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Carbon Dioxide And Water Exchange Rates By A Wheat Crop In NASA'S Biomass Production Chamber: Results From An 86-Day Study (January To April 1989)

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ABSTRACT

Gas exchange measurements were taken for a 20 m^2 wheat stand grown from seed to harvest in NASA's Biomass Production Chamber. Respiration of the wheat stand caused the CO_2 concentrations to rise an average of 440 ppm during the 4-h dark period each day, or 7.2 umol m^{-2} s^{-1}. Dark period respiration was sensitive to temperature changes and could be increased 70-75% by raising the temperature from 16°C to 24°C. Stand photosynthesis (measured from the rate of CO_2 drawdown immediately after the lights came on each day) peaked at 27 umol m^{-2} s^{-1} at 25 days after planting and averaged 15 umol m^{-2} s^{-1} throughout the study. By combining the average light period photosynthesis and average dark period respiration, a net of 860 g or 470 liters of CO_2 were fixed per day. Stand photosynthetic rates showed a linear increase with increasing irradiance (750 umol m^{-2} s^{-1} PPF the highest level tested), with an average light compensation point after day 30 of 190 umol m^{-2} s^{-1}. Stand photosynthesis decreased slightly when CO_2 levels were decreased from 2200 to 800 ppm, but dropped sharply when CO_2 was decreased below 700-800 ppm. Water production from stand transpiration peaked at 120 L day^{-1} near 25 days and averaged about 90 L day^{-1}, or 4.5 L m^{-2} day^{-1} throughout the study.

INTRODUCTION

An important objective for NASA's Controlled Ecological Life Support System (CELSS) research program is the documentation of mass flows of gases in a closed plant growing system. The plants

in a CELSS would be used to provide food, water, and oxygen for humans, while removing carbon dioxide (CO_2) (MacElroy and Bredt, 1985). Exchange rates of carbon dioxide and water are especially important and photosynthesis is thus the focal event in the plant growing portion of a CELSS. Carbon dioxide is the primary gaseous constituent used by plants in building sugars for metablolic needs, while large water fluxes through the biomass from transpiration are a result of the plants' need to maintain open stomata (leaf pores) to sustain CO_2 uptake (Coombs et al., 1985).

Traditionally, closed atmospheric studies of plant growth have been limited to small-sized chambers (Dutton et al., 1988; Knight et al., 1988). However, with the construction of the Biomass Production Chamber (BPC) at the Kennedy Space Center, FL, closed system studies of atmospheric mass flow are now possible for large plant stands. The BPC is a two-storied cylindrical steel chamber (7.5 m high and 3.6 m diameter), which has been fitted with electric lighting, air handling, and nutrient solution delivery systems to sustain plant growth. The current configuration includes 64 0.25-m^2 hydroponic trays for growing the plants. When the gaps between the trays are included, approximately 20 m^2 can be covered by plants. Total chamber volume, including the air handling systems has been calculated to be 112.6 m^3 with a leakage rate of less than 10% of the volume per day (Sager et al., 1988). More thorough descriptions of the BPC's construction and capabilities have been reported by Prince et al. (1987), Sager et al. (1988), and Prince and Knott (1989).

A preliminary plant study in the BPC began with wheat in January, 1987. This was followed by a second study with wheat in May of 1988. In both of these early trials, only the upper portion of the chamber was functional and no attempts were made to rigorously seal the atmosphere of the chamber. A third wheat study was planted the fall of 1988 using the entire chamber and pneumatic gaskets to prevent leakage around the doors. Results of this third test showed that when wheat plants were grown under a diurnal cycle of 20 h light, 4 h dark, CO_2 would rise in a linear fashion during the dark cycle (up to 600 ppm above the initial set point). Immediately after the lights were turned back on, the CO_2 would draw back down to the set point. There the control system would maintain the set point by injecting CO_2 from an external compressed gas source. This repeating pattern of dark increase followed by light ("morning") drawdown was determined by the rate of the wheat crop's respiration and photosynthesis (Fig. 1).

As described by Coombs et al. (1985), changes in CO_2 in closed systems can be used to calculate plant photosynthesis, provided the chamber volume is known (to convert concentrations to a mass or molar basis), and a vegetative area can be assigned in the chamber. In the case of small gas cuvettes, area corresponds to the amount of exposed leaf surface (Coombs et al., 1985). When measuring crop or "community" photosynthesis (which is the more pertinent measurement for CELSS; Bugbee and Salis-

bury, 1988; Gerbaud et al., 1988), the value would then equate to the entire area covered by growing plants. In the case of the BPC, this is about 20 m^2.

A second approach to calculating photosynthesis in a closed system would be to monitor the rate of CO_2 flow into the chamber that is needed to exactly balance the uptake rate by the plants. These have been called "semi-closed" systems (Coombs et al., 1985). Although the BPC currently has this capability, mass flow measurements of CO_2 were not available during early testing. Consequently, in the study described in this report, CO_2 exchange was tracked solely by quantifying the rate of rise during the dark period and the subsequent drawdown when lamps were turned on each day.

MATERIALS AND METHODS

On January 19, 1989, seeds of wheat (Triticum aestivum L. cv Yecora Rojo) were planted into hydroponic growing trays as described by Mackowiak et al. (in press) (see also, Prince and Knott, 1989). Trays were covered for 120 hours (5 days) with translucent acrylic lids to maintain high humidity around the germinating seeds. A complete nutrient solution (Mackowiak et al., in press) was pumped continuously to the slightly elevated end of each tray and then flowed passively to the lower end where the solution was returned to a reservoir for recirculation. Water (volume) taken up by the plants from the nutrient solutions was replenished on a daily basis, while mineral nutrients were replenished twice weekly. The chamber was kept dark for 72 hours

after planting after which a 20-h light / 4-h dark photoperiod was imposed. Because of poor germination in some trays, 12 trays were reseeded on day 6 after the initial planting. Lighting was provided by 96 400-W high pressure sodium (HPS) lamps. Using the dimming capabilities of the HPS ballasts, input power to the lamps was lowered as the plants grew in an attempt to keep PPF constant at the top of the plant canopy. PPF throughout the study averaged 534 umol m^{-2} s^{-1} ($\pm$ 42 umol m^{-2} s^{-1} difference between the growing levels).

For the first 34 days after planting, air temperature and humdity were held constant at 20°C and 80% relative. After 34 days, temperature set points were switched to 20°C in the light and 16°C in the dark. Atmospheric CO_2 was maintained at 1000 ppm throughout the study by injecting pure CO_2 from a compressed supply outside the chamber. Throughout the study, temperatures averaged 20.3°C ($\pm$ 0.4°C difference between levels) for the 20-h light cycle, and 16.8°C ($\pm$ 0.5°C) for the dark cycle. Humidities averaged 81% $\pm$ 4% and 82% $\pm$ 6% for the light and dark cycles. During the dark cycle, concentrations rose above the 1000 ppm set point from plant respiration and no external CO_2 was required. Throughout the study, CO_2 averaged 1160 ppm $\pm$ 238 in the light and 1380 $\pm$ 310 in dark. The large standard deviations reflect episodes of CO_2 manipulations to study stand photosynthesis in the light and the respiration-caused increases of CO_2 in the dark.

At 84 days after planting, water supply to the plants was turned off to hasten drying of the biomass. No gas exchange data were collected after this point. On day 86, lights were turned off and trays were harvested over the next 3 days.

Gas exchange measurements. Respiration and photosynthesis of the wheat stand were calculated from rates of changing CO_2 during the dark-increase and morning-drawdown cycles each day, respectively. The part-per-million readings from the CO_2 analyzer (Anarad, Inc., Santa Barbara, CA) were converted to equivalent molar quantities using the chamber volume (112,600 L) and the following relationships:

1 ppm = 1 uL / L

at 20° C and 1 atm, there are 24.0 uL / umol

and at 16°C and 1 atm, there are 23.7 uL / umol

then for any gas in the BPC where the
the volume = 112,600 L

1 ppm = (1 uL / L) X (1 umol / 24 uL) X 112,600 L

or 1 ppm = 4692 umol (at 20° C)

(and 1 ppm = 4751 umol at 16° C)

Plant stand transpiration was determined by measuring the condensate produced from the "cold" coils of the air heat exchange system. Condensate tank volumes for both the upper and lower air handling systems were recorded each day and then emptied. Calculations for both CO_2 and water fluxes assumed a plant stand area of 20 m^2. All the data presented are based on the dynamic responses of the crop in the BPC and hence have not been evaluated statistically.

RESULTS AND DISCUSSION

Background assumptions. It is well known that CO_2 concentrations have profound effects on the rate of photosynthesis and the degree of stomatal opening of plant leaves (Acock and Allen, 1985; Coombs et al., 1985). Because closed gas exchange systems use a change in CO_2 concentration over time to calculate photosynthesis, the drawdowns must be taken across a range where the changing CO_2 itself does not impose a significant effect. To study this, at 25 days after planting the CO_2 level was raised to approximately 2200 ppm and then allowed to draw down to near the compensation point (point where no net CO_2 uptake occurs). As shown in Fig. 2, the rate (slope) of the drawdown remained relatively constant from 2200 ppm down to approximately 800 ppm. Below this level, the rate of the CO_2 drawdown decreased, indicating an increasingly slower photosynthetic rate at the lower CO_2 concentrations. A comparison of the slopes from the drawdown against CO_2 concentration (i.e. the 1^{st} derivative of a polynomial fit to Fig. 2) shows that the slope and hence

photosynthetic rate decreased slightly from 1500 to 800 ppm and then decreased precipitously below about 500 ppm (Fig. 3). These results are typical of most C-3 plant species, where at moderate irradiance, photosynthesis shows CO_2 saturation near 1000 ppm and a compensation point near 50 ppm (Ehleringer and Bjorkman, 1977; Coombs et al., 1985; Sage and Sharkey, 1987). For the purpose of this paper, it will be assumed that above 1000 ppm, the CO_2 concentration itself had little effect on stand photosynthetic rate. As will be noted later, manipulations of irradiance (PPF) to study CO_2 drawdown rates were all conducted above 1000 ppm to minimize the CO_2 effect.

Because the photosynthesis data were measured from a morning drawdown (lasting about 1 to 2 hrs), a second important assumption was made. Namely, the rate of photosynthesis remained relatively constant across the day, i.e. there was no diurnal change in CO_2 uptake by the stand. This is generally not true in the field where irradiance, water vapor pressure deficit, and plant water status change throughout the day (Larcher, 1980). But in controlled environments such as the BPC, irradiance and vapor pressure deficit can be held constant, and subsequent tests with a wheat crop at similar conditions in the BPC have shown that CO_2 uptake by photosynthesis does indeed remain constant across the day (K. Corey, 1989).

Carbon Dioxide Exchange

Dark period respiration. A record of dark period respiration rates throughout growth is shown in Fig. 4. Respiration (shown as negative CO_2 exchange) increased until about 20 days after

planting (to about 13 umol m^{-2} s^{-1}) and then showed a gradual decrease with time as the stand matured. When averaged across the entire life cycle of the crop, CO_2 rose about 440 ppm during the 4-h dark period each night, or about 7.2 umol m^{-2} s^{-1}. A large drop in dark period respiration occurred at 34 days, when the night temperature was lowered from 20°C to 16°C (Fig. 4). Tests conducted later in growth showed that respiration was strongly influenced by temperature, where increasing the temperature from 16°C to 20°C raised respiration by 65% at 5-weeks-age, and 45% at 10-weeks-age (Fig. 5). Raising temperature from 16° C to 24° C increased respiration by 70% at 5 weeks and 75% at 10 weeks (Fig. 5).

Photosynthesis. Net photosynthetic rates of the wheat stand through time are also shown in Fig. 4. Carbon dioxide uptake from photosynthesis rose very rapidly during early growth, peaking near 27 umol m^{-2} s^{-1} at 25 days and then gradually declined with age. In similar studies with wheat, Gerbaud et al. (1988) showed peak CO_2 uptake later in development, but their plants were spaced much wider than the plants in this study (80 plants m^{-2} vs. 1500 plants m^{-2}). Thus the difference between the two studies likely lies in the time required to reach full canopy ground cover, when the stand intercepts the maximum amount of radiation. The low CO_2 uptake prior to 15 days likely reflects the incomplete ground cover early in stand development (Bugbee and Salisbury, 1989).

The average photosynthetic rate across the life cycle for the wheat crop was approximately 15 umol CO_2 m^{-2} s^{-1} (this was averaged from day 10 through day 84; Fig. 4). This equals about 21.6 moles CO_2 fixed during the 20-h light period; after subtracting 2.1 moles respired during the 4-h dark period, a net of 19.5 moles CO_2 was fixed per day (about 860 g or 470 liters per day). Assuming most of the plant biomass is carbohydrate, if the mass of CO_2 fixed X 0.68 = mass of carbohydrate produced (Charles Edwards et al., 1986), then 860 X 0.68 = 585 g carbohydrate per day X 75 days = about 44 kg of biomass from the crop (75 days for days 10 through 84). Harvest results showed that about 40 kg of total biomass were produced. Thus the estimate of biomass from photosynthesis was approximately 10% higher than the actual yield. Several factors may contribute to this overestimate, including: the 5 to 10% chamber leak rate, which would tend to overestimate photosynthesis and underestimate dark respiration; and the possibility that photosynthesis was slightly higher early in the day when rates were measured, as observed in some studies at Utah State (B. Bugbee, personal communication). In addition, losses of biomass due to respiration prior to harvest (during the last three days) and during oven drying would cause the actual yield data to be lower than gas exchange predictions made during active growth. However, the fact that the prediction from this gas exchange analysis and the actual yield are close suggests that the gas exchange data were accurate.

At 28 days (Fig. 4), a large drop in net photosynthesis (CO_2 uptake) occurred when the lamps were dimmed to lower the irradiance (from 695 to 480 umol m^{-2} s^{-1}). Two other temporary drops in photosynthesis also are noticeable circa 50 and 60 days. In each of these instances, the CO_2 supply to the chamber ran out and photosynthetic rates temporarily decreased.

Several tests were conducted at different stages of growth to study photosynthesis at different PPF levels. To do this, the CO_2 was raised to about 2000 ppm and then allowed to drawdown while the lamps were dimmed to different intensities. Each PPF level was maintained for at least one hour and the resulting CO_2 exchange rate tracked (Fig. 6). These tests showed that stand CO_2 uptake rates rose linearly as PPF increased from 60 to 750 umol m^{-2} s^{-1} (Fig. 7). The PPF or light compensation point (point where net CO_2 uptake is zero) occurred near 200 umol m^{-2} s^{-1}. Repeating the drawdown tests at different ages indicated that the light compensation point remained relatively constant throughout growth, averaging 190 umol m^{-2} s^{-1} (Fig. 8). As the stand approached senescence, the largest absolute drops in CO_2 uptake occurred at the highest PPF levels (Fig. 9).

As with the CO_2 response data, the light responses are quite typical of many plant leaves (Larcher, 1980), except for the light compensation point. In contrast to the stand light compensation point of 190 umol m^{-2} s^{-1}, light compensation points for single wheat leaves can be as low as 20 umol m^{-2} s^{-1} (Azcon-Bieto, 1983). The difference lies in that gas exchange for the BPC represents an entire stand of plants with multiple layers of

leaves, roots, stems, and microorganisms in the nutrient solution. Stand light compensation points as high as 500 to 600 umol m^{-2} s^{-1} have been measured with high density wheat stands grown at high irradiance (B.G. Bugbee, 1990). Thus compensation points for entire stands appear to be greatly influenced by the lighting during development, which affects total shoot biomass and thus dark respiration.

As noted earlier, lowering the PPF from 695 to 480 umol m^{-2} s^{-1} on day 28 caused net photosynthesis to drop from 24.7 to 15.3 umol m^{-2} s^{-1}. Such a large decrease (38%) in net photosynthesis is somewhat surprising when viewed in terms of the absolute decrease in PPF (30%). However, if the the PPF difference is normalized for the stand light compensation point (180 umol m^{-2} s^{-1} at that time), then the change might be interpreted as [(695-180) - (480-180)] / (695-180), or a 42% drop in PPF above the compensation point, which agrees more closely with the decrease in net photosynthesis.

Water Exchange

A comparison of condensate production and the water added to the nutrient solution through time is shown in Fig. 10. Prior to 12 days, extra water was added to the atmosphere from supplemental humidification and more condensate was produced than water added to the nutrient solutions. After this point, condensate directly related to water transpired from the wheat stand. As with stand CO_2 uptake (photosynthesis), stand water production (transpiration) peaked at 120 L day^{-1} near 25 days when ground cover was complete. Unlike photosynthesis, however,

stand transpiration continued at relative constant level until the onset of senescence. An average of about 90 L of water were transpired from the stand each day. Based on a stand area of 20 m^2, the average transpired water in the BPC was 4.5 L m^{-2} day^{-1}. Gerbaud et al. (1988) reported that wheat stand transpiration peaked near 9 L m^{-2} day^{-1}, with an entire growth cycle average of about 5 to 6 L m^{-2} day^{-1} (their Fig. 2).

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FIGURE CAPTIONS

Fig. 1. Carbon dioxide (CO_2) concentration in the Biomass Production Chamber with a stand of wheat. CO_2 increased during the 4-h dark cycle each day and would quickly draw back down to the set point of 1000 ppm when the lights came back on. Data show the trend from three consecutive days (28 through 30).

Fig. 2. Photosynthetic drawdown of carbon dioxide in the Biomass Production Chamber by stand of wheat.

Fig. 3. CO_2 exchange rate (net photosynthesis) of a stand of wheat in response to changing atmospheric CO_2 concentration. Data were derived from the slope of the drawdown curve shown in Fig. 2. Photosynthetic rate increased rapidly from 115 ppm up to about 700-800 ppm, and then increased slowly in response to further CO_2 increase.

Fig. 4. CO_2 exchange rates throughout the growth cycle for a stand of wheat. Open symbols indicate CO_2 uptake (net photosynthesis) rates during the 20-h light cycle each day. Closed symbols indicate CO_2 production (respiration) during the 4-h dark cycle each day. At 28 days after planting, lights were dimmed resulting in a large drop in net photosynthesis. At 35 days, night temperatures were lowered from 20°C to 16°C resulting in a decrease in respiration. Effects of three controlled temperature tests and two uncontrolled losses of CO_2 supply are also noted.

Fig. 5. Effect of temperature on dark period respiration rates of a stand of wheat. Increasing the temperature from 16°C to 24°C caused a 70-75% increase in respired CO_2. Respiration at all temperatures showed a decrease as the stand aged (e.g. 5 wks vs 10 wks).

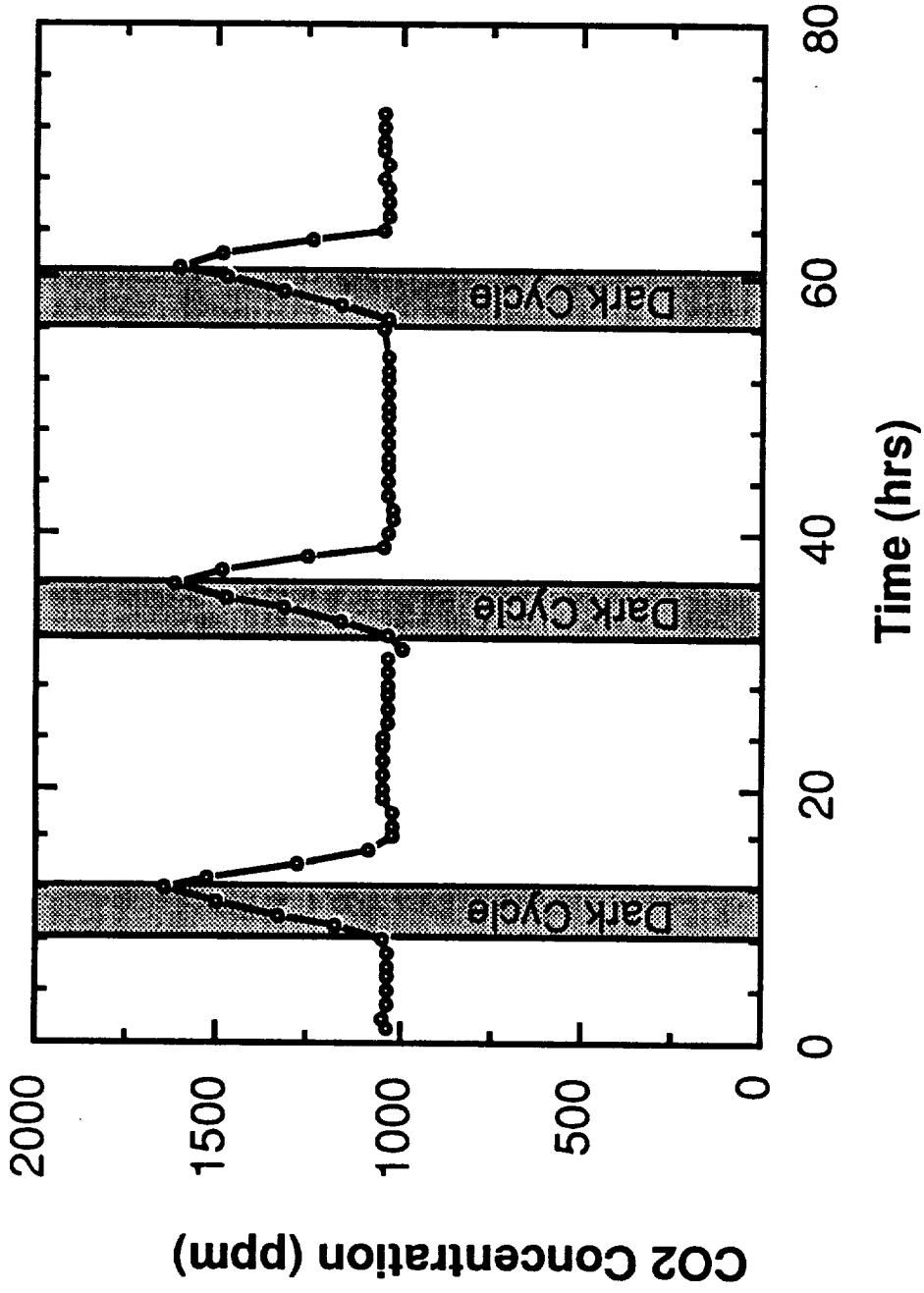
Fig. 6. Effect of changing the photosynthetic photon flux (PPF) on the rate of CO_2 drawdown (photosythetic rate) of a stand of wheat. PPF levels could be changed rapidly by dimming the high pressure sodium lamps. At a PPF of 60 umol m^{-2} s^{-1}, a net production of CO_2 occurred indicating that 60 was below the light compensation point.

Fig. 7. CO_2 exchange rate of a stand of wheat in response to photosynthetic photon flux (PPF). CO_2 exchange showed a linear increase between 60 and 750 umol m^{-2} s^{-1}. Zero net CO_2 uptake (the light compensation point) occurred near 180 umol m^{-2} s^{-1}. Measurements were taken at 41-days-age.

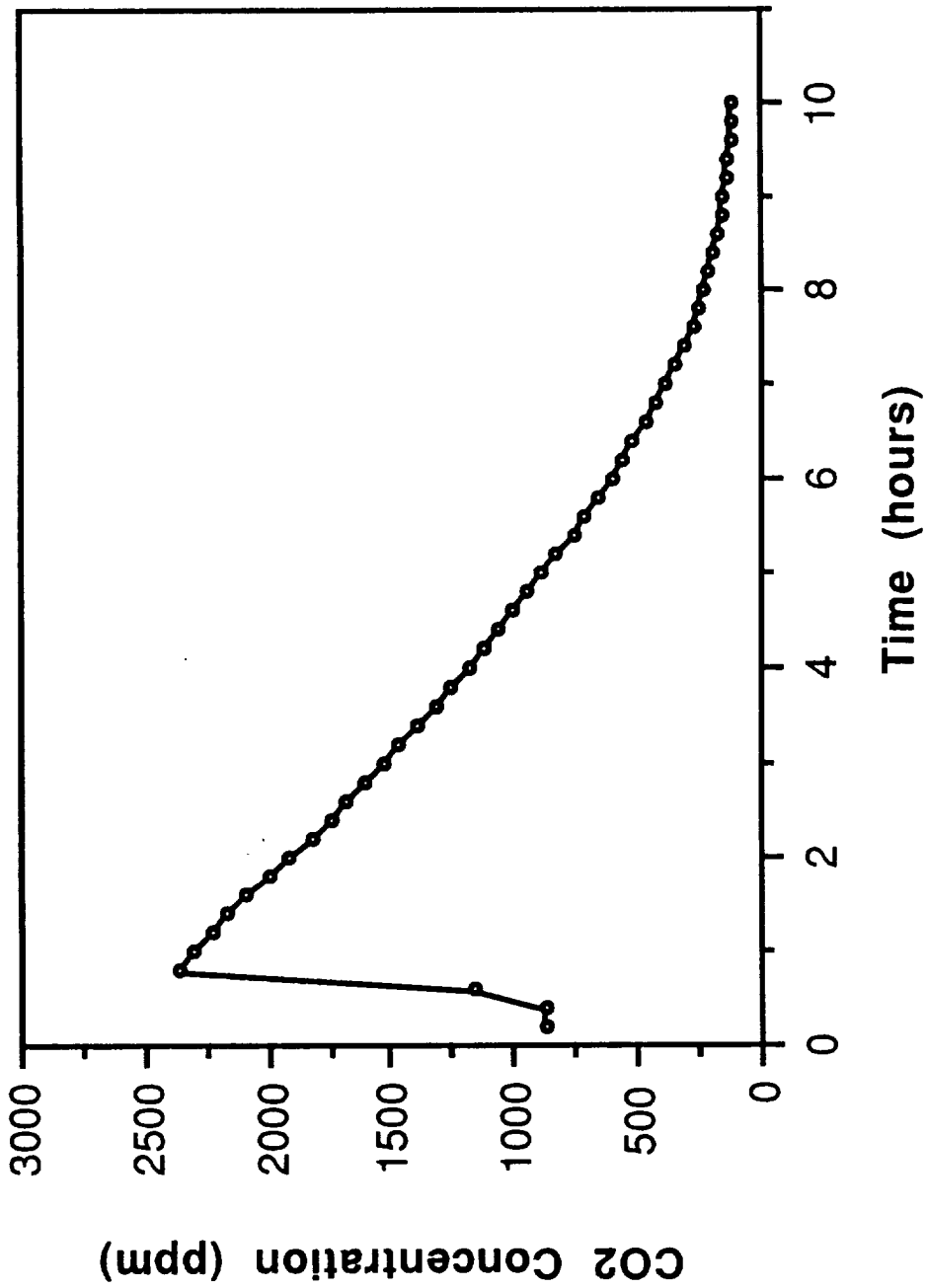
Fig. 8. Light compensation point of a stand wheat over time. At the light compensation point, photosynthesis and respiration balance and no net CO_2 uptake occurs.

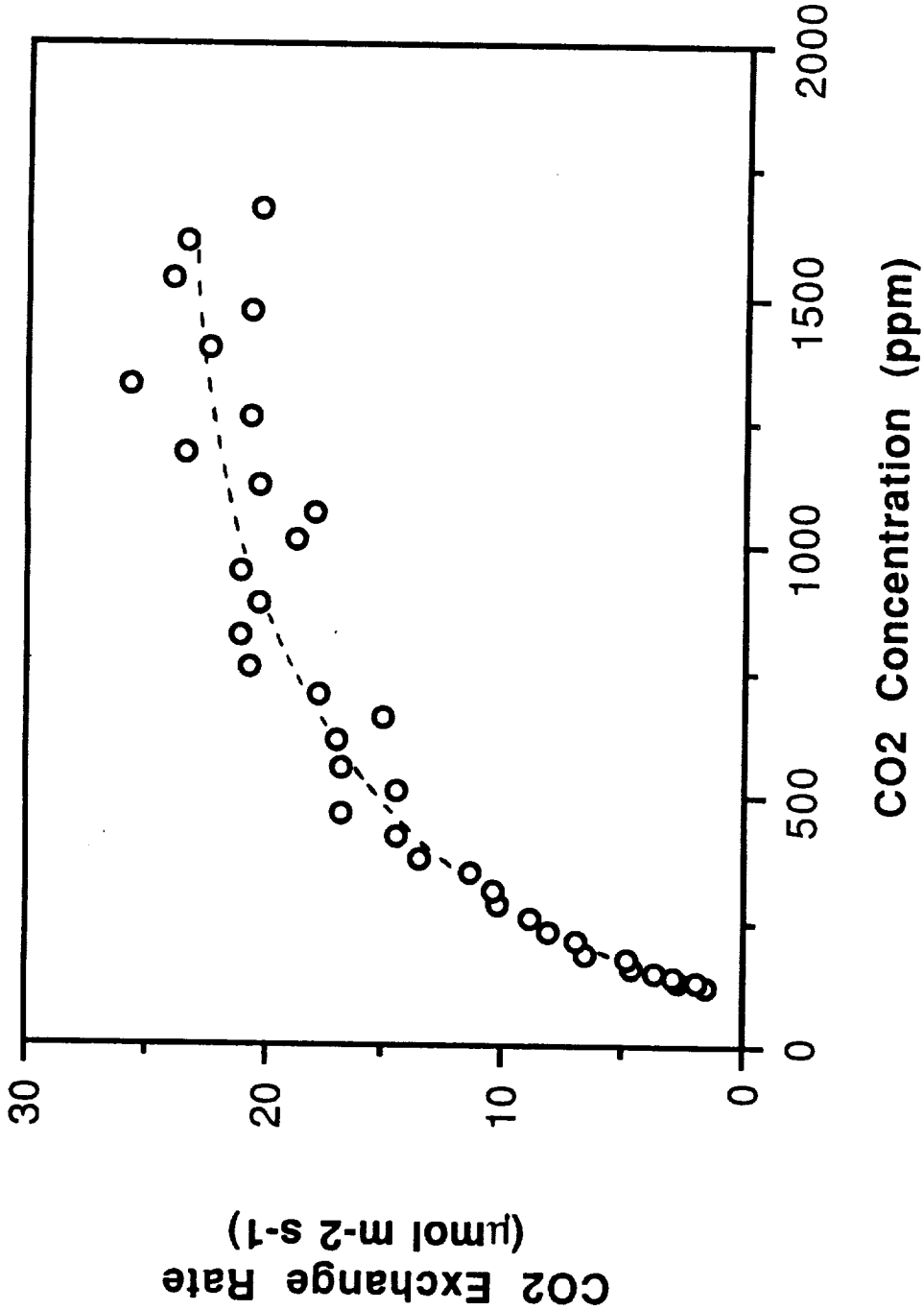
Fig. 9. Predicted CO_2 exchange rates of a stand of wheat at different PPF levels through time. After 50 days, CO_2 uptake decreased steadily at the higher PPF levels (500 and 750 umol m^{-2} s^{-1}). Plants were harvested at 86 days.

Fig. 10. Water production by a 20 m^2 stand of wheat through time in the Biomass Production Chamber. Open symbols represent the water added to nutrient solutions supplied to the plants. Closed symbols represent the amount of water condensed from the chamber atmosphere. Prior to about 15 days, supplementary humidification was provided in the chamber and more water was condensed than was added to the nutrient solutions. After this time, the amounts of water added and water recovered are nearly equal and represent the transpiration of the wheat stand.

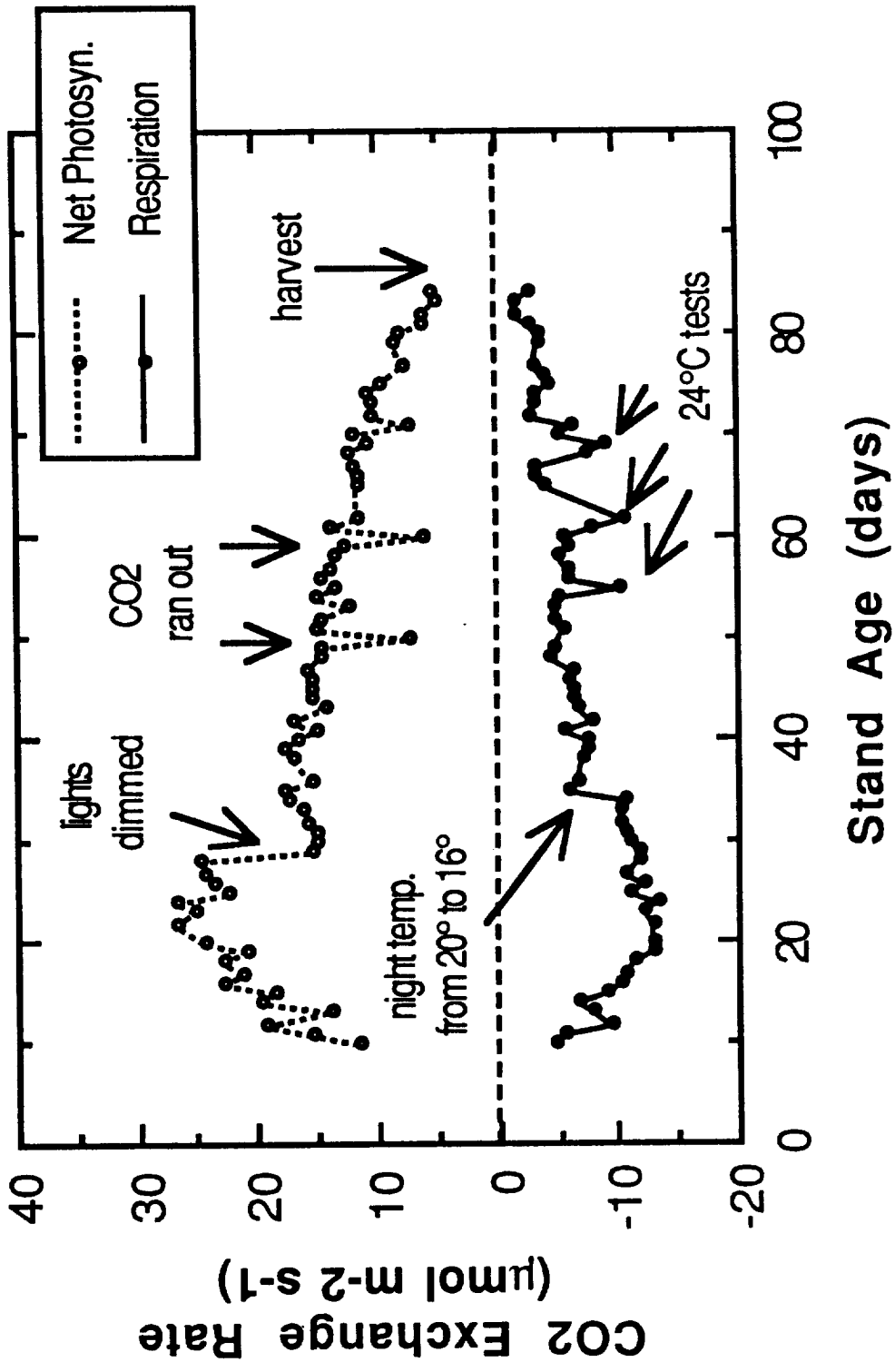

CO2 Concentration (ppm)
2000
1500
1000
500
0
0
20
40
60
80
Time (hrs)
Dark Cycle
Dark Cycle
Dark Cycle

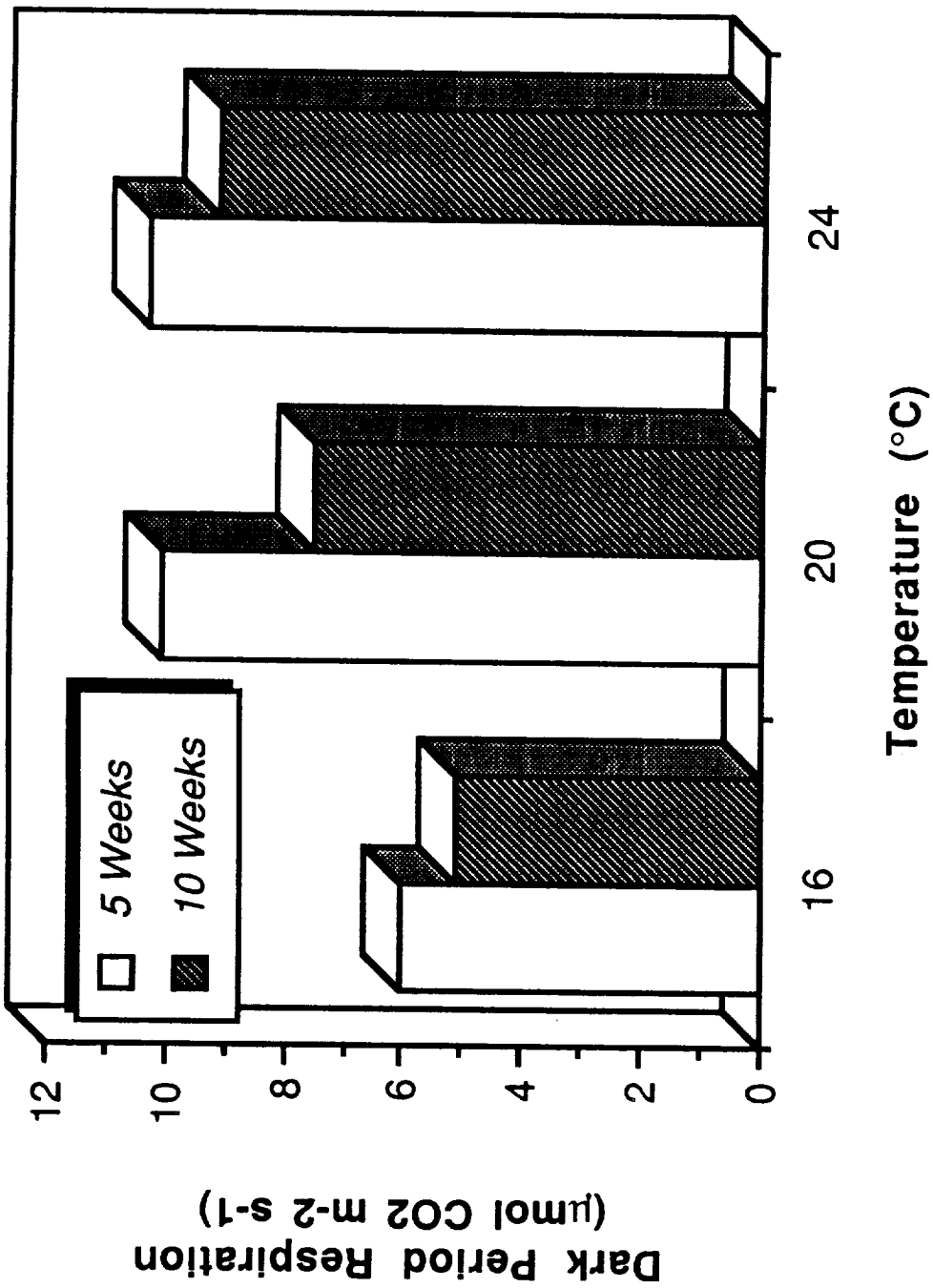
(Figure 2)


CO2 Concentration (ppm)
3000
2500
2000
1500
1000
500
0
0
2
4
6
8
10
Time (hours)

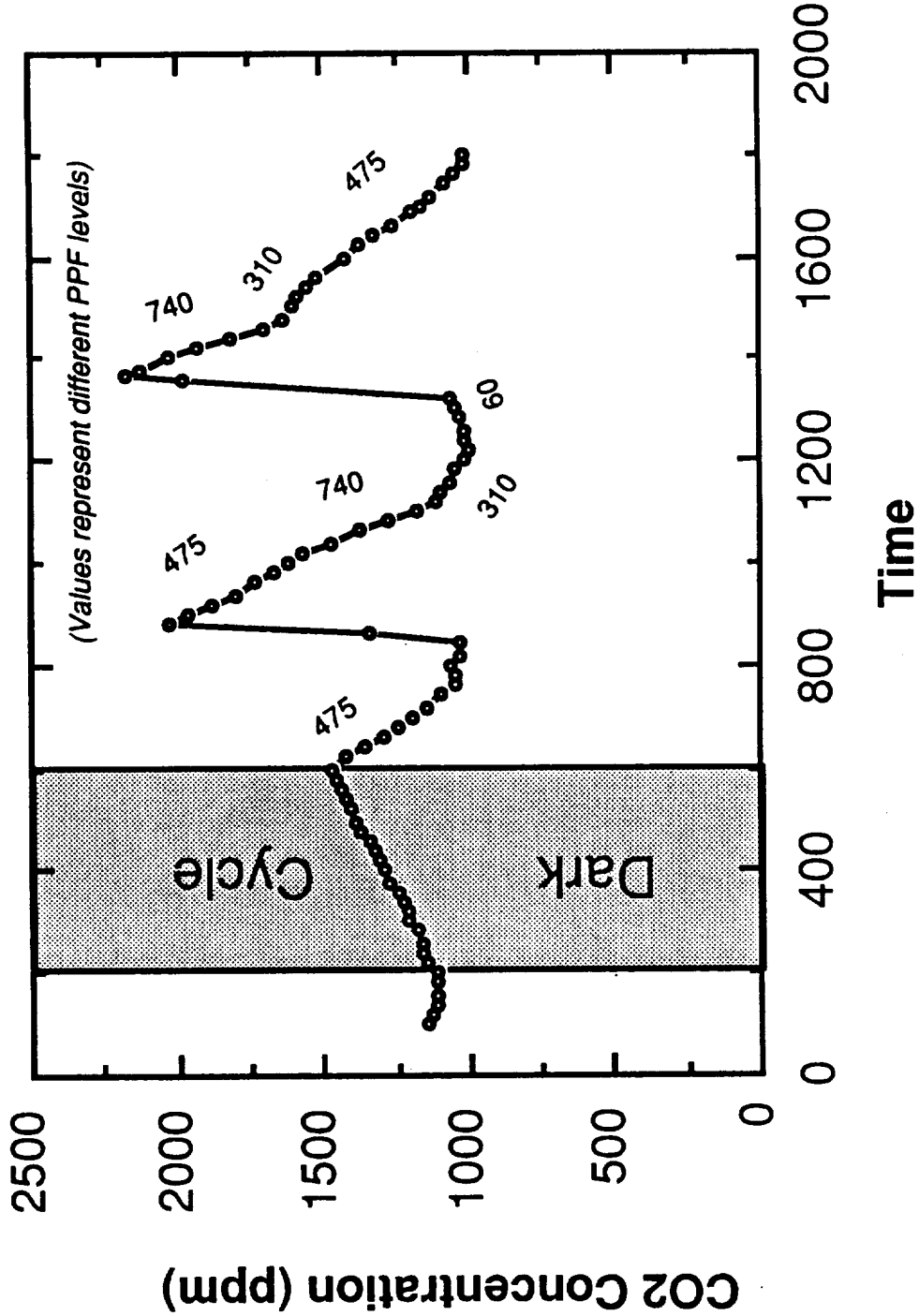

CO2 Exchange Rate
(μmol m-2 s-1)
30
20
10
0
0
500
1000
1500
2000
CO2 Concentration (ppm)

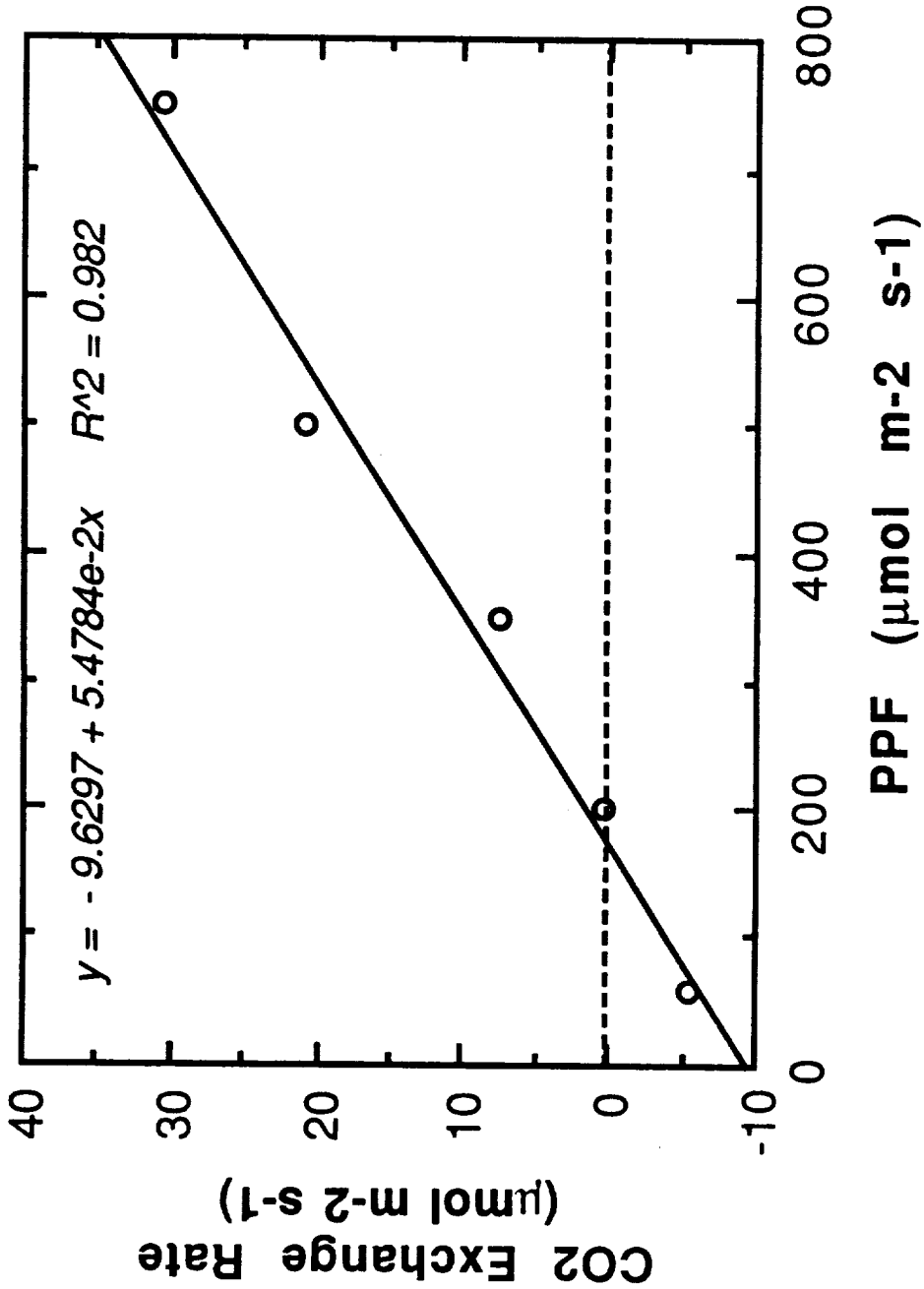
(Figure 4)


Net Photosyn.
Respiration
lights dimmed
CO2 ran out
harvest
night temp. from 20° to 16°
24°C tests
CO2 Exchange Rate (μmol m-2 s-1)
Stand Age (days)
40
30
20
10
0
-10
-20
0
20
40
60
80
100

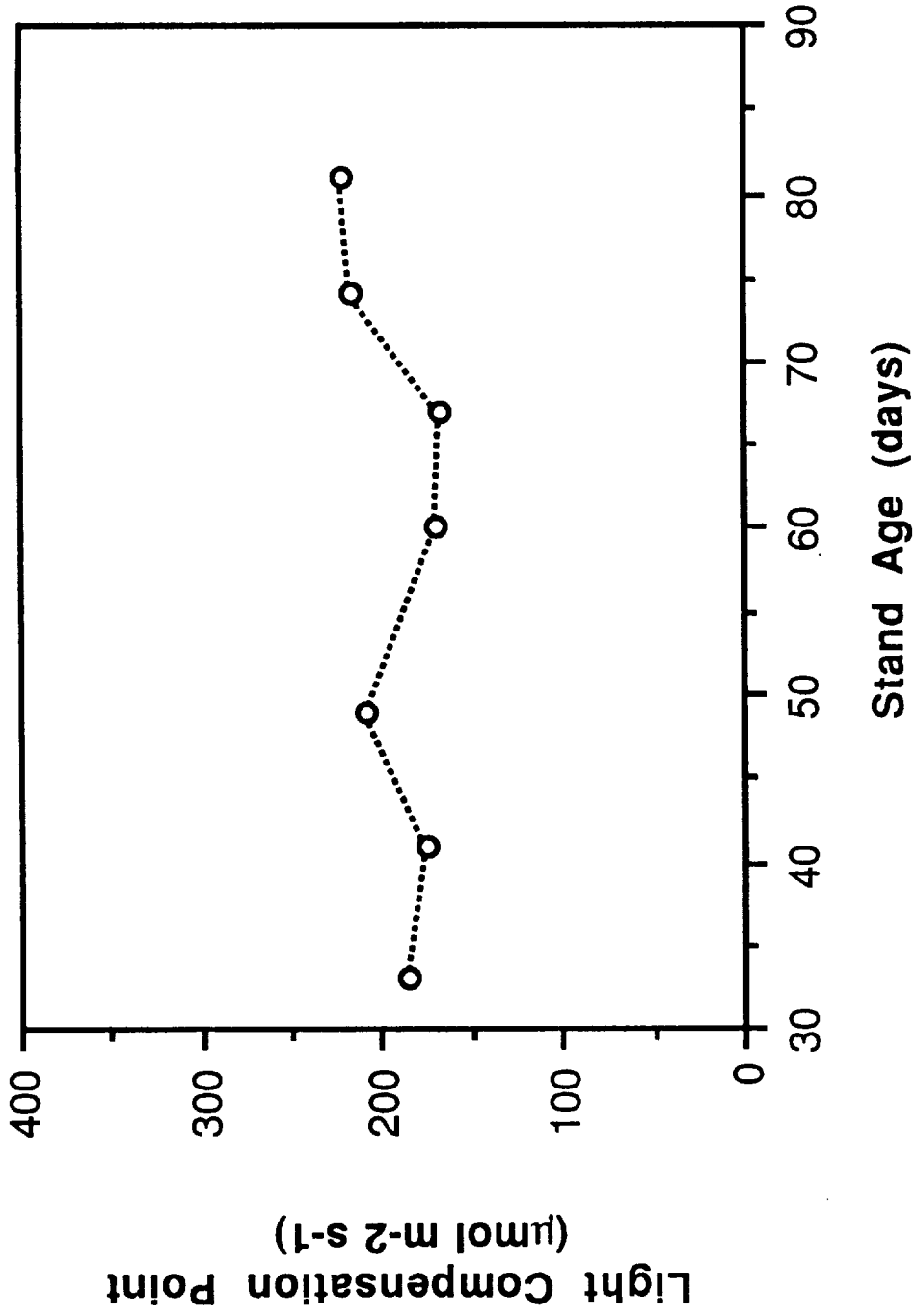

Dark Period Respiration
(μmol CO2 m-2 s-1)
0
2
4
6
8
10
12
5 Weeks
10 Weeks
16
20
24
Temperature (°C)

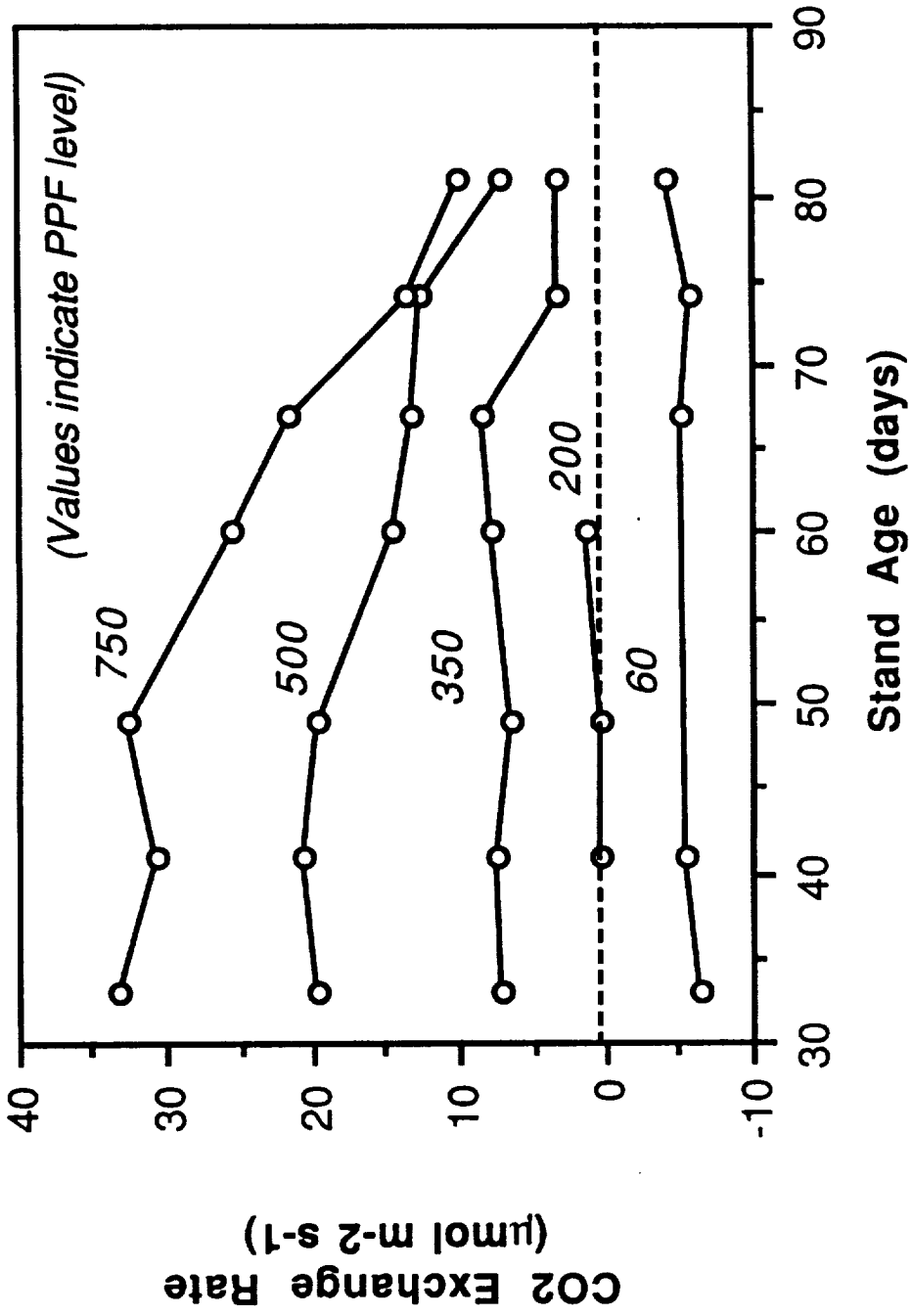
(Figure 6)


CO2 Concentration (ppm)
2500
2000
1500
1000
500
0
0
400
800
1200
1600
2000
Time
Dark
Cycle
(Values represent different PPF levels)
475
310
740
60
740
310
475
475

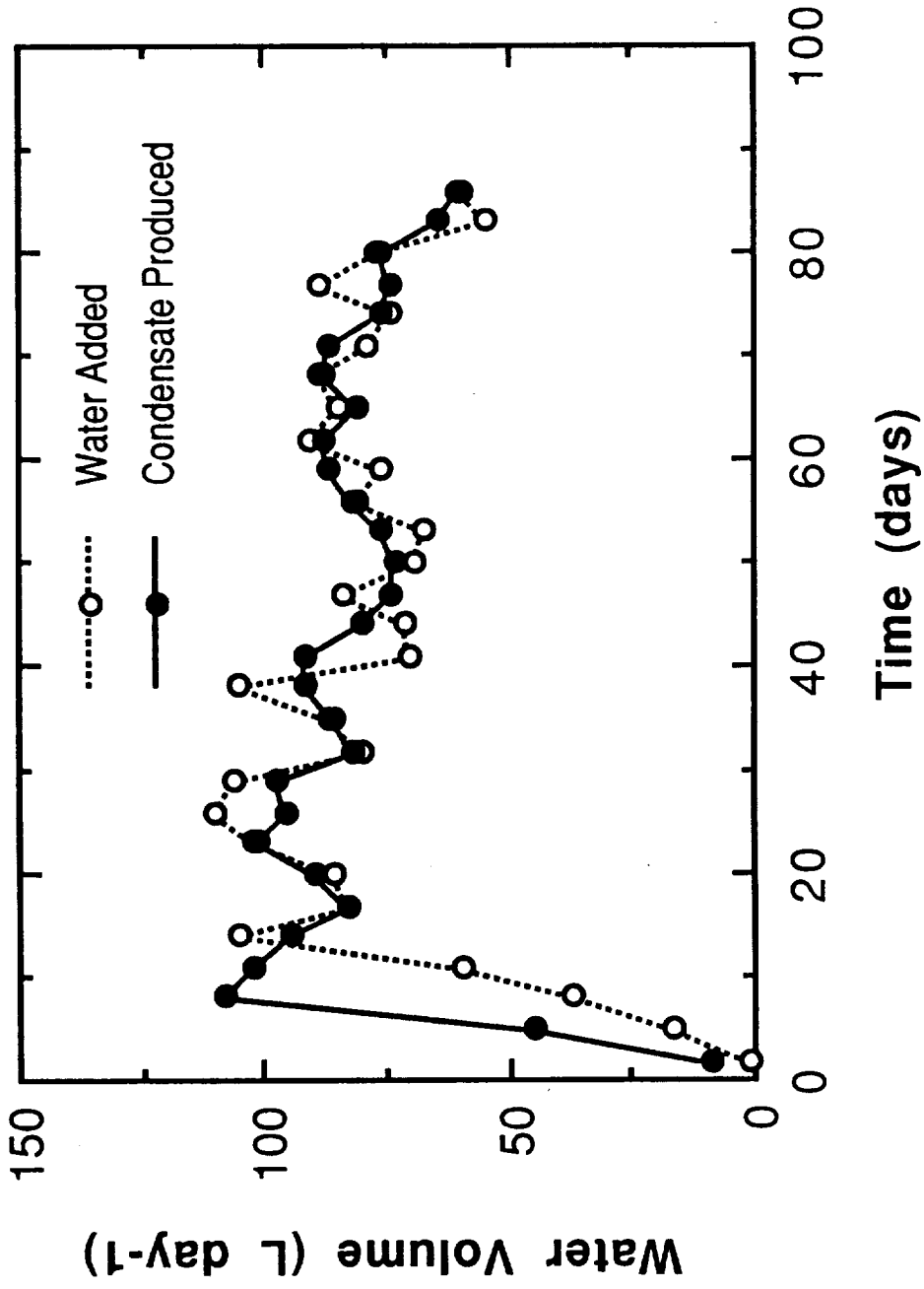

CO2 Exchange Rate
(µmol m-2 s-1)
40
30
20
10
0
-10
0
200
400
600
800
PPF (µmol m-2 s-1)
y = - 9.6297 + 5.4784e-2x R^2 = 0.982

(Figure 8)


Light Compensation Point
(μmol m-2 s-1)
400
300
200
100
0
30
40
50
60
70
80
90
Stand Age (days)


CO2 Exchange Rate
(µmol m-2 s-1)
40
30
20
10
0
-10
30
40
50
60
70
80
90
Stand Age (days)
(Values indicate PPF level)
750
500
350
200
60

(Figure 10)


Water Volume (L day-1)
150
100
50
0
0
20
40
60
80
100
Time (days)
Water Added
Condensate Produced

NASA National Aeronautics and Space Administration

Report Documentation Page

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15. Supplementary Notes

16. Abstract

Gas exchange measurements were taken for a 20 m^2 wheat stand grown from seed to harvest in NASA's Biomass Production Chamber. Respiration of the wheat stand caused the CO_2 concentrations to rise an average of 440 ppm during the 4-h dark period each day, or 7.2 umol m^{-2} s^{-1}. Dark period respiration was sensitive to temperature changes and could be increased 70-75% by raising the temperature from 16°C to 24°C. Stand photosynthesis (measured from the rate of CO_2 drawdown immediately after the lights came on each day) peaked at 27 umol m^{-2} s^{-1} at 25 days after planting and averaged 15 umol m^{-2} s^{-1} throughout the study. By combining light period photosynthesis and dark period respiration, a net of 860 g or 470 liters of CO_2 were fixed per day. Stand photosynthetic rates showed a linear increase with increasing irradiance (750 umol m^{-2} s^{-1} PPF the highest tested), with an average light compensation point after day 30 of 190 umol m^{-2} s^{-1} PPF. Stand photosynthesis decreased slightly when CO_2 levels were decreased from 2200 to 800 ppm, but dropped sharply when CO_2 was decreased below 700-800 ppm. Water production from stand transpiration peaked at 120 L day^{-1} near 25 days after planting and averaged about 90 L day^{-1}, or 4.5 L m^{-2} day^{-1} throughout the study.

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