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DYNAMICS OF CARBON DIOXIDE EXCHANGE OF A WHEAT COMMUNITY GROWN IN A SEMI-CLOSED ENVIRONMENT

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ABSTRACT

A wheat (Triticum aestivum 'Yecora Rojo') community was grown in the semi-closed conditions of the NASA/KSC Biomass Production Chamber (BPC). Experiments were conducted to determine whole community carbon dioxide exchange rates as influenced by growth and development, carbon dioxide concentration, time within the photoperiod, irradiance, and temperature. Plants were grown at a population of about $1500/m^2$ using a 20 hour light/4 hour dark daily regime. Light was supplied by HPS vapor lamps and irradiance was maintained in the range of 590 to 675 $\mu mol/m^2/s$. The temperature regime was 20 C light/16 C dark and nutrients were supplied hydroponically as a thin film.

Fractional interception of PPF by the community increased rapidly during growth reaching a maximum of 0.96, 24 days after planting. This time corresponded to canopy closure and maximum rates of net photosynthesis (NP). Net daily CO_2 utilization rates were calculated to day 48 and a 4th order regression equation integrated to obtain total moles of CO_2 fixed by the community. This procedure may be useful for monitoring and prediction of biomass yields in a CELSS.

Results of 5, 1-hour photosynthetic drawdowns of CO_2 during the photoperiod and from the data log of mass flow injections of CO_2 into the chamber indicated a constant rate of NP during the photoperiod. Net photosynthesis appeared to be relatively linear with CO_2 concentration down to about 400 ppm, suggesting minimal enhancement of NP by supra-ambient CO_2 concentrations with the light regime used. The CO_2 compensation point (CCP) was in the range of 45 to 55 ppm and was independent of irradiance. Carbon dioxide exchange rates were related linearly to irradiance up to 750 $\mu mol/m_2/s$, indicating that growth was not light saturated. Light compensation points (LCP) of the whole community were in the range of 193 to 223 $\mu mol/m^2/s$ and did not appear to change during growth between days 13 and 41. Net photosynthetic rates for a fully developed canopy were maximized between 16 and 20 C and dark respiration was minimized at 16 C.

This study resulted in the development of a broad database for the CO_2 exchange dynamics of a wheat community and will be valuable in the selection of environmental conditions in future biomass production efforts for CELSS. The work also demonstrated the unique research capabilities of the BPC and suggested an approach to the monitoring and prediction of crop biomass.

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LIST OF ABBREVIATIONS AND ACRONYMS

BPC	Biomass Production Chamber
CER	Carbon dioxide Exchange Rate
CCP	Carbon dioxide Compensation Point
CELSS	Controlled Ecological Life Support System
conc	concentration
DR	Dark Respiration
f	fractional interception
HPS	High Pressure Sodium
I	Incident PPF
IRGA	Infra-red Gas Analyzer
LCP	Light Compensation Point
NCU	Net Carbon dioxide Utilization
NP	Net Photosynthesis
PAR	Photosynthetically Active Radiation
PHICS	Plant-Human Integration in Closed Systems
PLC	Programmable Logic Controller
PPF	Photosynthetic Photon Flux
ppm	parts per million
R	Reflected PPF
RH	Relative Humidity
T	Transmitted PPF

I. INTRODUCTION

1.1 BACKGROUND

Humans living for long durations on lunar or planetary bases, on planetary missions, and in space colonies will require the use of controlled ecological life support systems (CELSS) to produce, process, and recycle biomass (1,2,3). An idealized CELSS would sustain human life indefinitely without the necessity for materials resupply. Human oxygen and nutritional requirements would be met by the production and processing of plant biomass. Carbon dioxide from the respiratory activity of humans and other heterotrophic organisms would provide the necessary carbon for photosynthesis while nutritional requirements of plants would be supplied by recycling of human and plant wastes.

An important step by NASA in the development of a bioregenerative life support system was the initiation of the CELSS Breadboard Project (4,5) which has as its primary goals the design, construction, and evaluation of systems and techniques for the production, processing, and recycling of biomass. Implementation of these goals began with the construction and testing of a pre-prototype biomass production chamber (6). A hypobaric test vessel used in the Mercury and Gemini programs was modified and systems constructed for heating, ventilation, and air conditioning (HVAC), lighting, and nutrient delivery (6). In addition, the BPC was provided with capabilities for the monitoring and control of atmospheric variables (temperature, relative humidity, and carbon dioxide and oxygen concentrations), nutrient solution variables (quantity, flow rate, temperature, pH, and conductivity), and irradiance (PPF).

Currently, the BPC is being tested under semi-closed conditions for the production of wheat (Triticum aestivum) and it is planned that future tests will include other staple crops such as soybean (Glycine max), Irish potato (Solanum tuberosum), and sweet potato (Ipomeae batatas). A major constraint imposed on these crop evaluations is that they are conducted in just one experimental unit. However, relative to studies in conventional growth chambers, the high degree of environmental control and the large size of the plant community combine to provide the BPC with the advantage of a well-integrated sample. Moreover, the BPC has been designed and constructed to be operated as a closed, nearly gas-tight system. This characteristic is particularly valuable for the conduct of short term experiments involving the monitoring of gas exchange processes as influenced by environmental variables.

An important aspect of environmental control in a CELSS will be the monitoring and regulation of atmospheric gases (7) at concentrations necessary for the maintenance of all life forms. For example, it is important to know the rate of carbon dioxide utilization by a crop community under various environmental conditions so that appropriate designs and control systems for maintaining oxygen and carbon dioxide mass balances can be achieved. Major variables that influence the carbon dioxide exchange rates of plants are temperature, irradiance, and carbon dioxide concentration. Results of small-scale growth chamber studies (8,9) can provide the appropriate ranges of these variables to select for use in community-scale studies with the BPC. The unique capabilities of the BPC can then be used for the conduct of non-steady state gas exchange experiments with relatively large crop samples.

1.2 OBJECTIVES

The overall objective of this study was to begin the contruction of a gas exchange database for wheat grown in a semi-closed environment. Specific objectives were to determine: a) rates of net photosynthesis (NP) and dark respiration (DR) during growth and development, b) influence of irradiance on carbon dioxide exchange rates, c) carbon dioxide and light compensation points of the whole community, and d) effects of temperature on net photosynthesis and dark respiration.

II. MATERIALS AND METHODS

2.1 PRODUCTION REGIME

The hard red spring wheat cultivar Yecora Rojo was planted in the Biomass Production Chamber (BPC) in the Life Sciences Support Facility, Hangar L, Kennedy Space Center (KSC) on May 30, 1989. Seed presoaked for 30 min and held for 4 days at about 3 C, were planted at a rate of 1900 to 2000/m^2 into strips of polyethylene (white top/black bottom) attached to "T" shaped PVC support pieces crossing the tray tops. Seed were suspended above the tray bottom by opposing strips. The trapezoidally shaped trays were 5 cm in depth and each provided approximately 0.25 m^2 growing area. Each of the 4 levels in the BPC contained 16 trays, providing a total growing area of 16 m^2 excluding areas between trays and outside trays where foliage extended during growth.

Germinating seedlings were covered and maintained in the dark for 2 days following planting at a RH of 90 % and a temperature of 24 C in the BPC. Following an additional 2 days at 24 C, covers were removed and a daily temperature regime of 20 C light/16 C dark was used throughout growth and development except for 3, 3-day spans when temperature was varied. Relative humidity in the BPC was reduced to approximately 70 % on day 7 and maintained as such thereafter. An average stand of 1488 plants/m^2 was measured from a sample of 8 trays following emergence.

The nutrient delivery system consisted of supplying a thin film of a modified half-strength Hoagland's (10) solution at a flow rate of 1 liter/min/tray. The pH of the nutrient solution was maintained in the range of 5.8 to 6.2 through automatic injections of HNO_3 as the pH increased upon crop uptake of NO_3^--N.

The wheat community was provided with a daily regime of 20 hour light/4 hour dark. Lighting during the 20 hour photoperiod was supplied by high pressure sodium (HPS) vapor lamps attenuated when necessary to provide an average canopy top irradiance of about 600 $\mu mol/m^2/s$.

Carbon dioxide concentration was maintained at 1000 ± 50 ppm throughout growth and development except during daily dark respiration and photosynthetic drawdown episodes and when experimental drawdowns were conducted. Establishment of set-points, ranges, and timing of events for all BPC subsystem variables was directed by programmable logic controllers (PLC).

2.2 EXPERIMENTAL

2.2.1 IRRADIANCE MEASUREMENTS. Instantaneous photosynthetic photon flux (PPF) measurements were made at least once weekly using a sunfleck ceptometer (model SF-40, Decagon Devices Inc., Pullman, WA 99163). The ceptometer measures irradiance in the wavelength region of 400 to 700 nm or photosynthetically active radiation (PAR). An average of 5 readings from each of the 64 trays was taken in each of 3 positions; 1) upfacing ceptometer at the canopy top, termed the incident PPF (I), 2) upfacing ceptometer at the canopy bottom or transmitted PPF (T), and 3) inverted ceptometer at the canopy top, or reflected PPF (R). Calculations of the fractional interception, f, were made from the following equation using averages of all readings.

$$f = 1 - T/I - R/I$$

After 21 days from planting, irradiance levels at the canopy bottom approached zero and measurements of T were taken from only 4 trays on each level.

2.2.2 RATES OF NET PHOTOSYNTHESIS (NP) AND DARK RESPIRATION (DR). Daily determinations of the rates of NP and DR were made from changes in CO_2 conc in the upper and lower levels of the BPC atmosphere. Carbon dioxide conc was monitored with infra-red gas analyzers (IRGA) and computer-logged at 4-min intervals. At 0200 hr each day, the lights were set to turn off and the CO_2 conc in the BPC increased linearly due to respiratory evolution. At 0600 hr, the CO_2 conc was above the 1000 ppm setpoint, the lights turned on, and a linear decrease (photosynthetic drawdown) in CO_2 conc occurred. Carbon dioxide conc at 20-min intervals between 0300 and 0500 hr and at 12-min intervals between 0628 and 0728 were used to obtain slopes of equations fit by linear regression. Whole community rates of NP and DR were calculated from the slopes assuming a BPC volume of 112,060 liters (7). Leak rates of CO_2 over the short time span from which calculations were made were assumed to be negligible. A BPC leak rate of 0.417 %/hr was measured in April, 1989 following the retrofitting of inflatable door seals (John Sager, personal communication).

On days 44-48, 4 trays representing approximately 6 % of the total chamber biomass were removed for study of downward rolling of leaves. Data for NP and DR were corrected for the biomass removed during that period by using the factor 64/60 (1.0667).

Calculations of rates of NP for the 20 hr photoperiod and of DR for the 4 hr period on a whole chamber basis were made to determine a net daily rate of CO_2 utilization (NP - DR). A polynomial was fit to the net daily rates of CO_2 utilization (NCU) and the resulting function integrated over time to obtain a total quantity of CO_2 fixed. A solution to the definite integral was obtained using the Math CAD software program (Mathsoft, Inc., Cambridge, MA 02139).

2.2.3 DIURNAL CO_2 EXCHANGE RATES (CER). On day 36, photosynthetic drawdowns of CO_2 conc were measured during 5 time intervals of the photoperiod; 0628 - 0728, 1012 - 1112, 1508 - 1608, 2018 - 2118, and 0006 - 0106 (day 37). Linear regressions were fit to 6 equally spaced points over each 60-min interval. Prior to each drawdown, CO_2 conc in the BPC was increased to about 1200 ppm and the flow valves closed to avoid PLC-directed injection of CO_2 upon depletion of CO_2 below the 1000 ppm setpoint. Rates of DR were determined before and after the photoperiod.

2.2.4 DETERMINATION OF CO_2 COMPENSATION POINT (CCP). On days 18 and 19, the CCP of the wheat community was approximated at 2 irradiance levels (I = 675 µmol/m^2/s on day 18 and I = 497 µmol/m^2/s on day 19). This was achieved by closing the CO_2 injection flow valves, and allowing the BPC CO_2 conc to decline. The barrier separating the upper and lower levels of the BPC was removed to facilitate mixing of gases in the entire chamber. Carbon dioxide drawdowns were conducted until the rate of CO_2 decrease approached zero. On day 19, one of the flowmeters for CO_2 injection was slightly open and a period of injection occurred when the CO_2 conc was below 500 ppm. In handling this data, a 90 min segment of CO_2 conc data was spliced out in order to approximate the time-dependent drawdown pattern.

2.2.5 EFFECTS OF IRRADIANCE ON NP. On days 13, 20, 27, and 41, irradiance was varied by dimming the HPS lamps to provide 5 irradiance levels. At the start of the experiment, BPC CO_2 conc was increased to approximately 2000 ppm and then allowed to change for 1 hr at each irradiance. Carbon dioxide conc at 8 min intervals for a 32 min time span near the midddle of each PPF drawdown event was used in calculations of CER. Measurements of incident PPF for each irradiance level were made for all 64 trays the day after the experiment. Light compensation points for the community were calculated (x-intercept) from the linear regressions of CER vs. PPF.

2.2.6 EFFECTS OF TEMPERATURE ON NP AND DR. On days 21 - 23 and 41 - 43, temperature of the BPC was varied. For each 3-day experiment, temperature was set at 24 C for day 1, 20 C for day 2, and 16 C for day 3. Rates of NP and DR were calculated as described previously.

2.2.7 MASS FLOW MEASUREMENTS. Data logged for a cumulative record of CO_2 injected into the BPC was retrieved and used to calculate NP during uninterrupted times when the chamber was sealed. Calculations of NP from mass flow data were compared with those made from drawdown measurements.

III. RESULTS AND DISCUSSION

3.1 IRRADIANCE

Irradiance incident at the canopy top was maintained between 590 and 675 µmol/m^2/s throughout growth and development (Table 3-1). As the wheat plants increased in height, it was necessary to alter the dimming levels of the light banks in order to remain within this range. Sharp decreases in the irradiance transmitted to the bottom of the canopy (T) and reflected (R) at the top of the canopy occurred after day 9. During this rapid growth phase of the wheat community there was a near doubling in the fractional interception (f) of PPF by the canopy. Canopy closure occurred after about 3 weeks as indicated by f values of 0.94 to 0.96. After 24 days, transmitted PPF declined to negligible levels and remained negligible until day 42. It is anticipated that both transmitted and reflected PPF will increase during senescence of the canopy.

Table 3-1. Incident (I), transmitted (T), and reflected (R) PPF and fractional interception (f) in the BPC during growth and development of a wheat community.

DAYS AFTER PLANTING	PPF (µmol/m^2/s)[ab]			
	I	T	R	f
9	628 ± 44	317 ± 28.0	104 ± 11.2	0.34
11	665 ± 42	173 ± 22.0	46 ± 5.5	0.67
14	675 ± 47	66 ± 9.0	26 ± 2.1	0.86
17	675 ± 30	37 ± 2.6	13 ± 2.9	0.93
21	620 ± 27	5 ± 0.6	30 ± 2.0	0.94
24	659 ± 33	2 ± 0.7	27 ± 1.3	0.96
28	610 ± 17	ND	ND	ND
31	601 ± 28	1 ± 0.5	22 ± 0.5	0.96
36	590 ± 30	1 ± 0.5	26 ± 3.3	0.96
42	616 ± 42	1 ± 0.5	36 ± 9.8	0.94

[a] Values represent the means of 4 levels ± 1 standard deviation.
[b] ND=no data.

3.2 GROWTH AND DEVELOPMENT - NP AND DR

Wheat seedlings became photosynthetically competent 6 days after planting. At this stage it was possible to obtain photosynthetic drawdown rates following the dark respiration period. The rate of NP increased sharply up to about 15 days and then remained in the range of 30 to 35 $\mu mol/m^2/s$ for about 3 weeks, followed by a gradual downward trend up to day 48 (Figure 3-2). Rates of NP reported herein from whole community CO_2 drawdowns are comparable to those reported for single leaf blades (11). The trend for rates of dark respiration early in development was similar to that observed for rates of NP. After 2 weeks the rate of DR remained relatively constant. During the interval of days 6 to 14, day-to-day variability in rates of NP and DR were low. Subsequent fluctuations in the daily rates are attributable to the conduct of temperature experiments (days 22-24 and days 42-44), changes in canopy geometry (growth) with respect to lighting, and periodic adjustments in lamp output to maintain a relatively uniform level of canopy top irradiance throughout growth.

Maximum daily rates of CO_2 utilization (35 mol/chamber/day) occurred between 3 and 4 weeks after planting (Figure 3-3). The equation fit to the data in figure 3-3 is:

$$Y = -39.912 + 10.129\ X - 0.496\ X^2 + 0.010331\ X^3 - 0.000079541\ X^4,$$
$$R^2 = 0.881.$$

This equation can be integrated to obtain the total moles of CO_2 fixed by the entire wheat community. Solving the definite integral of the above equation between days 6 and 48 yields a total CO_2 fixed of 1,202 moles or 52.9 kg. Assuming that 1 mole of CO_2 yields 1 mole of CH_2O, then 52.9 kg of CO_2 should yield 36.1 kg of carbohydrate (12). Upon obtaining a complete growth and development data set, this procedure may be used in conjunction with data on ash and total N as percentages of dry weight to predict total community biomass.

A gradual downward trend in NP (Figure 3-2) is expected to occur. However, a gradual decrease in NP may be accompanied by a sharp increase in DR as the plants senesce leading to a large decrease in the daily net fixation of carbon dioxide.

3-3 DIURNAL PATTERN OF CARBON DIOXIDE EXCHANGE RATES

A question that arose from using morning photosynthetic drawdown rates of CO_2 as a measure of the daily rate of NP was the following. How representative of the daily rate was a 1 hr segment of CO_2 conc changes obtained at the beginning of a 20 hr photoperiod? Measurements of NP obtained from the beginning and end of the photoperiod and 3 intermediate times revealed some variation in the rate of NP computed in this manner, but not enough to discern any diurnal pattern in the rate (Figure 3-3). The regions of the dotted lines represent presumed extrapolations of the data. Actual plant reponses could differ only slightly from these extrapolations. The absence of a distinct diurnal pattern in NP for plants grown at constant irradiance and angle of incidence on the canopy contrasts with photosynthetic responses of plant canopies receiving only solar radiation, since the angle of incidence and the intensity of solar radiation varies throughout a day.

Further evidence to claim a relatively constant rate of NP was obtained from mass flow data logged during a complete photoperiod when the BPC doors remained sealed (Figure 3-4). The rate of NP calculated from the slope of the line presented in Figure 3-4 was 420 µmol/chamber/s as compared to a rate of 467 µmol/chamber/s obtained from the morning photosynthetic drawdown data. The disparity between the two methods of calculating rates of NP may derive from several sources. First, the leak rate of carbon dioxide from the chamber over a period of 18 hours used in the mass flow method of calculation could cause a significant error in the measurement. This should lead to an overestimate of the true rate. However, the drawdown computation method yielded a higher value for NP and therefore suggests that other factors contribute to the disparate measurements. Another possibility is the variability in IRGA measurements used to obtain the drawdown data. The IRGA is subject to drift and needs to be calibrated on a frequent basis to ensure consistency in the daily absolute values of CO_2 conc. Such instrument variability should be random and result in times when the mass flow method yields higher or lower measurements of the rate than the drawdown method. This contention was confirmed by comparison of data sets from other days and it was concluded that factors contributing to the disparity between methods were of a random nature.

3-4 CARBON DIOXIDE COMPENSATION POINT

Photosynthetic drawdowns of CO_2 at PPF values of 497 and 675 µmol/m^2/s were linear to CO_2 concentrations below 400 ppm, suggesting that CO_2 enrichment above ambient levels has a minor effect on the rate of NP of a wheat community at these irradiances and stage of development (Figure 3-6). However, it will be necessary to repeat this experiment, perhaps at a higher irradiance, to test this possibility.

The discontinuity in the presentation of the data for the 497 PPF treatment represents the time splice explained in section 2.2.4. The rate of CO_2 consumption was irradiance-dependent, but the CCP was irradiance-independent as indicated by the convergence of the two data sets after about 6 hours. The plateau portion of the plot approximates the CCP to be between 45 and 55 ppm which agrees with values reported previously for wheat and other C_3 plants (13). This range may be a slight overestimate of the CCP due to the long time required to ensure a complete drawdown. Such extreme drawdowns represent possible scenarios in a CELSS where atmospheric gas control systems may, on occasion, not be altered in response to significant changes in the proportions of

CO_2 evolved and utilized, or when resources (e.g. CO_2 supply, energy) become limiting and appropriate modifications must be made.

Additional CCP data obtained from complete drawdowns will need to be conducted under different temperature regimes and perhaps lower oxygen concentrations to broaden this database since CCP has been reported to be temperature- and oxygen- dependent (13,14,15,16). While decreased oxygen conc for C_3 plants such as wheat should improve photosynthetic efficiency by decreasing photorespiratory carbon loss, it would probably not be feasible to lower the partial pressure of oxygen in a CELSS with humans below about 0.15 atm, unless there was sufficient gas tight partitioning of human and plant atmospheres.

3-5 EFFECT OF IRRADIANCE ON NP

Carbon dioxide exchange rate was linearly related to PPF up to the approximately 750 $\mu mol/m^2/s$ limit used during the 4 separate irradiance experiments. An example of the results of one (day 41) of these experiments is presented in Figure 3-7. Irradiance levels used in this study were well below the light saturation levels suggested by growth responses measured at higher irradiances by Bugbee and Salisbury (9) and as summarized by Larcher (17).

Following canopy closure (about 20 days), there was an increase in the light compensation points (LCP) of the whole wheat community (Table 3-2).

Table 3-2. Light compensation points (LCP) of a wheat community during growth and development. See 2.2.5 for experimental details and calculations.

DAYS AFTER PLANTING	LCP (µmol/chamber/s)
13	209
20	193
27	229
41	223

Since fractional light interception by the canopy did not increase after about 20 days (Table 3-1), it would be expected that light would eventually become limiting considering that irradiance was nonsaturating and that continued increases in biomass were taking place. In general, the whole community LCP values reported here are substantially higher (about 5-fold) than those reported for single flag leaves (11) or those assumed for wheat in growth experiments (9). It is expected that a community LCP would be higher than that measured for single leaves or plants exposed to a higher irradiance than the average irradiance recieved by all leaf surfaces in a dense canopy.

Additional determinations of LCP later in development will need to be made to determine if changes occur during grain fill and senescence.

3-6 EFFECTS OF TEMPERATURE ON NP AND DR

Net photosynthetic rates for the 6-week old canopy was lowest at the highest temperature (24 C), but decreased when the temperature was lowered from 20 C to 16 C (Figure 3-8), suggesting an optimum temperature between 16 and 20 C for NP. The rate of DR increased with increasing temperature. The net daily rates of carbon dioxide utilization were 28.6, 29.6, and 22.6 mol CO_2/chamber/day for 16, 20, and 24 C, respectively. At 16 C, the rate of DR is decreased more than the rate of NP relative to 20 C, which explains the small difference between the 2 temperatures in the daily rate of CO_2 utilization. Considering this minor difference in carbon-fixation, it may be more economical from the perspective of energy efficiency to use 16 C as a growth temperature for wheat in a CELSS. It will also be important to conduct similar temperature experiments at different stages of development to determine if the same trend is observed.

IV. CONCLUDING REMARKS

The biomass production chamber served as an excellent pre-prototype CELSS test chamber for making determinations of the rates of carbon dioxide exchange of a wheat community as influenced by environmental variables. When sealed, carbon dioxide exchange studies in the BPC may be conducted in a non-steady state mode whereby CO_2 injection is prevented, or in a quasi-steady state mode whereby CO_2 injections are made to maintain near constant concentrations. In the quasi-steady state mode, absolute quantities of CO_2 injected can be used to calculate assimilation rates. The non-steady state mode allows rapid determinations of CO_2 utilization and evolution rates following alterations in environmental variables.

The whole community gas exchange responses measured in the BPC are judged to be more representative of crop responses than studies involving single leaf or single plant measurements. Daily measurements of NP and DR enable constant monitoring of crop 'activity' and may furthermore be used to estimate crop biomass at any stage of development using straightforward analytical techniques. Similar gas exchange studies conducted in the BPC with other crops selected for CELSS should provide valuable databases. However, the constraints of one experimental unit and the time required for conducting these studies necessitates judicious selection of variables and treatments.

An additional avenue of research that should be pursued during the BPC crop evaluations is the acquisition of gas exchange data for an integrated system of plants and humans. Plant-human integration in closed systems (PHICS) will enable experimental human ratings of the test chamber and also will serve to cross verify measurements of gas exchange rates of each biotic component measured in isolation.

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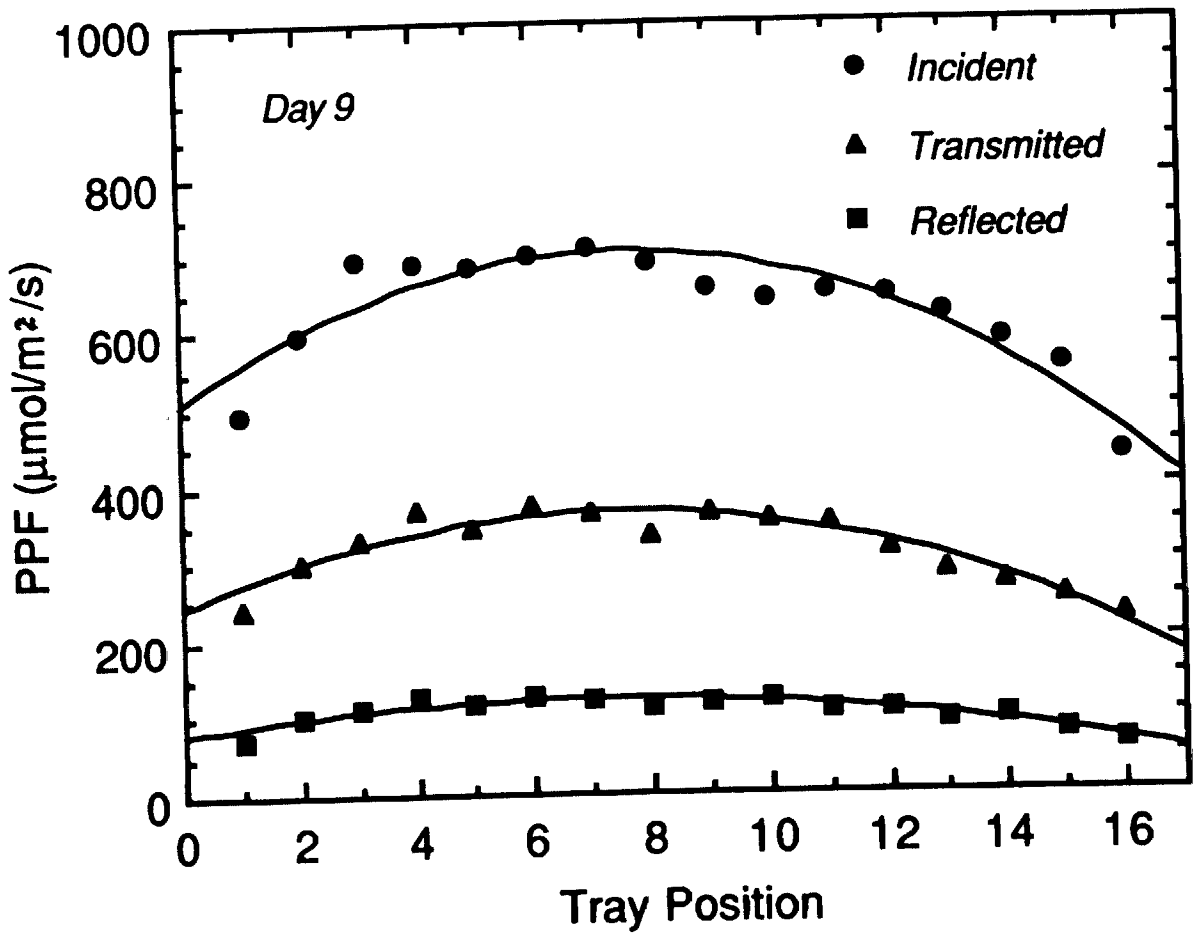

Figure 3-1. Irradiance levels under HPS lamps at various locations in the BPC.

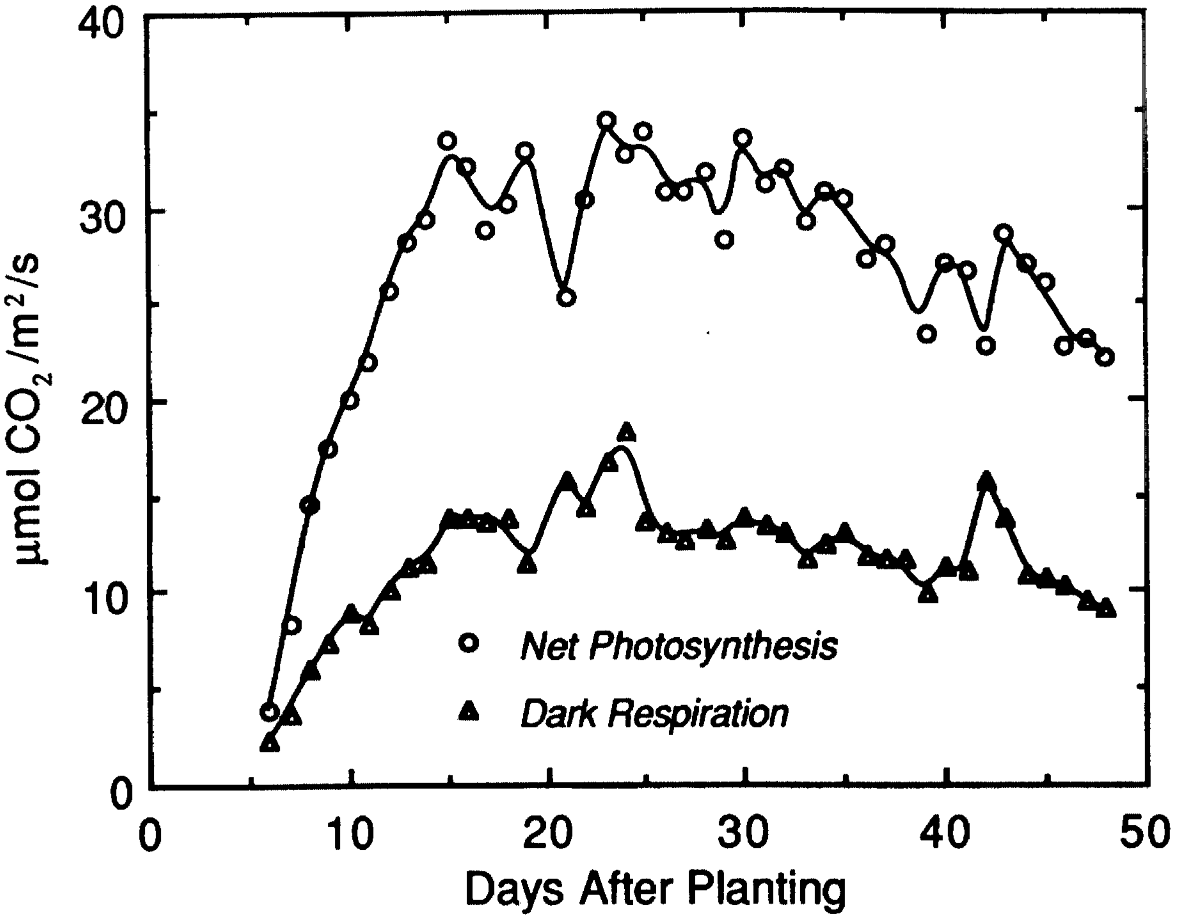

Figure 3-2. Rates of NP and DR during growth of a wheat community.

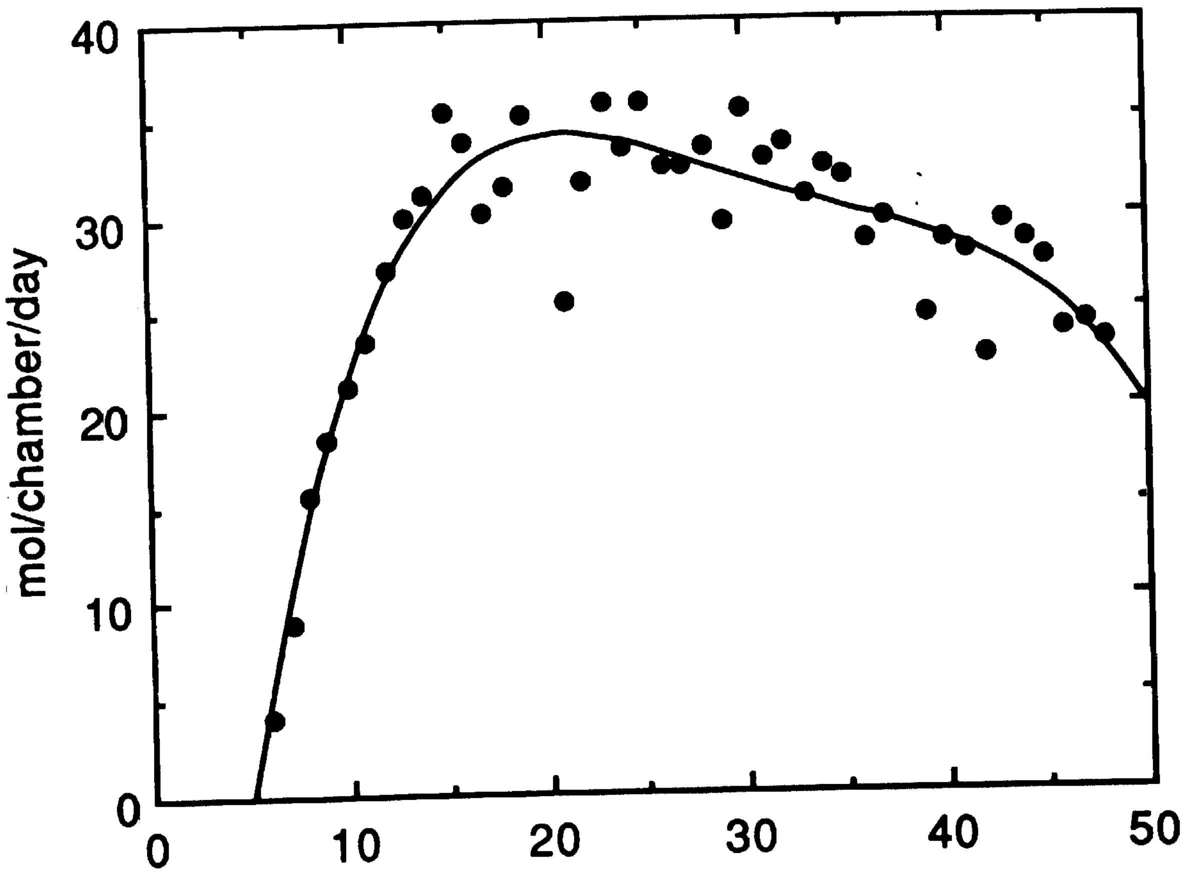

Figure 3-3. Net daily carbon dioxide utilization during growth of a wheat community.

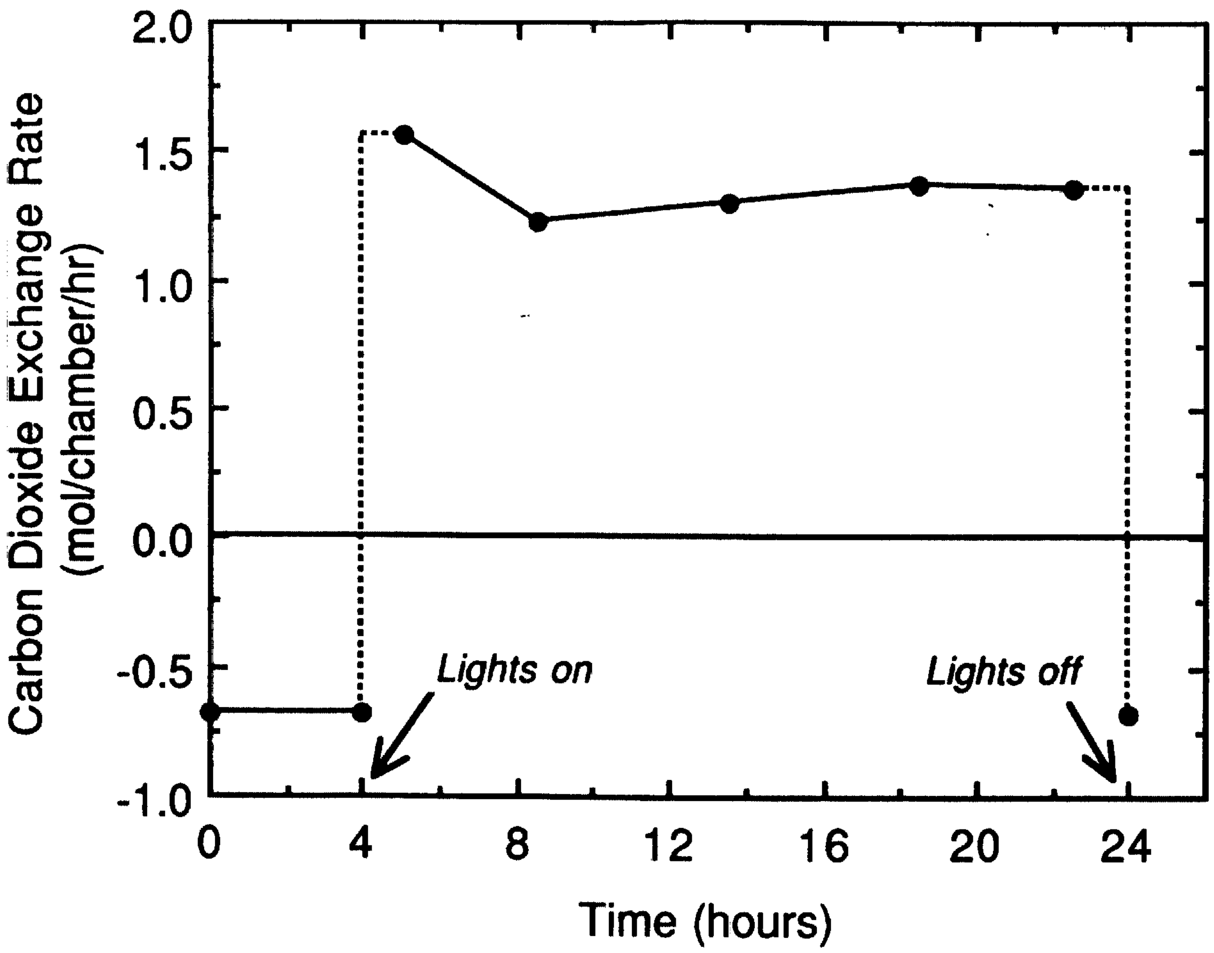

Figure 3-4. Daily pattern of carbon dioxide exchange rates.

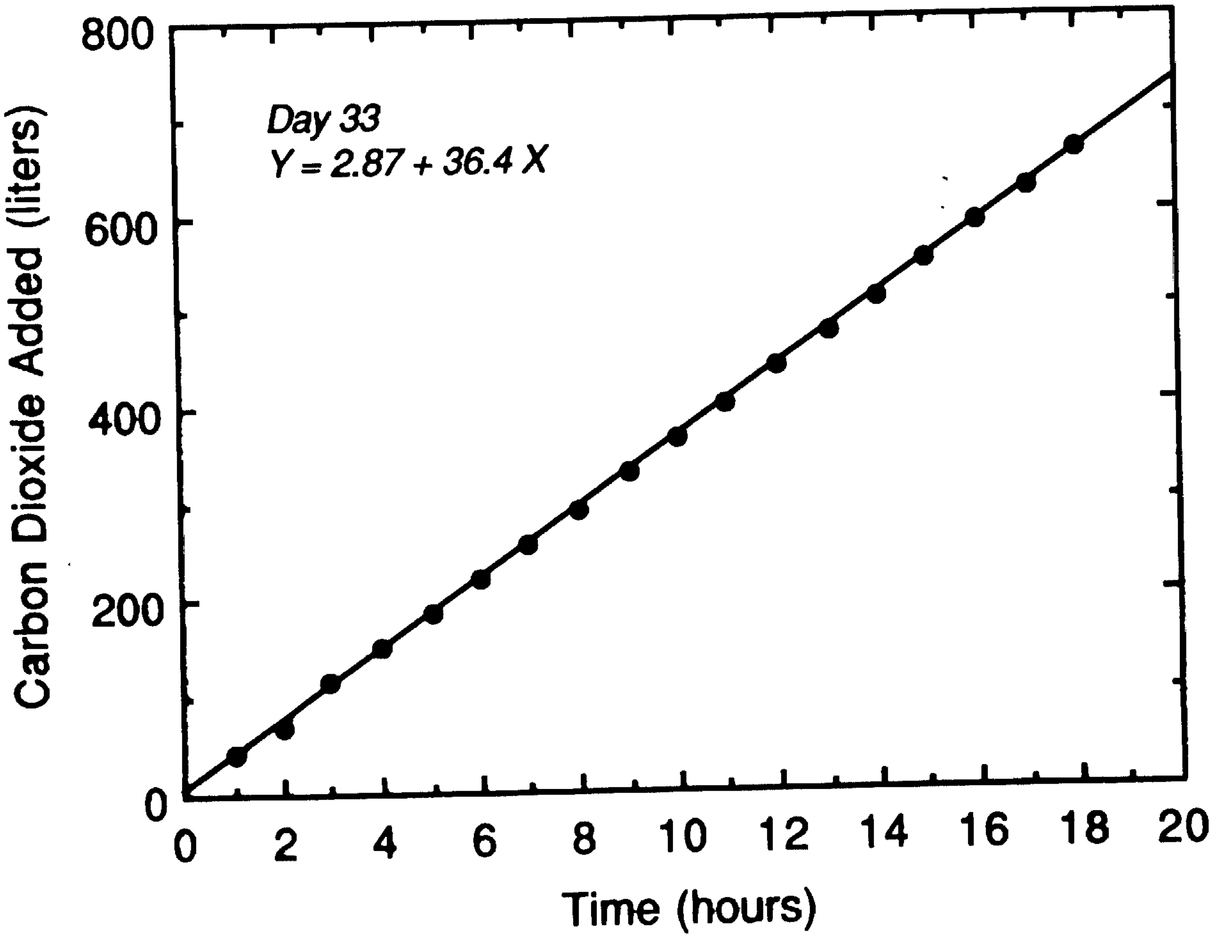

Figure 3-5. Cumulative additions of carbon dioxide to the BPC atmosphere during the photoperiod.

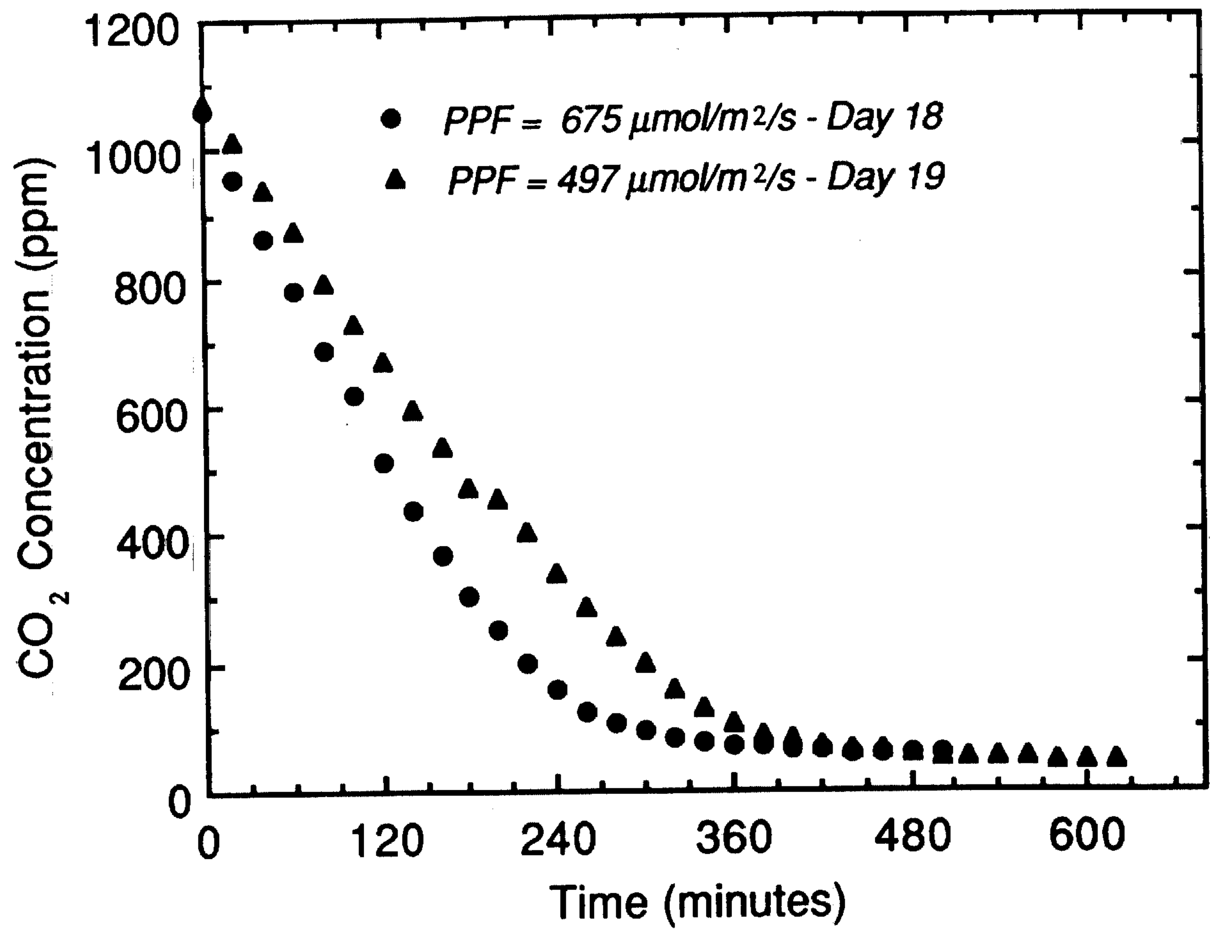

Figure 3-6. Photosynthetic drawdowns of CO_2 by a sealed wheat community at 2 irradiance levels.

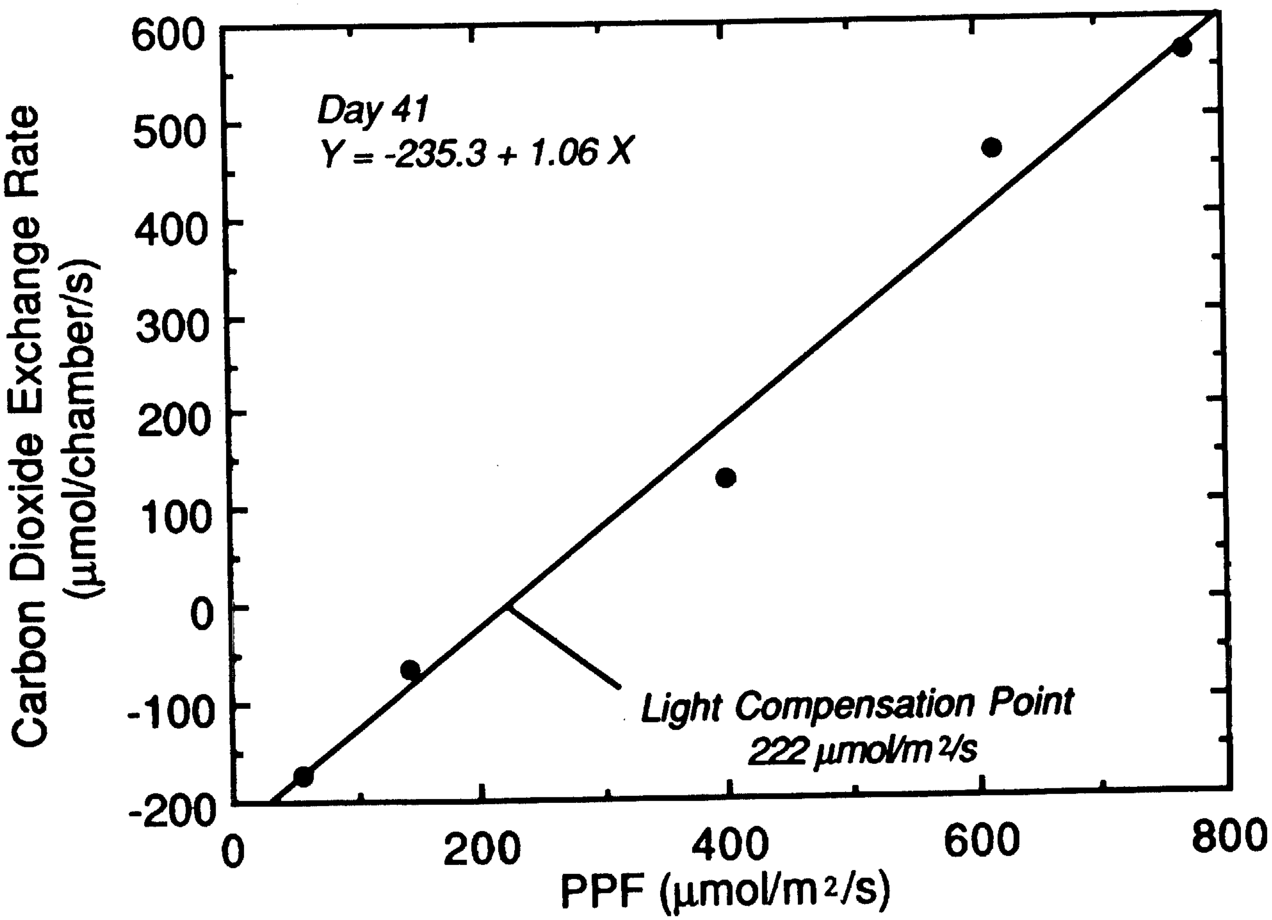

Figure 3-7. Relationship of carbon dioxide exchange rate with irradiance.

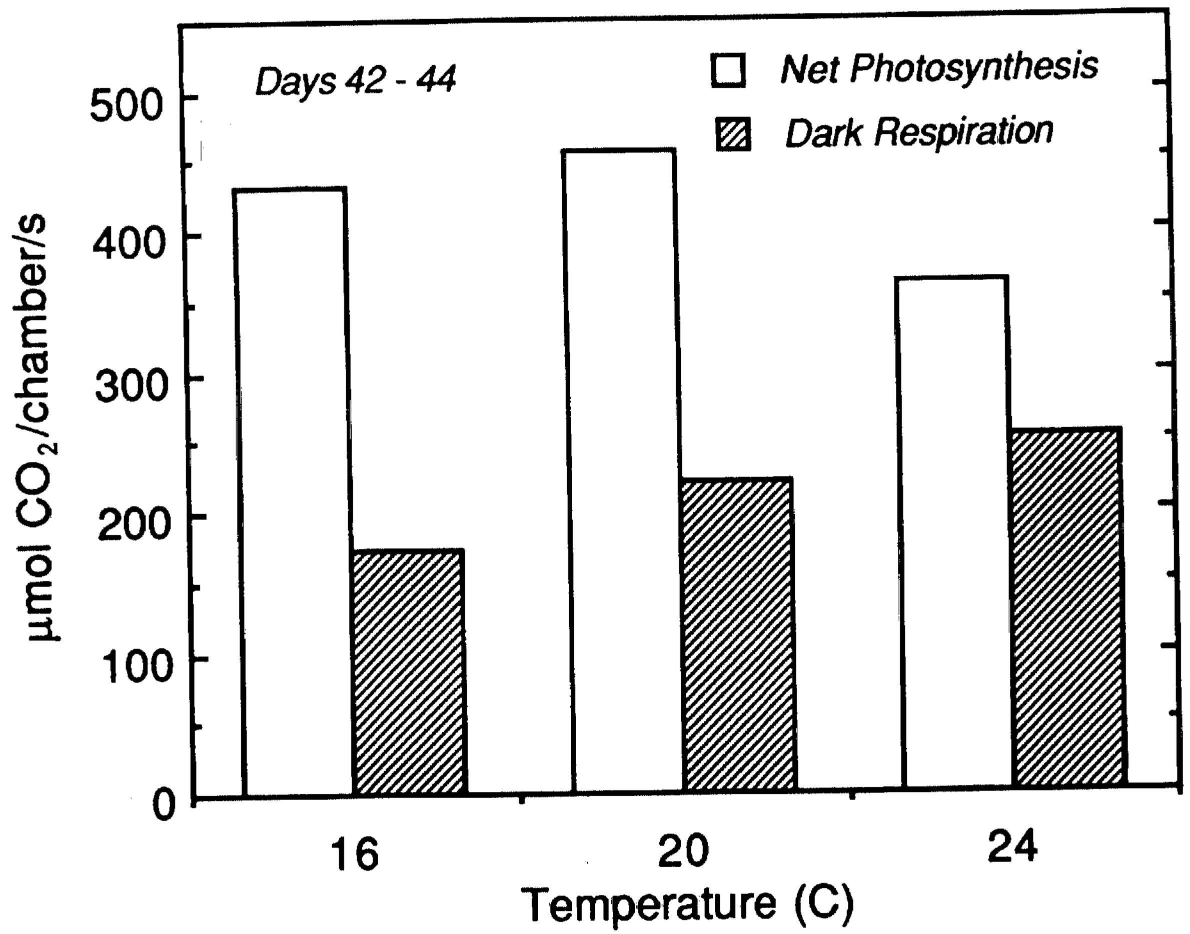

Figure 3-8. Effects of temperature on rates of net photosynthesis and dark respiration.