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# Exploring the Limits of Crop Productivity[1]

## I. PHOTOSYNTHETIC EFFICIENCY OF WHEAT IN HIGH IRRADIANCE ENVIRONMENTS

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### ABSTRACT

**The long-term vegetative and reproductive growth rates of a wheat crop (*Triticum aestivum* L.) were determined in three separate studies (24, 45, and 79 days) in response to a wide range of photosynthetic photon fluxes (PPF, 400–2080 micromoles per square meter per second; 22–150 moles per square meter per day; 16–20-hour photoperiod) in a near-optimum, controlled-environment. The $CO_2$ concentration was elevated to 1200 micromoles per mole, and water and nutrients were supplied by liquid hydroponic culture. An unusually high plant density (2000 plants per square meter) was used to obtain high yields. Crop growth rate and grain yield reached 138 and 60 grams per square meter per day, respectively; both continued to increase up to the highest integrated daily PPF level, which was three times greater than a typical daily flux in the field. The conversion efficiency of photosynthesis (energy in biomass/energy in photosynthetic photons) was over 10% at low PPF but decreased to 7% as PPF increased. Harvest index increased from 41 to 44% as PPF increased. Yield components for primary, secondary, and tertiary culms were analyzed separately. Tillering produced up to 7000 heads per square meter at the highest PPF level. Primary and secondary culms were 10% more efficient (higher harvest index) than tertiary culms; hence cultural, environmental, or genetic changes that increase the percentage of primary and secondary culms might increase harvest index and thus grain yield. Wheat is physiologically and genetically capable of much higher productivity and photosynthetic efficiency than has been recorded in a field environment.**

The influence of factors limiting crop productivity could be better assessed if the maximum potential productivity was known. Physiologists have long been interested in the efficiency of photosynthesis in single leaves and over a quarter century ago estimated the maximum photosynthetic rate (carbon fixed g $m^{-2}$ $d^{-1}$) by a community of plants in the field (28). Loomis and Williams (13) appear to be the first to calculate maximum potential productivity based on incident PPF[2] rather than total radiant energy. They estimated the maximum quantum yield of a single leaf, PPF absorption, and respiration and determined a potential growth rate of 15.4 $\mu$g per calorie total radiation. They assumed an incident PPF of 43.2 mol $m^{-2}$ $d^{-1}$ (500 cal $cm^{-2}$ $d^{-1}$) and calculated a potential CGR of 77 g $m^{-2}$ $d^{-1}$.

The past two decades of research have provided the data to make more accurate estimates of potential growth rate. Because average radiation levels vary widely among geographic locations, it is useful to calculate maximum growth rate per unit of incident radiation (efficiency), rather than an absolute maximum growth rate. This efficiency has been calculated as g of biomass per MJ total radiation (7, 16), but photosynthetic photon flux is the most direct measure of useful radiation, and efficiency is better expressed as g per mol of photosynthetic photons. The estimate of Loomis and Williams (13) is about 1.78 g $mol^{-1}$ of photons.

Although the theoretical minimum quantum requirement is 8 mol of photons per mol of $CO_2$ fixed, the lowest quantum requirement measured in intact leaves has been about 12.5, and this has been possible only in 2% oxygen atmospheres (6, 19). Monteith (16) conservatively estimated that a photosynthetic efficiency of 1.28 g $mol^{-1}$ of photons was obtainable with a quantum requirement of 20, but Ehleringer and Pearcy (6) obtained a quantum requirement of 13.7 at 16°C in normal atmospheric conditions and their data suggest that a quantum requirement of 13 might be achievable in C3 plants at about 13°C. Assuming a quantum requirement of 13, 95% absorption of the incident PPF, a respiratory carbon use efficiency of 75%, and 40% carbon in the plant mass (23, 26), results in a maximum growth rate of 1.64 g per mol of photons. This is very optimistic but is slightly lower than the widely cited value obtained by Loomis and Williams. This growth rate would be possible only with low-lipid plants in which the respiratory carbon use efficiency can be high.

Efficiency can be expressed as a percentage if the energy content of the dry biomass and the spectral distribution of the radiation are known. A good estimate of the combustible energy content of the biomass of low-lipid plants is 17.2 MJ $kg^{-1}$ (11), and the average energy content of photosynthetic photons is about 217 kJ $mol^{-1}$ (14). The resulting conversion efficiency (from 1.64 g $mol^{-1}$) is thus 13% of the photosynthetically active radiation and about 6% of the total radiation.

How achievable is the calculated maximum efficiency in the field? At 1.64 g $mol^{-1}$ a PPF of 43.2 mol $m^{-2}$ $d^{-1}$ results in a potential growth rate of 71 g $m^{-2}$ $d^{-1}$, but some agricultural areas have daily PPF levels of over 55 mol $m^{-2}$ $d^{-1}$, resulting in a potential productivity of over 90 g $m^{-2}$ $d^{-1}$. Monteith (15) rigorously reviewed the studies on maximum CGRs (by communicating with the original authors) and determined that guard-row effects or sampling errors (experimental error) contributed to overestimates of CGR in several studies. After unreliable data were discarded, the maximum short-term CGRs were 34 to 39 g $m^{-2}$ $d^{-1}$ for $C_3$ crops and 51 to 54 g $m^{-2}$ $d^{-1}$ for C4 crops. Loomis and Gerakis (12) thoroughly discussed the problems associated with obtaining reliable data on maximum crop efficiency. One of the problems was that measurements of incident radiation

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[2] Abbreviations: PPF, photosynthetic photon flux (400–700 nm; $\mu$mol $m^{-2}$ $s^{-1}$); HPS, high pressure sodium; CGR, crop growth rate; LAI, leaf area index; SLA, specific leaf area; PLM, percent leaf mass; LAR, leaf area ratio.

were not always available with data on high growth rates. Radiation can be estimated, however, from the location of the study, and it appears that the highest, short-term productivity achievable in the field has been 50 to 85% of the calculated potential (7 to 11% conversion efficiency of PAR; 5, 12, 15).

It is often argued that the calculated potential growth rates are unrealistically high. The assumptions that result in a potential growth rate of 1.64 g $mol^{-1}$ of photons are optimistic even in a single leaf at PPFs below 150 $\mu mol\ m^{-2}\ s^{-1}$. To predict that photosynthesis, respiration, and PPF absorption can all occur with maximum efficiency in every leaf of a plant community at high PPF levels is even more optimistic. Fully developed canopies, however, have approached this potential for short periods of time so it appears that the calculated potential is realistic. The most significant problem appears to be maintaining this efficiency throughout the life cycle.

The best long-term crop growth rates (averaged over the entire life cycle) for several $C_3$ crops have been almost identical at 15 g $m^{-2}\ d^{-1}$, and maize had the highest average daily CGR for a $C_4$ crop at 28 g $m^{-2}\ d^{-1}$ (5, 12, 15). These long-term growth rates are about 20 to 40% of their potential (3–6% conversion efficiency of PAR).

Why is long-term productivity so much less than the calculated potential growth rates? Incomplete interception of incident PPF is a primary factor. Although a closed canopy can intercept over 95% of the incident radiation, interception begins at zero at germination and does not reach a maximum for several weeks. A crop plant community, grown at high density, intercepts about 50% of the incident PPF over the growing season. Leaf senescence prior to harvest also decreases absorbance by increasing the reflectance of individual leaves. Senescence in the final days before harvest also decreases photosynthetic efficiency but has been less well studied in canopies than PPF interception.

Even in the best conditions, field-grown plants endure unavoidable stresses that keep them from reaching their genetic potential. Controlled environments can be used to remove all the obvious environmental constraints to productivity, but there have been few attempts to determine the long-term genetic potential of plant canopies in optimal conditions at high irradiance levels. Two Soviet scientists (21, 22) have reported achieving 5 kg $m^{-2}$ of oven-dry wheat seed in 65-d in a $CO_2$-enriched, controlled environment. They did not include information on total biomass or the harvest index (edible grain/total biomass), but if a typical harvest index (45%) is assumed, the resulting CGR would have been 171 g $m^{-2}\ d^{-1}$. They used an exceptionally high PPF (1300 W $m^{-2}$; about 520 mol $m^{-2}\ d^{-1}$ from xenon lamps) so the yield was about 0.33 g $mol^{-1}$ and the conversion efficiency was 2.7% of PAR. They developed a new cultivar for high PPF and used a very high plant density (4000 plants $m^{-2}$), but the published reports (the most recent is an abstract) have not provided enough information to fully evaluate the research. One of the Soviet objectives was identical to our own: to determine the factors that result in maximum crop productivity for use in Controlled Environment Life Support Systems that would provide food from recycled wastes in a lunar station or similar environment.

The research reported in this paper characterized the long-term vegetative and reproductive response of a wheat community in a well-defined, near-optimum environment over a wide range of PPF levels (50–300% of the integrated daily photon flux available outside in the summer). Several preliminary studies were conducted to determine near-optimum levels of primary foliar and root-zone environmental parameters (2, 3, 24). We defined optimum environmental conditions as those that cause PPF to be the only factor limiting net carbon gain. Growth in an optimum environment would occur at the potentially achievable rate. We attempted to provide optimum conditions in this research.

## MATERIALS AND METHODS

Three studies were conducted in each of three, nearly identical, controlled environment chambers (Environmental Growth Chambers, model EGC-13)[3] that were modified to create the necessary optimal conditions. Two photon flux levels were developed in each of the three chambers by separating the chamber in the middle with reflective mylar film and then shading one or both halves with neutral density screen. This technique provided a total of six photon flux levels, from 400 to 2080 $\mu mol\ m^{-2}\ s^{-1}$. There are two replicate plots per PPF level. The chamber area, the growing area, and the harvested area are shown in Figure 1.

The three studies were identical except for three parameters: harvest data, photoperiod, and PPF level. The differences among studies are outlined in Table I.

The wheat cultivar Yecora Rojo (hard red spring wheat) was used for two reasons: (a) It is short (about 0.6 m tall in the field) and thus much easier to work with in the confined volumes of controlled environments. (b) Previous cultivar trials, in our near optimum conditions, indicated that it was consistently among the highest yielding cultivars (24). Other studies have indicated that Yecora Rojo lacks alternative pathway respiration (M Musgrave, personal communication), which may favor this cultivar in high $CO_2$ environments. Seeding rate in all studies was 2000 plants $m^{-2}$. All seeds were screened, and only seeds larger than 2.38 mm diameter (6/64 inch sieve) were planted.

**Foliar Environment: Radiation.** The highest PPF was provided by a mixture of two 1000-W HPS lamps, four 400-W HPS lamps, and four 400-W metal halide lamps. Radiation from these lamps was filtered through 40 mm of water cooled to 3°C below the air temperature in the chamber, thus removing much of the thermal load except for the PPF itself (2). The lower PPF levels were provided with 16 110-W, very-high-output, cool-white fluorescent lamps (1760 total watts) and four 400-W HPS lamps located in the corners of each chamber. A plexiglass barrier (without water) below the lamps in these chambers reduced the total radiation. These barriers did not significantly alter the spectral characteristics of the radiation in the visible region. The exact spectral and thermal effects of the barriers have been quantified (2).

**Photosynthetic Photon Flux.** PPF was measured at the top of the plant canopy with a quantum sensor (Li-Cor Instruments, model 190SB) and integrating quantum meter (Li-Cor, model 188B). The sensor had been recently calibrated by the manufacturer. The most difficult environmental parameter to accurately monitor and control over the life cycle was the PPF. High intensity discharge lamps are required to achieve a high PPF. High intensity discharge lamps radiate from a point source and are thus inherently less uniform than nonpoint sources (fluorescent lamps). We arranged multiple high intensity discharge lamps so that PPF in a horizontal plane about 300 mm below the barrier varied by no more than 7%. The top of the plant canopy was then raised (using an adjustable platform) until it intercepted the horizontal plane that provided the desired PPF. The adjustable platform was lowered daily as the plant canopy grew taller. The wheat canopy grew to 90% of its maximum height during the first 45 d of its life cycle. A uniform PPF at the top of the canopy was maintained by lowering the platform an average of 15.5 mm $d^{-1}$ over this period. PPF at the top of the canopy was remeasured at weekly intervals during early canopy development because measurements were as much as 10% higher because of

[3] Mention of trade names is to provide detailed information only and does not imply endorsement to the exclusion of other products that might also be suitable.

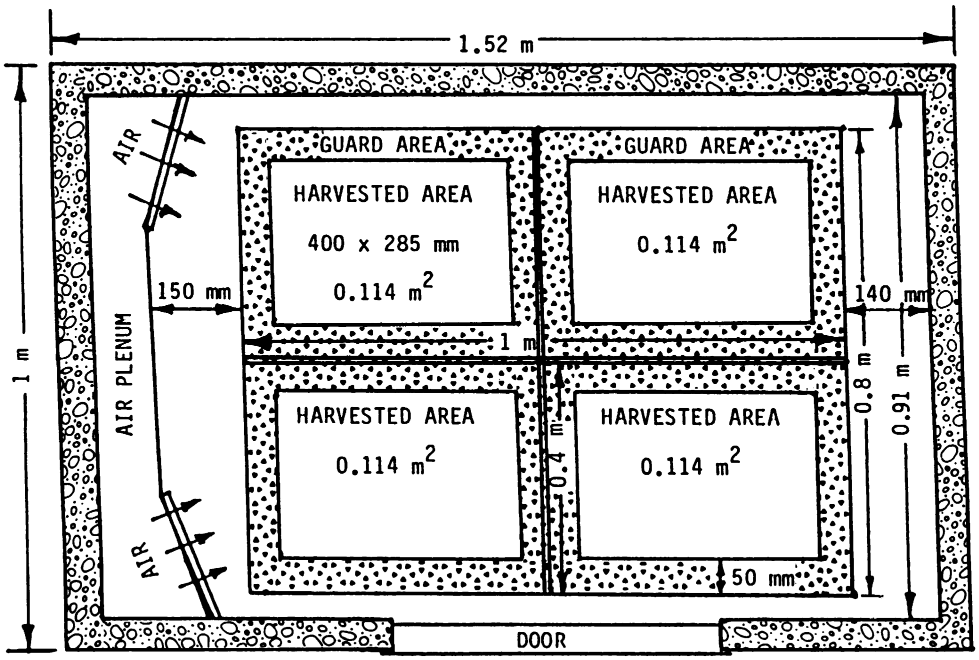


FIG. 1. A top view of the chamber area. The total growing area was 0.8 × 1.0 m, which contained four separate root-zone compartments. Note the guard row area of each section and the harvested center area that was used for analysis. Each chamber was divided in the middle making two replicate tubs per PPF level.

Table I. *Parameters that Differed Among the Three Studies*

Each study included a total of 12 experimental units (6 PPF levels × 2 replicate plots).

| Study Number | Days to Harvest | Growth Stage at Harvest | Photoperiod | Range of Instantaneous PPF | Range of Integrated PPF |
|---|---|---|---|---|---|
| | | | *h* | *μmol m$^{-2}$ s$^{-1}$* | *mol m$^{-2}$ d$^{-1}$* |
| 1 | 24 | Canopy closure | 16 | 400–1700 | 23–98 |
| 2 | 45 | Anthesis | 16 | 400–1600 | 23–92 |
| 3 | 79 | Physiological maturity | 20 | 480–2080 | 35–150 |

PPF reflected from the support media when there were no plants below the sensor. As the plant canopy developed, less of the incident PPF was reflected, and the PPF levels decreased. The PPF levels reported are the average of all the measurements made over the life cycle.

Integrated daily PPF (mol m$^{-2}$ d$^{-1}$) was calculated from instantaneous measurements (μmol m$^{-2}$ s$^{-1}$) multiplied by the daily photoperiod.

**Carbon Dioxide Concentration.** The $CO_2$ concentration was maintained at 1200 ±30 μmol mol$^{-1}$ of air by mixing pure $CO_2$ from compressed gas cylinders with filtered (25 μm) air pumped into the chambers from outside the building. The flows of both the outside airstream and the $CO_2$ gas were regulated with appropriately sized rotameters (Dwyer Instruments, Inc.). The $CO_2$ concentrations in all chambers were monitored with an infrared gas analyzer. A sample of the air from each chamber was cycled into the gas analyzer at 5-min intervals with solenoid valves controlled by a timer. $CO_2$ concentrations were continuously recorded on a strip-chart recorder. $CO_2$ cylinders were checked for trace contamination with ethylene (17) but none was found. Input airflow provided at least one exchange of chamber air every 5-min to avoid the possible buildup of volatile plant emissions and any other contaminants from the chamber itself.

**Temperature.** The temperature in all studies was measured at the top of the plant canopy with shielded thermocouples and maintained at 20°C day/15°C night. The average temperature variation among chambers (0.3°C) was always less than the temperature variation at different positions within chambers (±1°C). The high PPF levels caused large heat loads, which increased temperature gradients within the chambers. Temperature variability was minimized with rapid internal air circulation (0.4 m$^3$ s$^{-1}$, 800 ft$^3$ min$^{-1}$) and small chamber size (Fig. 1).

**Vapor Pressure Deficit.** The vapor pressure deficit in all studies was maintained at 0.5 to 0.9 kPa (5 to 9 mbars; about 60–80% RH) by humidifying the chambers when the plants were young and by increasing the chamber ventilation rate (to remove transpired moisture) as the plant canopy developed. The vapor pressure was monitored with a dewpoint hygrometer (General Eastern, model DEW-10). Gas samples from the chambers were cycled to the hygrometer using the same solenoid system that was used to monitor $CO_2$.

**Air Velocity.** The air velocity was measured with a hot wire anemometer (Hastings Instruments, model RM-1) and maintained at about 1 m s$^{-1}$ at the top of the plant canopy. Airflow was regulated with variable speed fans and was horizontal over the top of the canopy.

**Root-zone Environment.** A recirculating hydroponic system was used in all studies. The system was common to all three chambers and helped ensure that the observed treatment effects were not caused by variability in the root-zone environment. The system provided nutrient solution to four separate, root-zone compartments in each growth chamber (Fig. 1). Each compartment had a surface area of 0.2 m$^2$ and a depth of 0.16 m. The nutrient solution was pumped with an epoxy-coated, magnetic drive pump from a 0.1-m$^3$ reservoir into a distribution manifold in each compartment at a rate of 0.08 L s$^{-1}$. The rapid flow rate and the distribution manifold helped provide a highly uniform root-zone environment in which dissolved oxygen was always at least 85% of saturation (7 g $m^{-3}$ in Logan, UT; 8 g $m^{-3}$ at sea level) at all locations in the system. The solution was replenished with oxygen as it cascaded back into the reservoir. Composition of the nutrient solution is shown in Table II.

**pH Control.** The solution pH was maintained between 5.5 and 5.8 with an in-line electrode (Orion, model 91-06) and automatic pH controller (Chemtrix, model 45AR). When the pH increased to 5.8, the controller opened a solenoid that allowed nitric acid to flow into the bulk solution. After 20 d, the increase in plant growth caused the pH to change more rapidly than at first, and ammonium nitrate was added to the pH control solution in a 1:1 M ratio with nitric acid; after 30 d the ratio was increased to 2:1. Ammonium ions are taken up more rapidly than nitrate ions, which caused the pH to decrease about 0.2 pH units during a 1-h period until the solution contained very low levels of ammonium. Nitrogen uptake was then predominately from nitrate and the pH slowly increased until the set-point pH was reached and the cycle began again. This pH control method provided 25% of the total nitrogen as ammonium after the first 30-d of growth.

**Seed Germination and Plant Support.** Seeds were direct seeded into an expanded rockwool material (Grodan) suspended above the hydroponic solution.

**Harvest Procedure.** Guard rows were removed and measured separately. Carbon partitioning among plant parts in the first two trials was determined by conventional plant growth analysis. Immediately after harvest, leaves were separated from stems, and green leaf-area was measured with a leaf area meter (Li-Cor Instruments, model LI-5000). Root, leaf, and stem dry mass were measured separately.

Table II. *Composition of Nutrient Solution*

The ionic composition of the nutrient solution was based on the principle of mass balance. The ratio of nutrients in plant tissue that results in good growth is adequately established and salts were added to the nutrient solution in this ratio. Concentration in nutrient solution was calculated from the mol $kg^{-1}$ concentration in plant tissue by assuming that 200 kg of water are transpired in the process of creating 1 kg of plant dry mass (transpiration to photosynthesis ratio with $CO_2$ enrichment). This ratio can be as high as 400:1 in hydroponic culture with ambient $CO_2$. High transpiration ratios increase the solution electrical conductivity, but the ion ratios stay about the same. The concentration of the refill solution was altered as needed to maintain the electrical conductivity of the recirculating solution at 12 S $m^{-1}$ (1.2 mmhos $cm^{-1}$).

| Element | Desired Concentration in Plant Tissue | | Concentration in Nutrient Solution |
|---|---|---|---|
| | % | *mol kg⁻¹* | *mmol kg⁻¹ water* |
| N | 4.0 | 2.9 | 14.4 |
| P | 0.6 | 0.2 | 1.0 |
| K | 3.1 | 0.8 | 4.0 |
| Ca | 1.0 | 0.25 | 1.25 |
| Mg | 0.3 | 0.13 | 0.65 |
| S | 0.3 | 0.11 | 0.55 |
| | *μg g⁻¹* | *mmol kg⁻¹* | *μmol kg⁻¹ water* |
| Fe | 112 | 2.0 | 10 |
| B | 44 | 4.0 | 20 |
| Mn | 55 | 1.0 | 5 |
| Zn | 32 | 0.5 | 2.5 |
| Cu | 10 | 0.15 | 0.75 |
| Mo | 0.5 | 0.005 | 0.025 |
| Cl | | | 11 |
| Si | 420 | 15.0 | 75 |
| Na | | | 150 |

Samples were put into porous paper bags and loosely placed in a well ventilated drying oven at 74 ± 2°C until their mass was constant (usually 48-h). Drying techniques were rigorously observed for all samples because drying procedure has been shown to be a large source of variability (11).

The following quantities were derived from these primary measurements: average crop growth rate (CGR; g $m^{-2}$ $d^{-1}$), specific leaf area (SLA; leaf area per leaf dry mass, $m^{-2}$ $kg^{-1}$), percent leaf mass (PLM; leaf dry mass divided by total shoot dry mass, dimensionless), leaf area ratio (LAR; leaf area per plant dry mass, $m^2$ $kg^{-1}$), leaf area index (LAI; green leaf area, one side, per horizontal surface area, dimensionless).

Percent conversion efficiency was defined as the energy content of the total dry biomass divided by the incident photosynthetic energy (400–700 nm). The combustible energy content of the biomass was calculated using the following standard values: protein: 24.3 MJ $kg^{-1}$, carbohydrates: 17.6 MJ $kg^{-1}$, lipids: 38.9 MJ $kg^{-1}$ (29; Table III). Seed protein, calculated by multiplying the Kjeldahl nitrogen concentration (measured without nitrate) by 5.83 (the established value for wheat seed), ranged from 15.6 to 16.9% with a mean of 16.3%. Neither PPF nor culm category affected the percentage protein in seeds.

The energy content of seeds was calculated to be 18.76 MJ $kg^{-1}$, and that of stems, leaves, and roots was 17.04 MJ $kg^{-1}$. The calculated value for vegetative plant parts (17.04) is in close agreement with measured values of other annual species (11). Typical values (18) were used for the carbohydrate, lipid, and ash components (Table III). Small changes in the assumed fraction of the components does not significantly alter the biomass energy content.

The energy in photosynthetic photons was determined as 217 kJ $mol^{-1}$ ($E = hc/\lambda$; average wavelength: 550 nm; 14). The spectral distribution in the photosynthetic region was very similar among chambers (spectral data not shown). The average wavelength in all three chambers was close to 550 nm, which is very close to the average photosynthetic wavelength in the field. Because photosynthesis is driven by the photon flux rather than photosynthetic energy, we assumed that the energy per mol of photons was constant, thus facilitating comparisons of photosynthetic efficiency among chambers and the field.

Carbon partitioning to reproductive sinks in the third trial was determined by measuring the following yield components: heads $m^{-2}$; seeds $head^{-1}$, and mass $seed^{-1}$. Each of these components was measured separately for primary, secondary, and tertiary heads. Sterile culms were counted separately. The primary head is typically the tallest culm on each plant, and was defined as such in this study. Secondary heads were defined as coming from slightly shorter culms. The seeds in primary and secondary (but not tertiary) culms had reached physiological maturity (maximum seed dry mass) at harvest, as determined by the complete

Table III. *Measured and Assumed (18, 29) Composition of the Harvested Biomass*

The energy values are the bomb-calorimeter energy content of the component fraction.

| Component | Seeds | Leaves, Stems, and Roots | Energy Value |
|---|---|---|---|
| | % | % | *MJ kg⁻¹* |
| Protein | 16.3 | 8 | 24.3 |
| Carbohydrate | 79.7 | 82.5 | 17.6 |
| Lipid | 2 | 1.5 | 38.9 |
| Ash | 2 | 8 | 0 |
| | 100 | 100 | |
| Energy Content | | | |
| | *MJ kg⁻¹* | | |
| | 18.76 | 17.04 | |

loss of green color from the glumes and crease in the seeds (4, 8). Tertiary heads were defined as heads with seeds still showing some green color (in the glumes and crease) at harvest. Based on the criteria of Hanft and Wych (8), the tertiary seeds were at about 95% of the maximum mass at harvest. Tertiary culms are initiated later and are shorter than primary or secondary culms.

The sequential maturation of different categories of culms means that time of the highest yield per day (g $m^{-2}$ $d^{-1}$) could not be unequivocally determined without a series of harvests. Total yield would have increased slightly if harvest had been delayed until the tertiary culms were mature, but since the majority of the culms were fully mature, yield per unit time might have decreased if harvest had been delayed. However, extending the harvest date by a day or two probably would have a very small effect on average yield per day because yield and time would both increase. Yield from the highest PPF treatments, which had the highest yield from tertiary culms, would probably have increased the most had harvest been delayed.

Harvest index (seed mass/total plant mass) was determined for the entire crop (including roots) and for each category of culms (without roots). Spikelet number and spikelets with fertile seed were measured on primary heads.

It was not possible to separate the center section of roots from the guard row roots at harvest, so the mass of the center section of roots was determined by multiplying the total dry root mass by the fraction of the harvested area (57%). The root-zone was confined to the same area (0.2 $m^2$) as the top.

Each trial began with 12 separate experimental units, but poor germination in randomly located tubs resulted in missing data in all three trials. Sections with poor germination were allowed to grow to harvest, but the harvest parameters were not typical; the values were considered unreliable and were not included in the analysis. Germination occurred in the dark, so it was not affected by the PPF treatments. It now appears that nonuniform watering of the germination substrate caused poor germination. In the third trial a cooling fan malfunctioned, causing the temperature in the back of one chamber to rise to 30°C. The fan was replaced within 48 h, but the affected plants matured early and the data were discarded.

## RESULTS AND DISCUSSION

**Plant Density.** The effect of plant density was not evaluated in the trials reported here, but the plant density (2000 plants $m^{-2}$) was 4 to 10 times higher than field seeding rates. Previous studies indicated that this density (or higher) is necessary to achieve maximum yield (3). This seeding rate required 75 g of seed $m^{-2}$, which was from 1.5 to 5% of the final seed yield. Similar studies at even higher PPF levels used 4000 plants $m^{-2}$ (21, 22).

High plant densities result in high yields partly because of more rapid PPF absorption during early growth, but another important benefit may be to increase reproductive sink capacity. Carbon dioxide enrichment and high PPF levels increase photosynthesis (source strength). A concomitant increase in sink capacity may be necessary to prevent feedback inhibition of photosynthesis (1). Increasing head number per unit area increases sink capacity. Gifford et al. (7) have pointed out that a key to high yield has been to establish a large number of seeds before their rapid filling commences. Reproductive initiation in wheat begins 9 to 12 d after germination (24), so high plant densities increase head number and thus sink strength even during early growth. The number of heads per unit area is often closely correlated with yield in high-yielding field environments. In our near-optimum environments there has consistently been a high correlation between head number and yield ($r^2 = 0.96$ in this study). Although a single wheat plant can form multiple tillers (heads) at low plant densities, higher densities consistently increase head number per unit area. Plant densities above 600 plants $m^{-2}$ may not increase yield in the field because other factors, such as water or nutrients, may become limiting.

**Guard Row Effects.** Other authors (12, 15) have reviewed studies in which guard row effects contributed to artificially high yields in small plots. The guard rows indicated in Figure 1 were not included in yield calculations. The average yield $m^{-2}$ from the exterior guard rows was about 15% higher than from interior areas of each plot, and the difference would have been greater if the outside guard rows had not been so close to the exterior walls (Fig. 1). Yields from guard rows adjacent to another plot (on the inside of the plots) were usually similar to the yields from centers of the plots. Results of preliminary studies, in which single rows beginning with the outside guard row were individually harvested and analyzed, indicated that the guard row area removed in this study should have been sufficient to eliminate a guard row effect.

**Trial 1: 24 Days (Harvested at Canopy Closure).** The most striking finding from the first study was the linear response of CGR to PPF (Fig. 2). The percent conversion efficiency, however, decreased as PPF increased.

The analysis of canopy growth indicated that increasing PPF decreased PLM from 78 to 68% and decreased LAR from 30 to

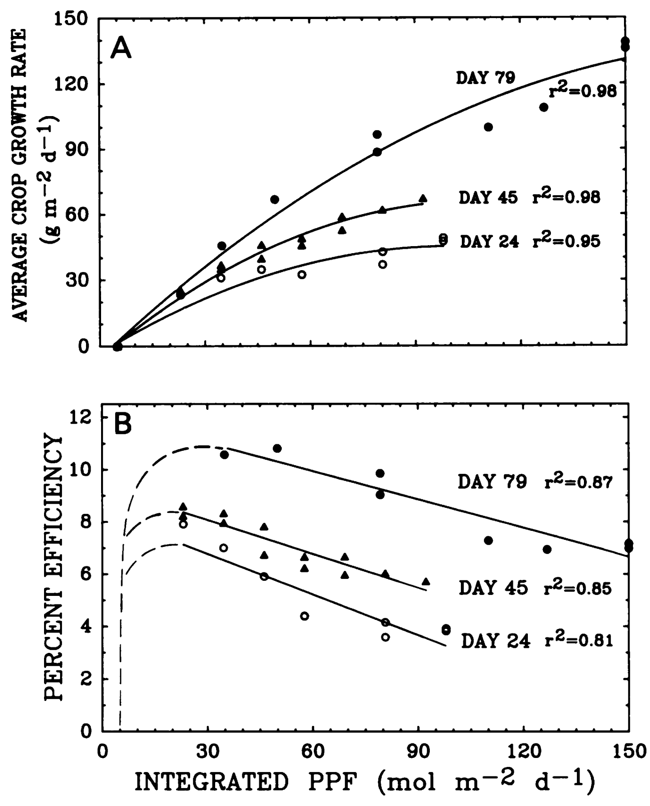


FIG. 2. Effect of daily PPF on average crop growth rate and percent efficiency at three different harvest dates. A canopy PPF compensation point of 5 mol $m^{-2}$ $d^{-1}$ (about 70 $\mu$mol $m^{-2}$ $s^{-1}$) has been assumed to facilitate curve fitting; all other values are measured. Efficiency was defined as the energy in the biomass divided by the energy in the photosynthetic photon flux. If efficiency were determined as a percent of total radiation (from the sun) the values would be reduced by about 50% (*i.e.* 5% maximum efficiency). The dashed lines indicate the effect of PPF levels lower than those used in these studies. The highest efficiency might occur at about 15 mol $m^{-2}$ $d^{-1}$ during early growth, and at about 20 to 40 mol $m^{-2}$ $d^{-1}$ during later growth. If respiration losses were not considered (photosynthetic efficiency only), the highest efficiency would occur at less than 5 mol $m^{-2}$ $d^{-1}$. Because the photoperiods varied in these studies, the instantaneous PPF was not identical across trials.

20 $m^2$ $kg^{-1}$ (Table IV). The plants more efficiently partitioned dry mass to leaf area at low PPF levels, but total leaf area (LAI) increased with PPF (Fig. 3). Crop growth rate doubled over the range of PPF levels. This was caused partly by the increased LAI (36%) and by an increase in photosynthesis rate.

**Trial 2: 45 Days (Harvested at Anthesis).** The photoperiod and PPF levels of the second trial were nearly identical to those in the first trial, but the plant canopy was allowed to grow to anthesis, which meant that the lower leaves were heavily shaded by the upper leaves during the last 25 d of growth.

Three findings are particularly significant. (a) Crop growth rate was again highly correlated with PPF and continued to increase up to the highest levels tested (Fig. 2). (b) Leaf area index was a linear function of PPF ($r^2 = 0.83$) and was unusually high (LAI = 30) at the highest PPF level (Fig. 3). (c) Head number per unit area, which is an indication of sink capacity, increased as a linear function of PPF (Fig. 4).

Wheat makes from 7 to 12 leaves before heading. The plants in this study consistently formed the minimum leaf number, but the high planting density nonetheless resulted in a high LAI.

Is an LAI of 30 higher than necessary? If the incident radiation were entirely direct-beam radiation from overhead, and the leaves were almost exactly vertical, an LAI of 30 would be useful. The radiation in controlled environments, however, does not come from a single point source and is thus not all direct beam radiation. Measurements of PPF at the bottom of the canopy indicated that, at all PPF levels, less than 1% of the incident PPF was transmitted from d 30 to d 45. Thus the LAIs were apparently higher than necessary because the lower leaves would have been below the PPF compensation point for photosynthesis. The lower leaves senesced prior to harvest, and the remaining LAI of green leaves at the top of the canopy was about 10 (Fig. 3). High plant density improves yield in spite of a super-optimum LAI.

Table IV. *Mean Values of Growth Analysis Parameters and Their Correlation with PPF at Two Harvest Dates*

| Parameter | Day 24 | | Day 45 | |
|---|---|---|---|---|
| | Mean | $r^2$ [a] | Mean | $r^2$ |
| SLA ($m^2$ $kg^{-1}$) | 33.9 | NS[b] | 36.4 | NS |
| PLM (%) | 72.8 | 0.73 | 32.6 | NS |
| LAR ($m^2$ $kg^{-1}$) | 24.7 | 0.55 | 11.9 | NS |
| % Roots (%) | 22.2 | 0.61[c] | 10.7 | NS |
| Height (mm) | 354 | NS | 631 | NS |

[a] The $r^2$ values indicate the correlation with integrated PPF. [b] Not statistically significant. [c] On d 24, the percent root mass increased from about 20% at low PPF to about 25% at high PPF. As expected, the percent root mass decreased with plant age to 10.7% on d 45 and to 3.5% at the final harvest on d 79.

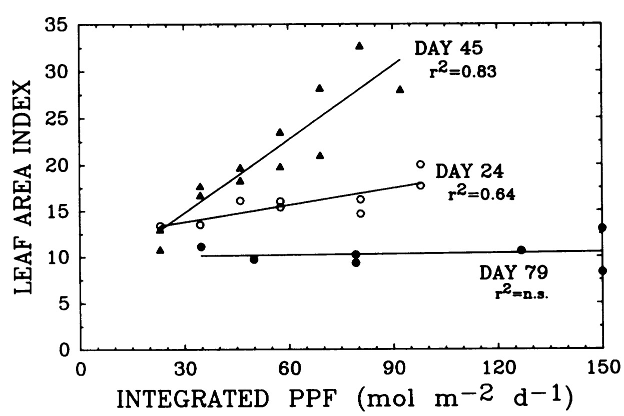


FIG. 3. Effect of PPF on leaf area index (one side of leaves). The canopy is not yet fully developed at d 24. At d 45, the leaf area index was much higher than in the field and was probably higher than necessary (see "Discussion" in text). The lower leaves were senesced at harvest (d 79), which resulted in an LAI of about 10 across all PPF levels (green leaves only).

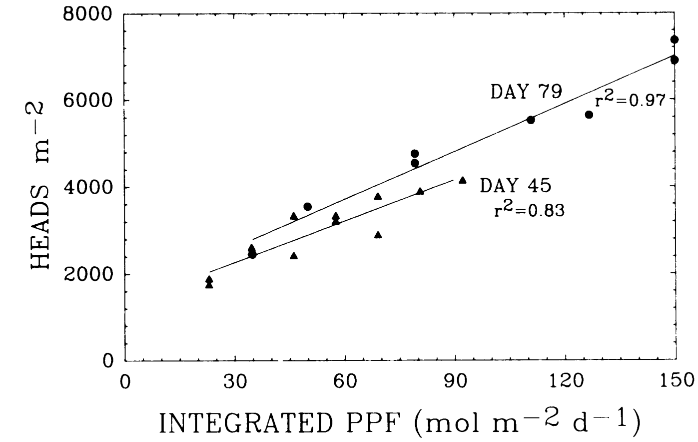


FIG. 4. Effect of PPF on number of heads per $m^2$. Head number was slightly higher in the 79-d trial, perhaps because a few additional late culms emerged that were not counted at d 45.

The vertical leaf orientation of wheat should be a distinct advantage in optimal environments in both growth chambers and in the field. About 60 to 90% of the radiation in the field during the summer months is direct beam radiation (14). During periods of maximum intensity (around solar noon) direct beam radiation penetrates deeper into vertical leaf canopies than diffuse radiation, and higher LAIs are beneficial. The ratio of direct to diffuse radiation in a growth chamber does not change with time of day and is probably similar (60–90% direct beam) to the ratio in the field. It has not always been possible to demonstrate that vertical leaf orientation is superior to horizontal leaf orientation in field studies, but this may be because factors other than PPF frequently limit productivity in the field. We are currently investigating the extinction of radiation in dense wheat canopies.

Although LAI was probably higher than necessary, photosynthetic efficiency (Fig. 2) at high PPF levels was higher at d 45 than at d 24. This increase was probably caused by the increase in PPF absorption after canopy closure, which occurred on about d 24.

As PPF levels increased, PPF saturation meant that the upper leaves would have fixed carbon less efficiently (per photon), and high LAI would cause the bottom leaves to be near the PPF compensation point with a photosynthetic efficiency near zero after subtracting for respiration. The combination of these two factors probably accounts for the reduction in efficiency at high PPF levels.

Wheat plants form tillers, or multiple heads, in response to favorable environmental conditions. The plant density was identical in all treatments, but tillering increased as PPF increased (Fig. 4). The increased number of heads would result in a dramatic yield increase if other yield components (seeds per head and mass per seed) remained constant. Tillering appears to have caused an increase in sink capacity to match source strength. The correlation between CGR and head number ($r^2 = 0.92$) was almost as high as the correlation of CGR with PPF ($r^2 = 0.96$).

**Trial 3: 79 Days (Harvested at Physiological Maturity).** In an attempt to saturate canopy growth rate, two factors were altered in the third trial. The photoperiod was increased from 16 to 20 h, and the plants in the high PPF chamber were allowed to grow closer to the lamps (0.2-m below the water barrier), thus increasing the instantaneous PPF level.

There were similar trends in all trials. CGR increased and efficiency decreased as PPF increased (Fig. 2). The growth rate did not appear to have reached a maximum even at the highest integrated PPF level. CGR and efficiency were considerably higher than in the two previous trials, partly because of improved interception of PPF (less than 1% of the incident PPF was transmitted during most of the life cycle), but also because grain fill may be more photosynthetically efficient than vegetative growth (LAI establishment).

Plant height at maturity was 700 mm in all units.

**Carbon Partitioning: Yield Components.** Figure 5 (a–d) indicates total grain yield and yield components from each of the three groups of culms. Yield components for each category of culms were very different. The number of primary culms was constant across all PPF levels, but the number of secondary and tertiary culms increased with PPF ($r^2 = 0.74$ and 0.91, respectively). Note that primary culms always contributed the most to total yield even though they were the fewest in number at the high PPF levels. The yield increase (as indicated by the slopes of the lines in Fig. 5a) with PPF level was similar in primary and tertiary culms. In primary culms, the yield increase was due entirely to increased seed set and seed mass; in tertiary culms the yield increase was due mostly to an increase in the number of culms.

By definition, each plant produced one and only one primary culm. The number of primary heads per unit area thus indicated the number of plants surviving to maturity (about 90% of planted seed). Plant survival was not affected by PPF.

It is interesting to note that significant tillering occurred even at the lowest PPF level (Fig. 5b), which is about half of the typical PPF in the field, and, yet, the planting density is at least 4 times higher than that used in field culture. This indicates the extent to which factors other than PPF limit tillering and yield in the field.

The dramatic increase in total heads $m^{-2}$ with PPF was largely due to tertiary culms. Sterile culms made up from 2 to 12% of the total number of culms and their production was not correlated with PPF. The total mass of sterile culms was small, but they reduced the harvest index by a few percent in each treatment.

The number of seeds per head produced by primary and secondary tillers tended to increase as PPF increased ($r^2 = 0.51$ and 0.53; Fig. 5c). At high PPF levels, however, the disproportionate increase of small tertiary culms meant that the mean number of seeds per head did not increase (all culms averaged together). The interaction of seed number per head in individual culm groups and mean seed number per head (averaged over culm groups) is a striking example of the need to quantify yield components for each culm category.

Yecora Rojo produces smaller heads than many other cultivars. The mean number of spikelets per head on primary culms was 16.1. The average number of sterile spikelets per head was 1.9, which is typical in field production. Neither the mean number of primary culm spikelets nor the number of sterile spikelets was affected by PPF. Mass per seed increased with PPF (Fig. 5d) probably because the supply of assimilates increased at high PPF.

The root dry mass at harvest decreased slightly from 3.7 to 3.1% of the total dry biomass as PPF increased. These percentages are less than reported in intensive field culture (5–20%) but are typical values in an optimal hydroponic root-zone environment. In an unfavorable root-zone environment the percent root mass increases, presumably in response to root-zone stress. During the final days before harvest, the roots change from turgid, white tissue to less turgid, brown tissue. This senescence probably decreases the final percentage root mass.

**Harvest Index.** The mean harvest index increased 3% as PPF increased ($r^2 = 0.72$; Fig. 6). The harvest indexes obtained in this study are typical for wheat grown in the field, and there is little indication that optimal environments improve edible yield by increasing harvest index. The harvest index for primary and secondary culms, however, was 11% higher than tertiary culms. Genetic, environmental, or cultural changes that reduce the formation of late forming tillers might thus be used to increase harvest index. Under optimal conditions, high planting densities may increase harvest index and yield by decreasing the percentage of tertiary culms. A high harvest index is particularly important in a Controlled Environment Life Support System, and we are currently investigating several methods of improving the edible biomass percentage.

**Nitrogen Concentration.** Figure 7 shows the nitrogen concentration of the flag leaf at different stages of growth. The high photosynthetic efficiencies may be due partly to the availability of ample nitrogen throughout the life cycle. Araus and Tapia (1) found that the photosynthetic rate of the wheat flag leaf increases rapidly up to nitrogen concentrations that reached 150 mmol $m^{-2}$ (3.5% N on a dry mass basis in their leaves), and their data suggest that higher photosynthetic rates occur with even higher flag-leaf nitrogen levels. The nitrogen concentration of well fertilized, field-grown wheat flag-leaves is about 3.5% at anthesis and gradually decreases to about 1.5% at maturity (1, 9, 25). The flag-leaf nitrogen concentration in this study declined before harvest but exceeded 3.5% for almost the entire life cycle. A continuous supply of nitrogen in the hydroponic solution may have contributed to leaf enzyme activity and photosynthetic efficiency, particularly in the final weeks before harvest. This hypothesis is supported by the results of a study by Smith *et al.* (25) in which a root-zone nitrogen level that maintained flag-leaf nitrogen at 4% (until harvest) increased growth rates, total biomass and yield compared to a root-zone nitrogen level in which flag-leaf nitrogen gradually decreased from 3.5 to 1.5%.

**Potential Productivity.** Recorded productivity in the field and in this study are compared with calculated potentially achievable productivity in Figure 8. The potentially achievable CGR (1.64 g $mol^{-1}$ of photons) is taken from the calculations in the introduction. This CGR is based on a quantum requirement of 13, which has not been achieved at an ambient $CO_2$ concentration. Carbon dioxide enrichment in controlled environments, however, means that a slightly lower quantum requirement can be obtained (6, 19). Crop growth rates higher than the potential shown in Figure 8 might thus be obtainable in $CO_2$ enriched environments. $CO_2$ enrichment is particularly important as PPF level increases. The highest short and long-term growth rates of $C_3$ and $C_4$ crops are taken from the studies discussed in the introduction (5, 12, 15).

The results of this study allow us to speculate on the factors limiting productivity and efficiency in the field. Most of the advantage of optimal environments is the result of increased photosynthetic efficiency, which may be primarily the result of $CO_2$ enrichment. The contribution of hydroponic culture to optimal plant water potential and a balanced nutrient uptake should not be overlooked, however.

The potentially achievable carbon use efficiency in respiration has been less well studied but is an important factor in maximum productivity (20, 26). A 30% efflux of carbon in respiration (carbon use efficiency = 70%) is a standard assumption in calculations of potential productivity. Carbon use efficiencies are typically less than 70% for most crops (20), but the following factors might increase carbon use efficiency in controlled environments.

(a) Much of the carbon used for maintenance respiration is thought to be associated with the continual synthesis of compounds to aid in the adaptation to changing environmental conditions. The constant conditions in controlled environments (water potential, PPF, temperature, *etc.*) might reduce the need

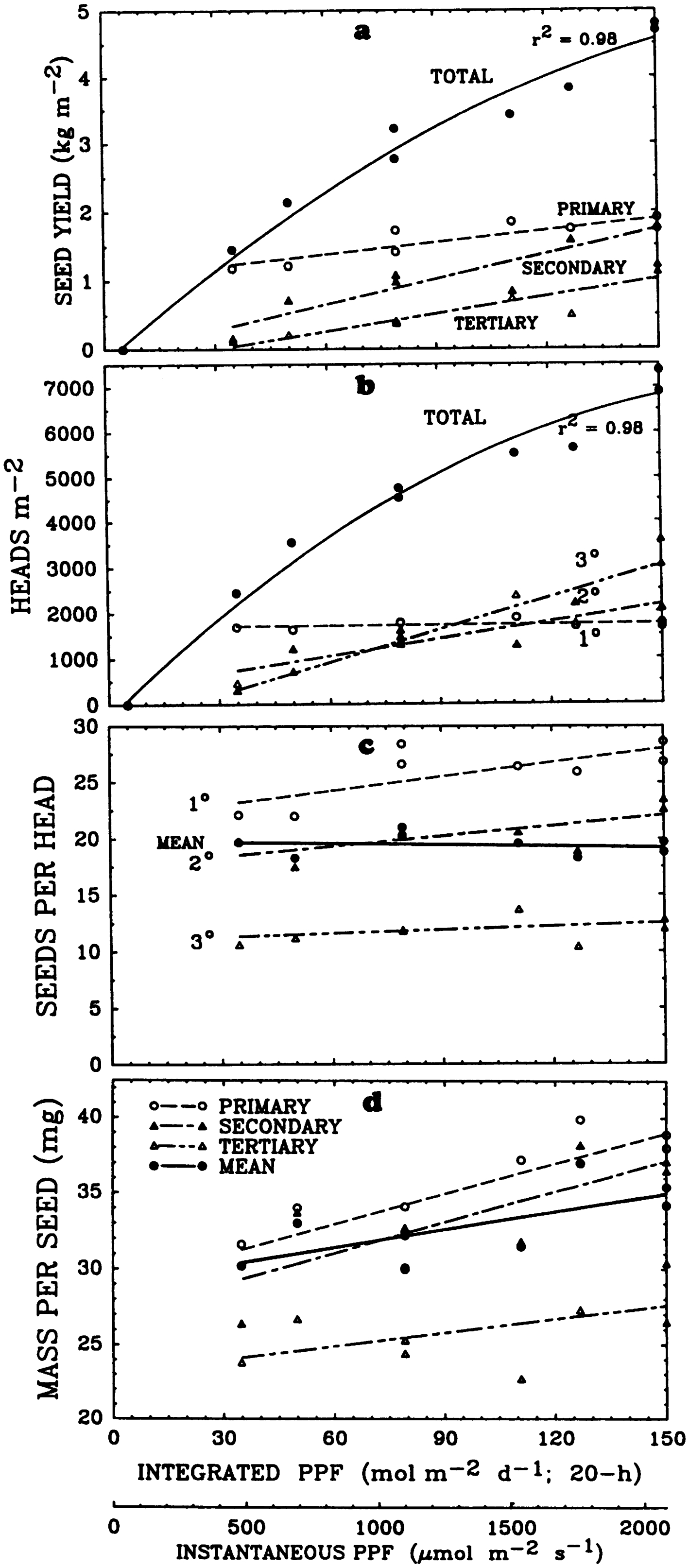


FIG. 5. Effect of PPF on total seed yield, and yield components in primary (1°), secondary (2°), and tertiary (3°) culms. (a) The yield of all three culm categories increased with increasing PPF. The yield increase of primary culms was entirely due to an increased seed number and seed mass, while the increase in secondary and tertiary culm yield was also due to an increase in head number. (b) The number of primary culms was constant across all PPF levels, because, by definition, each plant could produce only one primary head and the number of surviving plants was constant across all PPF levels. (c) Note the large difference among culm categories in number of seeds per head. Seed number per head increased with PPF within each culm category, but because of the disproportionate increase in tertiary culms at high PPF levels, the mean seed number per head decreased with increasing PPF. (d) Mass per seed increased rapidly within each culm category, but, because of the disproportionate increase in tertiary culms, the mean mass per seed increase was slower and was not statistically significant.

for new compounds and thus reduce the carbon used in maintenance respiration.

(b) Root respiration is normally much higher (per gram) than shoot tissue. An optimal, hydroponic root-zone environment means that carbon allocation to roots can be minimized.

(c) A higher percentage of nitrogen assimilation occurs in photosynthetic tissue in the light, and long photoperiods are commonly used in controlled environments. Promoting photosynthetic nitrogen assimilation may be particularly beneficial in view of several recent studies indicating excess electron transport capacity in saturating PPF and $CO_2$ environments (*e.g.* 10, 27).

Each of these factors may have only a small effect on carbon

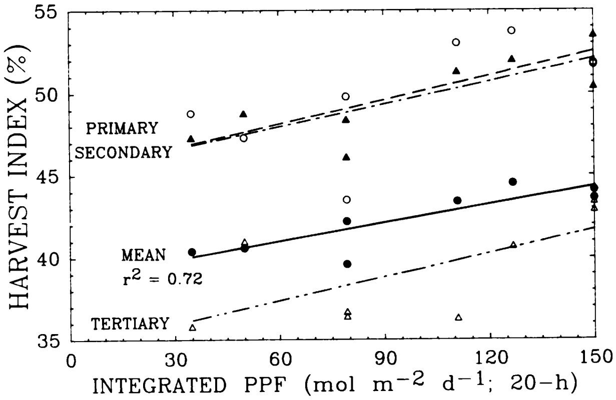


FIG. 6. Effect of PPF on harvest index. The harvest index for the primary and secondary culms was nearly identical, and both culm categories tended to increase to a harvest index of over 50% at the highest PPF levels. The mean harvest index in this Figure was calculated including the root mass (about 3.5% of total biomass) and the stem-base mass (about 2% of total biomass). Harvest index values for field culture are usually based on above ground biomass only. The values in this Figure would be about 2% higher if they had been calculated in the same way that field harvest index values are calculated. The regression coefficients for the individual categories of culms were not statistically significant at the 0.05 level. Note that the $Y$ axis does not start at zero.

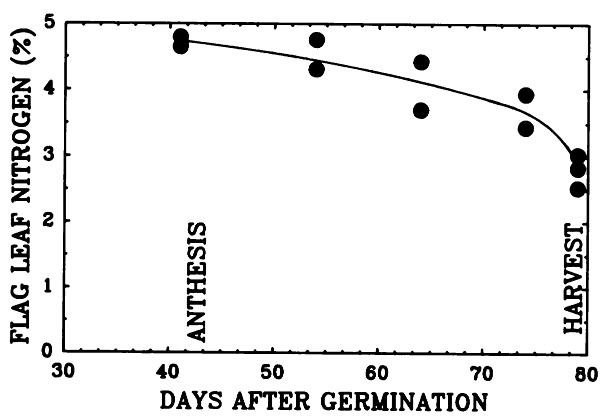


FIG. 7. Flag leaf nitrogen concentration from anthesis to maturity. Note the rapid decrease just before harvest as the leaves senesce. Nitrogen concentrations in this study were well above levels that are typical for field culture (1.5–3.5%; see "Discussion" in text).

use efficiency. Taken together, however, they could result in a significantly higher respiratory efficiency than is associated with field grown plants.

Productivity and canopy photosynthetic efficiency at PPF levels above 150 mol $m^{-2}$ $d^{-1}$ are not well characterized. Even higher growth rates may be obtainable as indicated by the Soviet studies noted in the introduction (21, 22). We hope to evaluate these effects in future trials. The results of this study indicate that the size of the food production component in a controlled environment life support system can be greatly reduced if adequate energy inputs are available.

## SOME IMPORTANT CONCLUSIONS

If other environmental conditions are nonlimiting, PPF limits the growth and yield of wheat, even when integrated daily PPF levels far exceed those encountered in the field. It should be noted, however, that high daily PPF levels were achieved by lengthening the photoperiod with an instantaneous PPF equal to the maximum in the field.

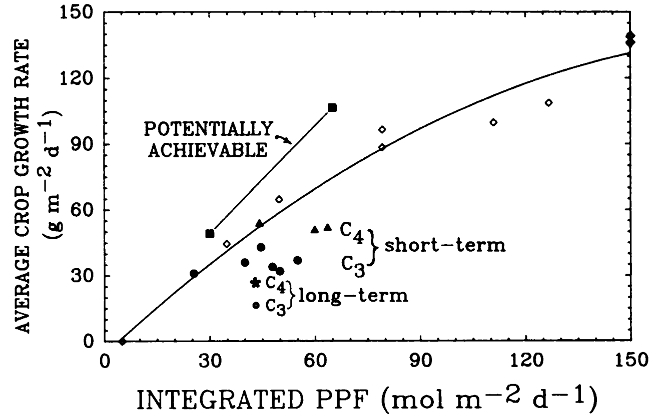


FIG. 8. A comparison of actual growth rates with potentially achievable growth rates. The highest recorded short-term growth rates for field-grown $C_3$ (●) and $C_4$ (▲) crops are indicated (data from Refs. 5, 12, 15). Both the mean PPF and CGRs for long-term productivity are lower than for short-term studies $C_3$ (○) and $C_4$ (★). The potentially achievable growth rate was calculated on the basis of 1.64 g $mol^{-1}$ of photons, which is obtained by assuming a quantum requirement of 13, 95% absorption of the photosynthetic photon flux, 75% respiratory carbon use efficiency, and 40% carbon in the plant mass (*i.e.* a low lipid concentration). Note that the yields obtained in this trial (◇) approach the calculated potential at low PPF levels and that the crop growth rate does not appear to saturate at the highest PPF level.

It may be unrealistic to hope to achieve the calculated maximum crop efficiency (1.64 g $mol^{-1}$ of photons) in the field, but this efficiency appears to be achievable in highly controlled environments. Carbon dioxide enrichment in controlled environments makes a slightly higher maximum efficiency possible.

The leaf area index increases in response to increased PPF, but photosynthetic efficiency is reduced at high PPF levels partly because PPF is distributed less uniformly within the plant canopy.

Tillering increases dramatically at high PPF levels, and the increased head number greatly increases sink strength. Although head number is closely related to yield, late developing culms have a lower harvest index and are thus less efficient. The results of this study suggest that cultural, environmental, or genetic changes that decrease the percentage of late developing culms might result in higher yields.

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