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EFFECTS OF ATMOSPHERIC CO_2 ON PHOTOSYNTHETIC CHARACTERISTICS OF SOYBEAN LEAVES

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ABSTRACT

Soybean (*Glycine max* cv. McCall) plants were grown at 500, 1000, and 2000 umol mol^{-1} CO_2 for 35 days and a photosynthetic photon flux (PPF) of 300 umol m^{-2} s^{-1}. Individual leaves were then exposed to step changes of CO_2 concentration and PPF to study CO_2 assimilation rates (CAR), i.e., leaf net photosynthesis. In general CAR increased when CO_2 increased from 500 to 1000 umol mol^{-1}, but not from 1000 to 2000 umol mol^{-1}. Regardless of the previous CO_2 level, all leaves showed similar CAR at similar CO_2 and PPF. This observation contrasts with reports that plants tend to become "lazy" at elevated CO_2 levels over time. Although leaf stomatal conductance (to water vapor) showed diurnal rhythms entrained to the photoperiod, leaf CAR did not show these rhythms and remained constant across the light period, indicating that stomatal conductance had little effect on CAR. Such measurements suggest that short-term changes in CO_2 exchange dynamics for a Controlled Ecological Life Support System (CELSS) can be closely predicted for an actively growing soybean crop.

INTRODUCTION

Soybean (*Glycine max* L.) is among the candidate crops currently under study for use in a Controlled Ecological Life Support System (CELSS; 1) and is tentatively scheduled for testing in the Biomass Production Chamber (BPC) at Kennedy Space Center in 1990. Preliminary tests with soybeans are currently underway in growth chambers at Kennedy Space Center in preparation for BPC studies. A major focus of these studies has been the effects of elevated CO_2 on plant development and biomass production. During all of these tests, leaf gas exchange (i.e. photosynthesis and transpiration) measurements were taken from plants grown under the different atmospheric CO_2 levels. In addition, the leaves were exposed to temporary changes in irradiance and atmospheric CO_2 to determine whether the growing environment had any effects on inherent photosynthetic capabilities of the leaves. The results should provide an indication of the effects of transient changes in either CO_2 or irradiance on the rate of CO_2 uptake by plants within a closed system. A set of follow-up measurements will be conducted during the BPC grow-outs to directly compare events at the leaf level with events at the plant canopy or community level.

METHODS AND MATERIALS

Soybean (Glycine max cv McCall) plants were grown in 0.25 m^2 plastic trays in a walk-in growth chamber using nutrient film technique and a complete nutient solution (2). A photosynthetic photon flux (PPF) of 300 ± 30 umol m^{-2} s^{-1} was provided by 30 VHO Vita Lite fluorescent lamps with a 12-hr light / 12-hr dark photoperiod. Temperatures were maintained at 26 ± 0.5 C during the light cycle and 20 ± 0.5 C during the dark; relative humidity was kept constant at 65% ± 5%. A series of three separate studies was conducted during which chamber CO_2 levels were maintained 500, 1000, and 2000 umol mol^{-1} (ppm) (set points held to within approximately ± 2% full scale). Carbon dioxide levels were monitored and controlled using an infrared gas analyzer (Anarad, Santa Barbara, CA) with a dedicated computer control system. Analyzer zero and span points were taken automatically each day to update the regression used for CO_2 determination, while manual adjustments for instrument drift were made as necessary.

At 36 days after planting, single fully-expanded leaves at the top of the canopy were selected for gas exchange measurements. Carbon dioxide assimilation rates (CAR) of the leaves were determined using an LCA2 portable photosynthesis system with a PLC model B leaf chamber (ADC Co., Hoddesdon, England). The incoming gas stream to the cuvette was provided from a CO_2-enriched (3510 umol mol^{-1}) compressed air supply. Different CO_2 concentrations were obtained from this air stream using an ADC GD600 gas diluter to selectively shunt portions of the flow through a soda lime column to remove CO_2. This system was used to provide gas supplies of 0, 255, 440, 695, 1040, 1290, 1480, and 2030 umol mol^{-1} CO_2. Higher levels were not used because of the inability to span the infrared analyzer unit beyond 2100 umol mol^{-1}. Different PPF levels were obtained by using the existing fluorescent radiation with neutral (metal) screening for levels less than 300 umol m^{-2} s^{-1} (63, 40, 28%), or with fluorescent plus supplemental radiation from a rheostat-controlled incandescent lamp with dichroic reflector and focused with a fiber optic guide. This supplemental radiation was filtered through a glass petri dish to reduce the long wave component. Cuvette temperatures could thus be kept within ± 0.3 C of the initial temperature. In addition to the radiation sensor on the ADC leaf cuvette unit, PPF levels were checked with a Li-Cor quantum sensor (Li-Cor Inc, Lincoln, NE).

Each single leaf was exposed to the entire set of CO_2 and PPF regimes, with a set of measurements lasting approximately 4 hours. This was done to expedite measurements during the middle of the photoperiod and to avoid leaf to leaf variability. This approach risked disturbing the leaf (e.g. closing leaf stomata) from the physical contact and/or altered environment of the cuvette. To avoid drying the leaf, the air stream desiccant loop of the gas supply system was bypassed thereby keeping cuvette relative humidities between 60 and 80%. To determine whether the measurements were themselves having any disruptive effects, measurements at the ambient CO_2 and PPF levels were taken before, in the middle, and at the end of each set of measurements. In all cases, initial photosynthetic rates were consistently repeatable even after 4 hours, indicating minimal effects of the physical measurements on leaf photosynthetic rates.

Carbon assimilation rates were calculated as the difference between incoming and outgoing CO_2 concentrations (on a molar basis) multiplied by the air stream flow rate (approx. 300 ml min^{-1}) and divided by the leaf area (6.25 cm^2) (3). No corrections were made for water interference in the readings.

RESULTS

Prior to testing leaf photosynthetic response to changing CO_2 and PPF levels, CAR was measured across the 12-hr photoperiod to determine whether any diurnal differences existed. As shown in Figs. 1 and 2, CAR measurements tended to remain constant across the light period, but stomatal conductance to water vapor showed a distinct diurnal rhythm, peaking prior to the middle of the light period and then decreasing with the onset of the dark period. Interestingly, changes in stomatal conductance had little effect on leaf photosynthetic rates (CAR) (Figs 1 and 2). However, to avoid any possible diurnal effects, all gas exchange data were taken within 2 hours of the middle of the photoperiod.

The effect of increasing CO_2 concentration at different PPF levels on leaf CAR for plants grown at 500 umol mol^{-1} CO_2 is shown in Fig. 3. Leaf CAR at the lower PPF levels tended to plateau at relatively low CO_2 levels, i.e. PPF was limiting and the CO_2 response was saturated. But at a PPF of 510 or 840 umol m^{-2} s^{-1}, no CO_2 saturation occurred, i.e. maximum rates were not achieved, even up to 1040 umol mol^{-1} CO_2. Leaves from plants grown at 1000 umol mol^{-1} CO_2 showed a similar trend of CO_2 saturation at lower PPF levels (Fig. 4). At a PPF of 510 or 840, CAR increased up to 1040 umol mol^{-1} CO_2, but did not increase when CO_2 was increased to 1290 umol mol^{-1}. Leaves from plants grown at 2000 umol mol^{-1} CO_2 also showed this trend, with peak CAR occurring at the highest PPF level near 1040 umol mol^{-1} CO_2 (Fig 5); raising the CO_2 higher than 1040 had no positive effect and tended to decrease leaf photosynthetic rates. A comparison of data from leaves taken from plants grown at the different CO_2 levels indicates that CAR was similar for similar combinations of CO_2 and PPF (Fig. 6).

DISCUSSION

The results suggest that regardless of the CO_2 concentration in the "native" environment, transient changes in the atmospheric CO_2 and irradiance have similar effects on carbon assimilation rates of healthy soybean leaves (Fig. 6). This contrasts with findings from other species in which CO_2 enrichment tends to reduce photosynthetic capacity with time (4). But recent field studies with soybeans have shown that long-term CO_2 enrichment had no adverse effects, and even increased photosynthetic capacity (5). From a CELSS perspective, it is noteworthy that the effects of transient changes on soybean CAR can be predicted independent of the crop's prior history. Thus, leaf systems may serve as useful models for testing transient changes in a closed life support module. However, this presumes that single-leaf gas exchange measurements closely reflect community gas exchange, which remains to be tested.

A comparison of CAR curves from Fig. 5 indicates that there is no advantage to raising the CO_2 much above 1000 umol mol^{-1} and that levels greater than this (e.g. 2000 umol mol^{-1}) may be supraoptimal. The drop in photosynthetic rates by increasing CO_2 from 1000 to 2000 umol mol^{-1} may be a result of some feedback inhibition, e.g. excessive starch accumulation in leaves (6,7). Aside from determining the optimum environment for photosynthesis, such data will be useful for the purposes of a CELSS, where plants may be subjected to transient changes in CO_2 levels, or levels much higher than have been traditionally studied (e.g. >1000 umol mol^{-1}).

Because the plants were all grown at a PPF of 300 umol m^{-2} s^{-1}, we can only speculate on the effects that a native lighting environment might have on photosynthetic capacities. It is likely that the lighting history would affect leaves differently than the CO_2 history because of irradiance effects on leaf chlorophyll content and chloroplast structure (8). However results from this study did show that when CO_2 levels were 440 umol mol^{-1} or greater, a PPF of 840 umol m^{-2} s^{-1} was still below the light saturation point for soybean leaves.

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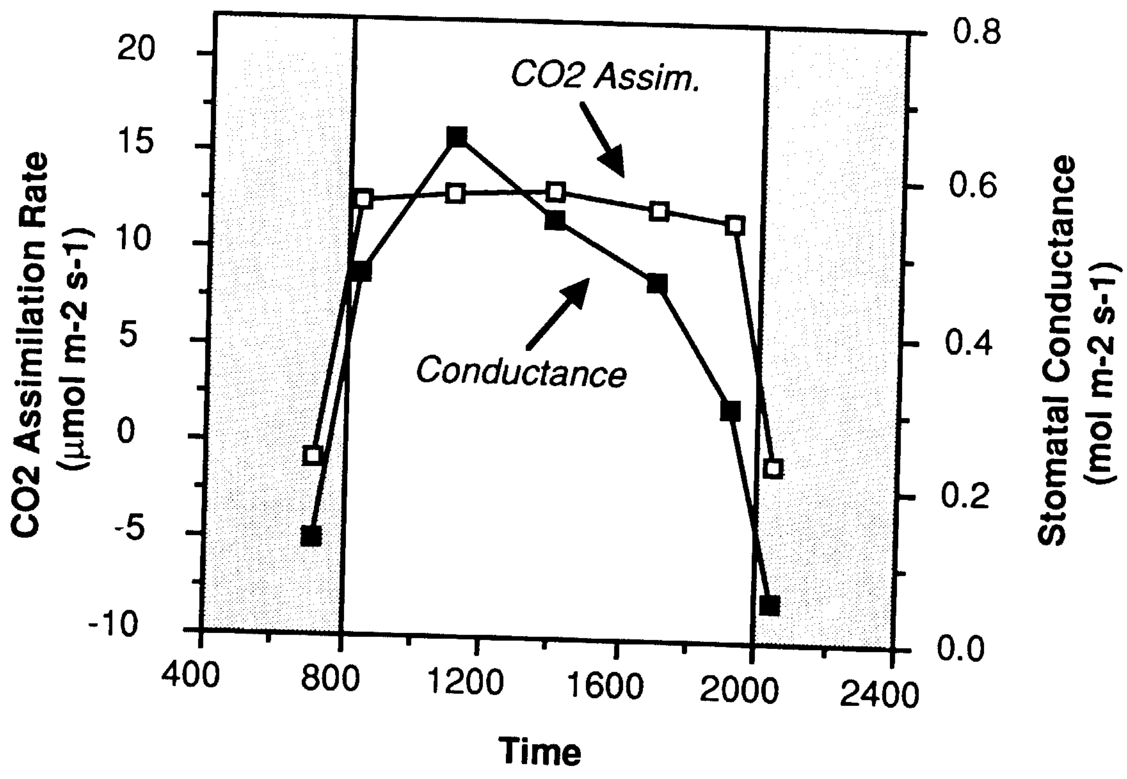

Figure 1. Diurnal trend of CO_2 assimilation (photosynthesis) rate and stomatal conductance of soybean leaves at 500 umol mol^{-1} CO_2. Photoperiod began at 0800 and ended at 2000 each day.

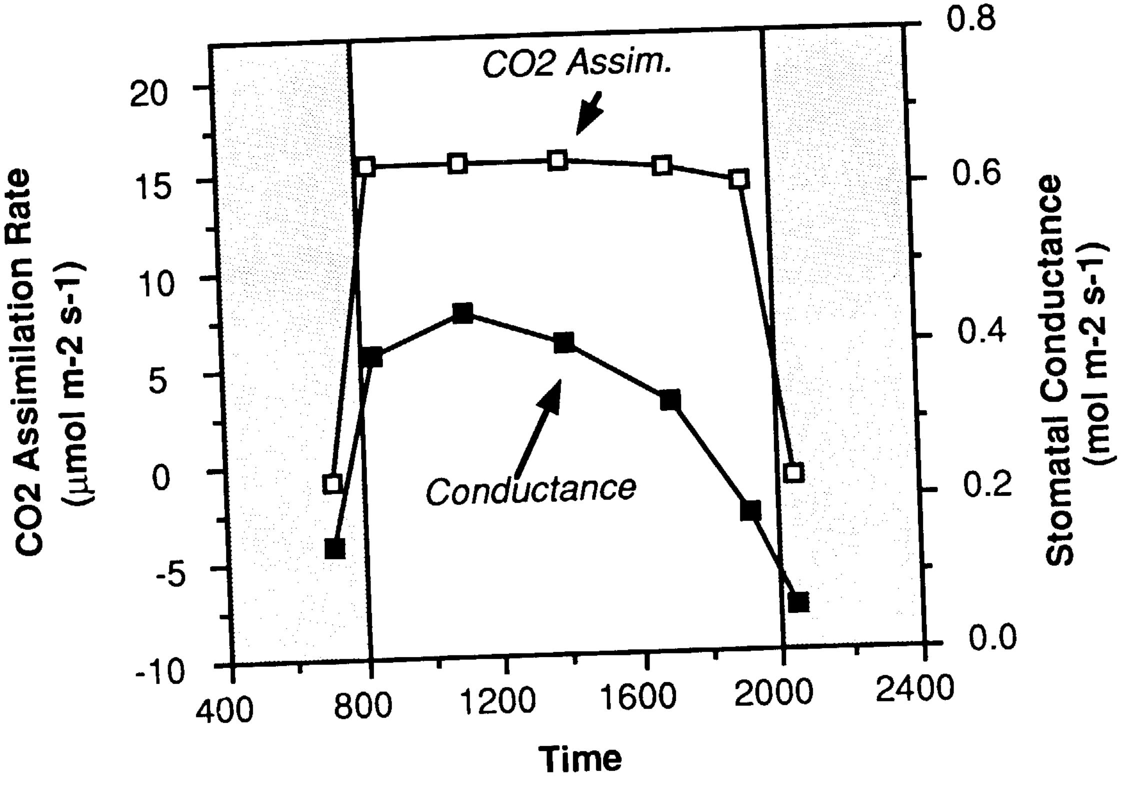

Figure 2. Diurnal trend of CO_2 assimilation (photosynthesis) rate and stomatal conductance of soybean leaves at 1000 umol mol-1 CO_2. Photoperiod began at 0800 and ended at 2000 each day.

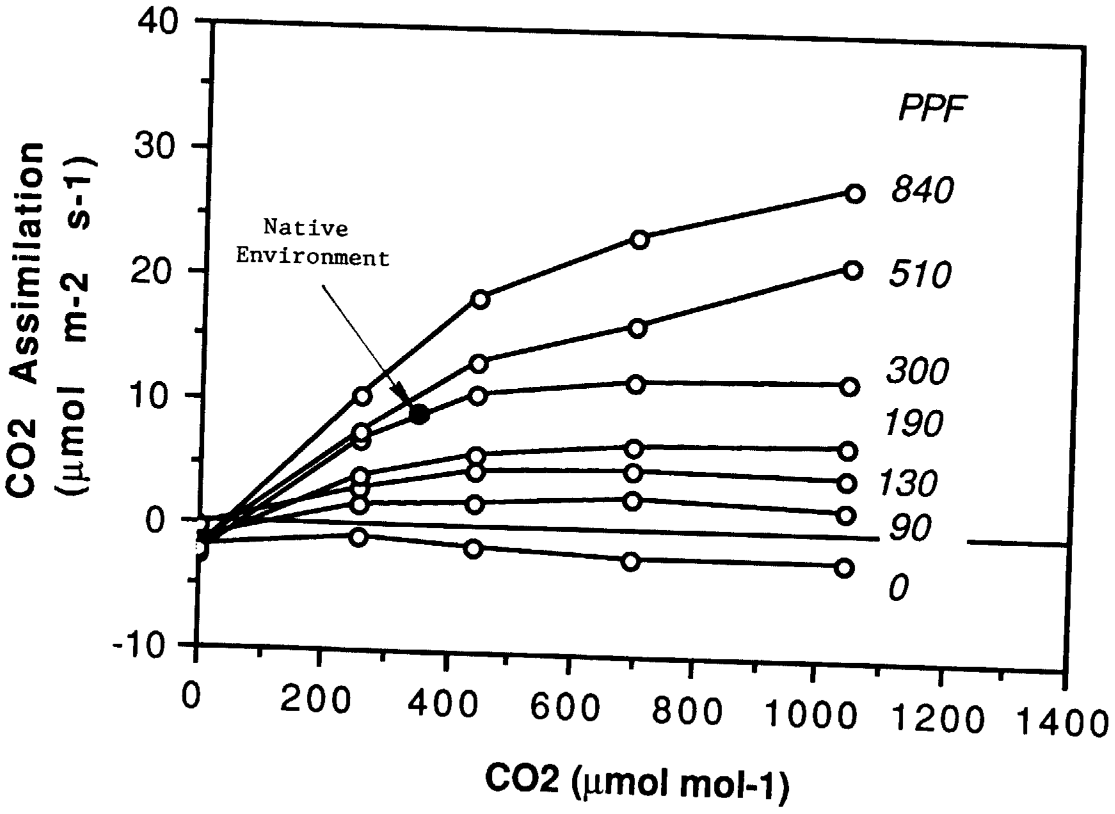

Figure 3. CO_2 assimilation (photosynthesis) rates of soybean leaves at different CO_2 and photosynthetic photon flux (PPF) levels. Plants were grown at 500 umol mol-1 CO_2.

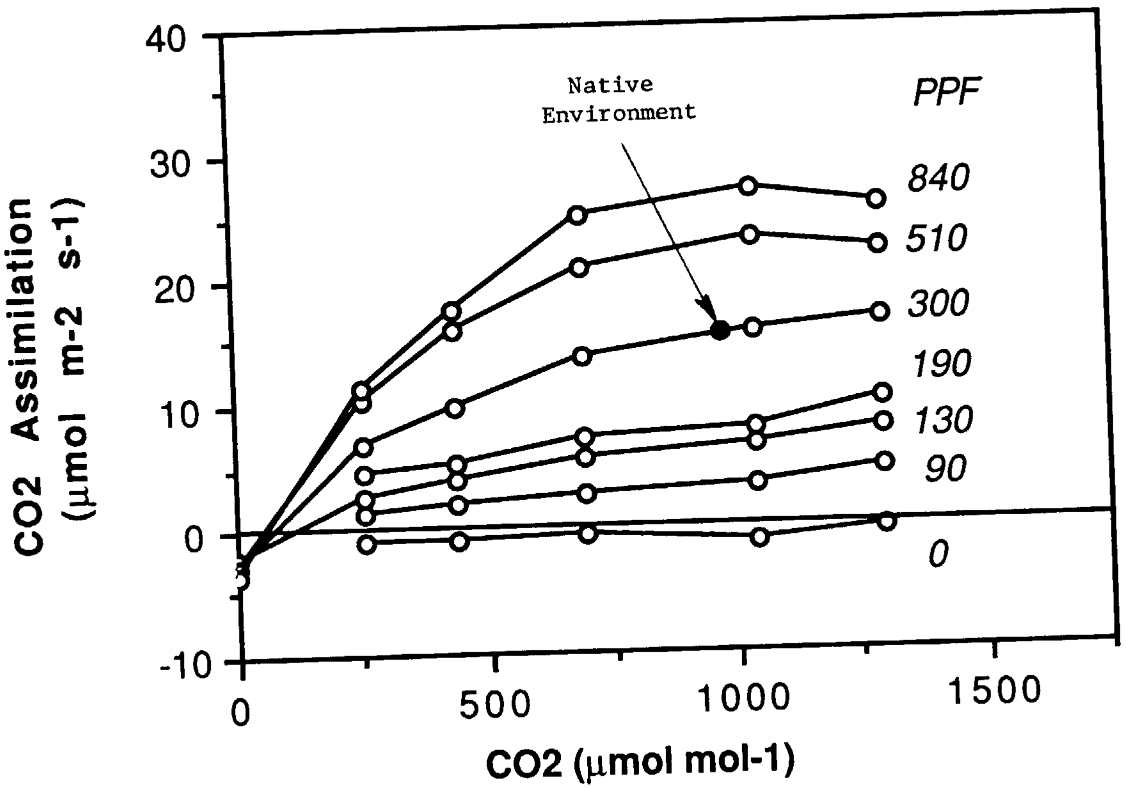

Figure 4. CO_2 assimilation (photosynthesis) rates of soybean leaves at different CO_2 and photosynthetic photon flux (PPF) levels. Plants were grown at 1000 umol mol^{-1} CO_2.

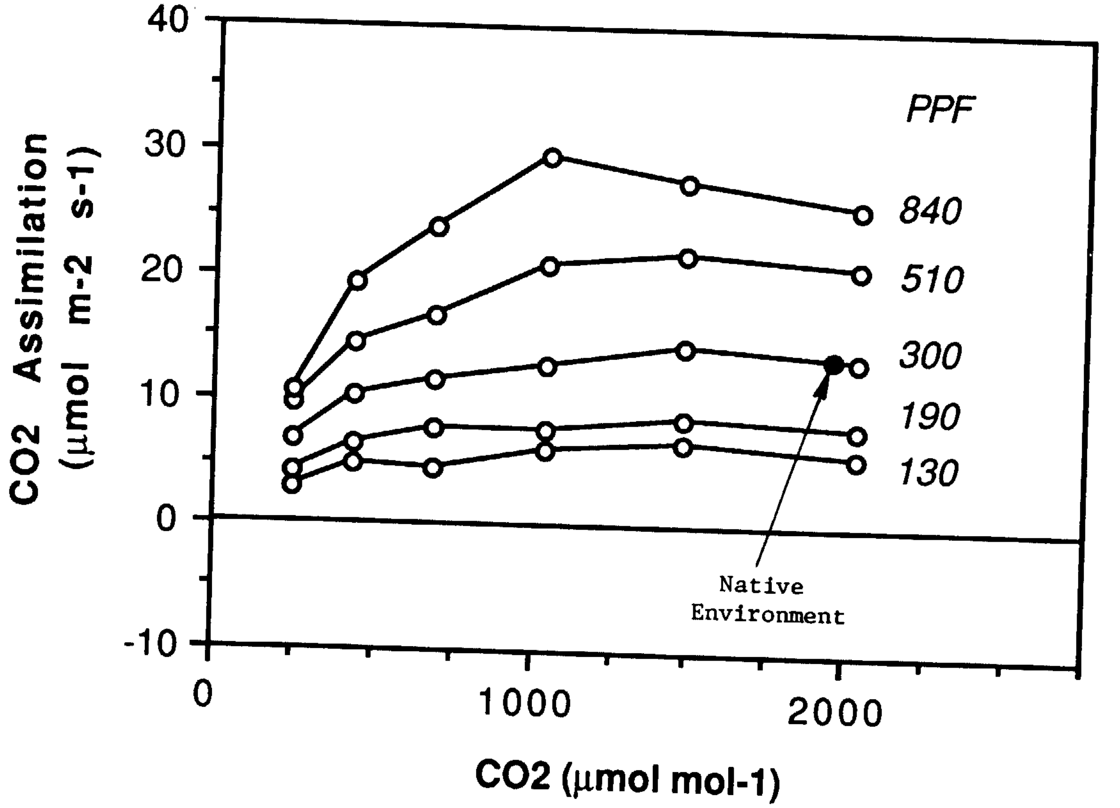

Figure 5. CO_2 assimilation (photosynthesis) rates of soybean leaves at different CO_2 and photosynthetic photon flux (PPF) levels. Plants were grown at 2000 umol mol^{-1} CO_2.

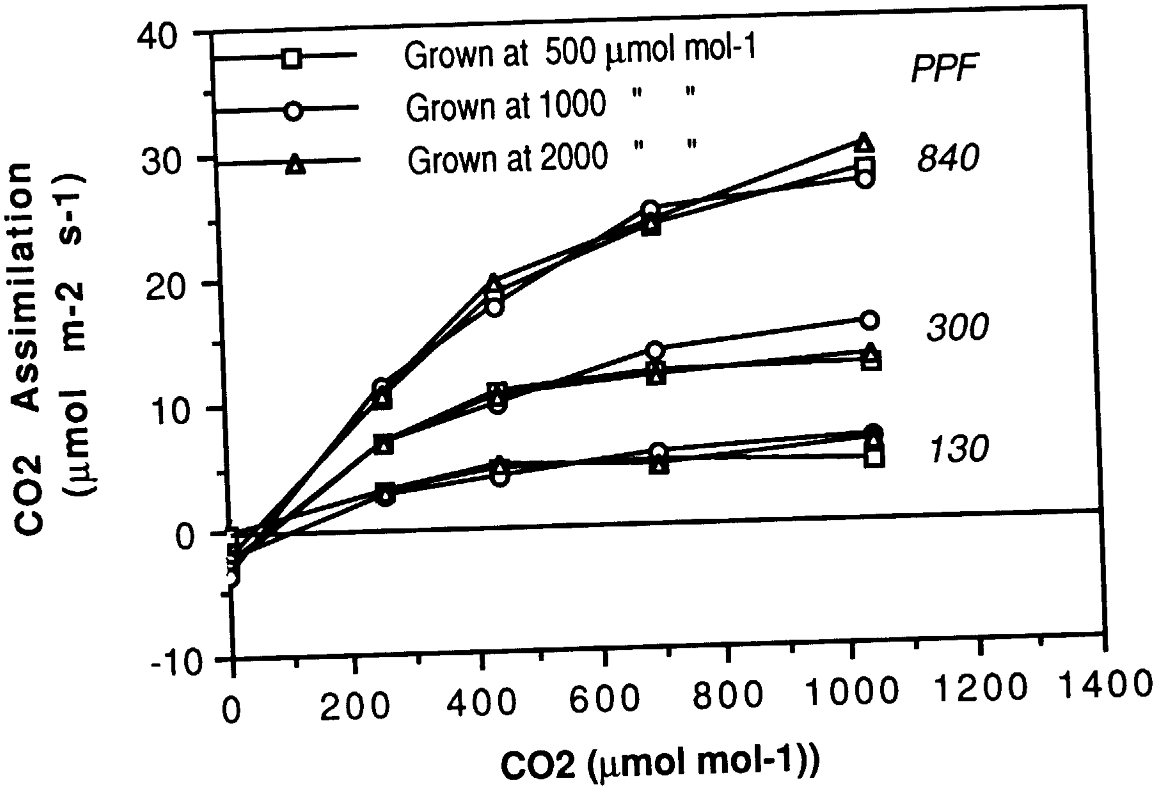

Figure 6. Comparison of CO_2 assimilation (photosynthesis) rates of soybean leaves at different CO_2 and photosynthetic photon flux (PPF) levels. Leaf measurements were taken from plants grown at 500, 1000, and 2000 umol mol^{-1} CO_2.