a good measure of crop growth rate.

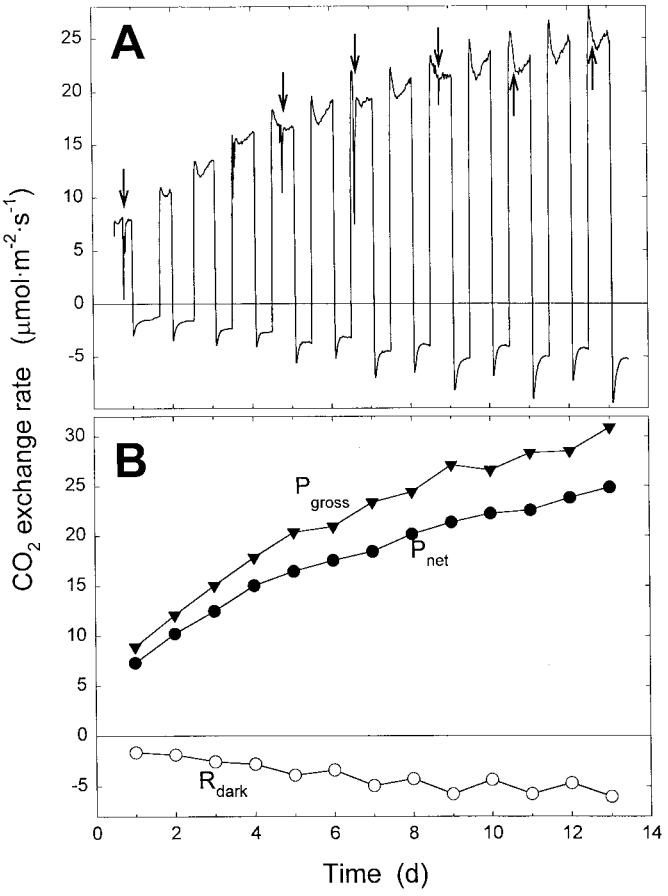


Fig. 3. Exchange rate of CO_2 of a petunia crop in a gas exchange chamber. The (**A**) raw data show the diurnal changes in gas exchange, while (**B**) daily means of net photosynthesis (P_{net}) and dark respiration (R_{dark}) are better suited to show long term changes. Gross photosynthesis (P_{gross}) was calculated as the sum of P_{net} and R_{dark}. All data are expressed per unit ground area. The first dark period was longer than subsequent ones due to a technical problem. In **A** arrows indicate the time of watering.

Both photosynthetic and respiratory rates are important in determining the growth rate of a crop, and from these two characteristics, carbon use efficiency (CUE, dimensionless), the ratio of C stored in biomass to total C fixed in photosynthesis (Amthor, 1989), can be estimated:

$$CUE = DCG/(P_{gross,avg} \times t_{light}) \quad \text{[Eq. 3]}$$

The assumption that respiration is constant in the light and dark is necessary for calculation of $P_{gross,avg}$, and thus for determination of CUE. Fortunately, changes in dark respiration during the light period have only a small effect on CUE. Because P_{net} is approximately four times as large as R_{dark} (Fig. 3), a 15% decrease (or increase) in whole-plant respiration during the light period changes CUE by only about 2% (when the photoperiod is 14 h).

We normally enclosed the pots with growing medium in the gas exchange chambers. Thus, soil and root respiration are included in the CO_2 exchange measurements. Since root respiration is part of whole plant metabolism, this must be included in whole plant measurements. Respiration by microorganisms in the root zone consists of two separate processes, respiration of organic compounds leaking from plants roots and microbial breakdown of organic matter in the growing medium.

Estimates of the quantity of organic compounds exuded by plant roots vary widely, but there is considerable evidence that carbon efflux increases when plants are under stress (Haller and Stolp, 1985; Smucker, 1984). Measurements of roots and microbes on healthy plant roots indicate that the fraction of carbon respired by root zone microorganisms is typically <2% of the total carbon fixed by the plants (Hojberg and Sorensen, 1993; Smart et al., 1995). Some experimental treatments can cause root-zone stress and this could significantly increase rhizosphere microbial respiration. It is important to realize that the carbon respired by rhizosphere microorganisms came from photosynthesis and it is thus necessary to include this respiration in the determination of P_{net}, $P_{gross,}$, R_{dark}, and CUE.

The efflux of CO_2 from microbial breakdown of soil organic matter also is included in the measured plant respiration, which could cause errors because this respiration is not related to plant metabolism. However, our measurements indicate that respiration caused by breakdown of soil organic matter normally accounts for <0.1% of the daily carbon gain of typical plant canopies (data not shown). Breakdown of organic matter will only have a significant effect on the measurements if very small plants are grown in a large volume of soil.

Results and Discussion

Typical CO_2 exchange data are shown in Fig. 3. Petunias (*Petunia ×hybrida*) were grown in a peat–perlite medium in a greenhouse. At the start of the experiment, 60 plants were placed in the gas exchange chambers. The *PPF* was 780 μmol·m^{-2}·s^{-1} (39.3 mol·m^{-2}·d^{-1}) at the canopy level, with a photoperiod of 14 h and constant temperatures during the light and dark periods (29/23 °C). Although 10 chambers were used in this experiment, data from only one set of plants is shown for demonstration purposes.

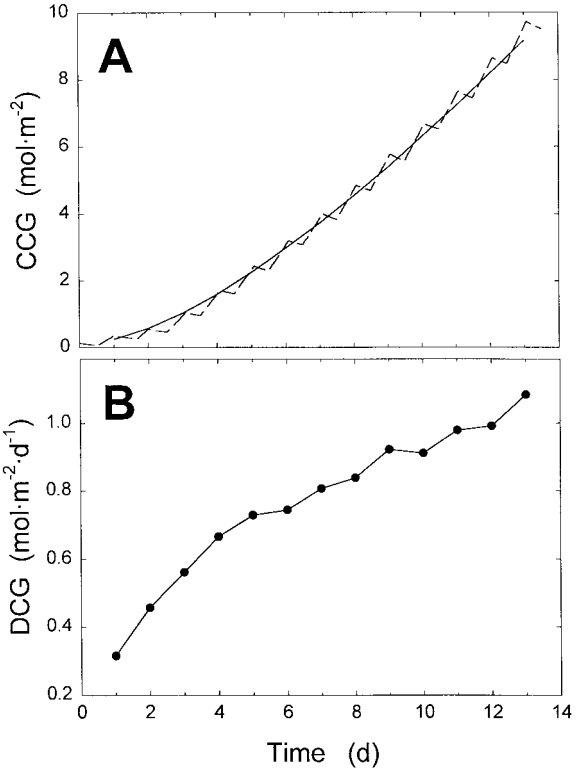


Fig. 4. (**A**) Cumulative carbon gain (CCG) and (**B**) daily carbon gain (DCG) of a petunia crop in a growth chamber. In **A** cumulative carbon gain was calculated as the cumulative value of DCG (solid line) and as the integral of the CO_2 exchange data (broken line). Note the decrease in CCG that occurs at night due to respiration when CCG is calculated as the integral of the CO_2 exchange data. All data are expressed per unit ground area.

A detailed description of this experiment has been published previously (van Iersel and Bugbee, 1996). Distinct diurnal changes occurred in photosynthetic and respiration rates (Fig. 3A). Photosynthesis generally was high at the start of the light period, but decreased during the next 4 h, probably because of feedback inhibition of photosynthesis (Greer, 1995). There was a consistent increase in P_{net} during the last 10 h of the light period, possibly due to increased light interception by the growing plants (Lawlor, 1995). Dark respiration was highest at the start of the dark period and then decreased slowly to a fairly constant rate during the rest of the night.

A sudden decrease in measured photosynthesis occurred immediately after the plants were watered with nutrient solution. At least two factors contributed to this. Water can contain significant amounts of bicarbonate, which can evolve CO_2 upon watering, thereby decreasing the measured photosynthetic rate. Since the solubility of bicarbonate in water is dependent on pH, CO_2 evolution after watering can be minimized by adjusting the pH of the water to 5.5 or less. However, this did not completely eliminate the decrease in P_{net} after watering. Another contributing factor may be the rapid displacement of air in the growing medium by water. The CO_2 concentration of air in the growing medium is likely to be high, due to root and microbial respiration, and a sudden displacement of this air would decrease measured P_{net}.

Plotting the raw data (collected at 15-min intervals) is useful to emphasize diurnal changes in CO_2 exchange, but daily averages are more suitable if long-term processes are of interest. Figure 3B shows the gradual increase in P_{net}, P_{gross}, and R_{dark} during development of the crop. Net and gross photosynthesis increase because of increasing leaf area which results in increased radiation interception by the canopy (Lawlor, 1995). Respiration increases, because larger plants have more maintenance respiration, while the higher growth rate of larger plants increase growth respiration (van Iersel, 1999b).

The CO_2 exchange data are then used to calculate DCG and CCG (Fig. 4). Cumulative carbon gain was calculated both as the cumulative value of DCG and as the cumulative value of the CO_2 exchange data. These two methods result in curves with the same long-term trend, but calculating CCG directly from the gas exchange data has the advantage that diurnal changes in growth are still apparent (Fig. 4A).

Carbon use efficiency is calculated from DCG and $P_{gross,avg}$ (Fig. 5) and distinct trends are apparent during plant development. Initially, carbon gain increased rapidly, possibly because the plants were acclimating to the conditions in the gas exchange chambers. Carbon use efficiency decreased from days 2 to day 9, but increased again thereafter. The range of calculated CUE values (0.67 to 0.79) is within the range of those determined for other crops, which were quantified by ^{14}C labeling or CO_2 exchange measurements (Amthor, 1989; McCree et al., 1990).

Uniformity among gas exchange rates measured in the 10 chambers is generally good. When the CO_2 exchange rates of 10 groups of plants (without any experimental treatments) are measured, the coefficient of variation generally is between 0.03 and 0.07 (standard deviation divided by the mean). In an experimental design with five treatments and two replications, significant differences in CO_2 exchange rates between treatments can be detected when differences are 10% to 15% or more. Detailed descriptions of different experiments and analyses with these systems have been published previously (Bednarz and van Iersel, 1998; Dougher and Bugbee, 1997; van Iersel and Bugbee, 1996, 1997; van Iersel, 1999a; van Iersel and Lindstrom, 1999).

In summary, multichamber continuous CO_2-exchange systems have many advantages over more commonly used single-leaf systems. They provide accurate measurements of crop growth and allow for determination of other variables (DCG, CCG, and CUE), that cannot be determined from short-term measurements of CO_2 exchange. Calibration is important to ensure the accuracy

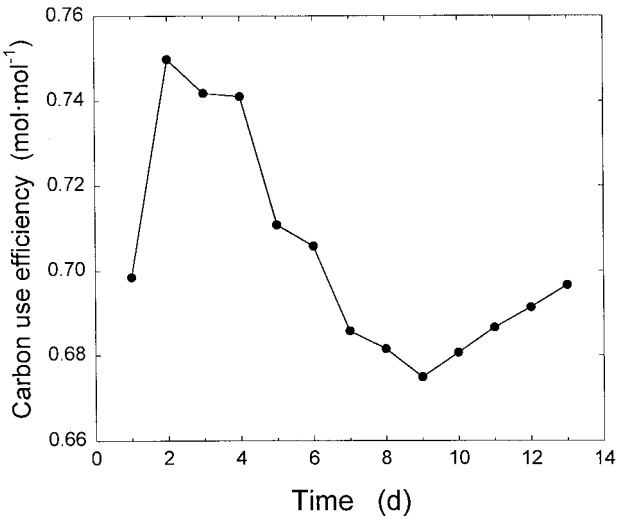


Fig. 5. Carbon use efficiency of a petunia crop as determined from CO_2 exchange data.

of the data, and can be achieved by simple means. All components needed to build these systems are readily available and the total cost in U.S. dollars in 1999 is approximately $35,000 (not including labor), comparable to the price of a single-leaf gas exchange system. Continuous, whole canopy CO_2 exchange measurements can provide valuable information that cannot be easily collected by other means and are a valuable complement to leaf photosynthesis measurements.

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