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EXPLORING THE LIMITS OF CROP PRODUCTIVITY:

A MODEL TO EVALUATE PROGRESS

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ABSTRACT

The productivity of higher plants is determined by the photo-synthetic photon flux (PPF) and the efficiency of the following four physiological processes: PPF absorption by photosynthetic tissue, carbon fixation (photosynthesis), carbon use (respir-ation), and carbon partitioning (harvest index). These constit-uent processes can be integrated to establish potentially achiev-able productivity, which is estimated to be 1.64 g mol^{-1} of photons. We obtained 1.3 g biomass mol^{-1} (0.56 g seed mol^{-1}) at a PPF of 50 mol m^{-2} d^{-1}, but this decreased to 0.8 g biomass mol^{-1} at a PPF of 150 mol m^{-2} d^{-1}. Photosynthetic and morphological measurements of wheat suggest that source strength (leaf area) greatly exceeds sink capacity (grain number) at high PPF levels. High plant densities improve sink strength, but result in exces-sive leaf area. Gradually decreasing temperature during the life cycle from 23°C to 17°C appears to improve yield by reducing maintenance respiration of the biomass. We are evaluating cul-tivars with reduced leaf size and number to decrease leaf area index at high plant densities. These cultivars may also have an improved harvest index. Hydroponic studies indicate that 1 mM nitrate in solution is adequate to support maximum growth in our systems, provided iron nutrition is adequate. Wheat does not accumulate nitrate in leaves even when the solution nitrate concentration is 15 mM. Long-term photosynthetic efficiency (g mol^{-1} of photons) and harvest index were not altered by photo-period (16, 20, or 24-h). Wheat does not need, nor benefit from, a diurnal dark period.

INTRODUCTION

Our goal has been to determine the limits of crop produc-tivity when all environmental constraints are removed. We define productivity as food output per unit of input, and are quan-tifying the output/input (efficiency) ratio for two of the most fundamentally limiting inputs to a CELSS: energy and volume.

Energy efficiency can be expressed as g of food per mole of photosynthetic photons or as percent (kJ food per kJ of photons).

Volume efficiency is best expressed as g m^{-3} d^{-1}, but the final volume of a production system depends on design factors that are difficult to estimate so we have measured volume efficiency as g m^{-2} (surface area) d^{-1}. These numbers can then be used to determine system volume. It appears that productivity m^{-2} could also be expressed m^{-3} because the production system could be about 1-m high (plants, lights, and roots).

Achieving high productivity and efficiency has required the development of unique apparatus to optimize environments, unusual cultural techniques and considerable genetic selection. Our studies have indicated that higher plant photosynthetic efficiencies can be similar to efficiencies obtainable with algae.

The following aspects of our approach are particularly important:

1. We have studied communities of wheat plants, rather than single plants, and can thus directly extrapolate to a larger scale from our small research plots (0.2-m). We were forced into this approach at an early stage because the morphology of a wheat plant is very different when it is grown without competition from neighboring plants. Findings based on individual plants are very useful for some types of studies, but they can be highly misleading when used to predict community productivity.

2. We have not tried to simulate field conditions. Part of yield optimization results from a significant departure from "normal" environmental conditions. The changes include elevated CO_2, 24-h photoperiod, high

photosynthetic photon flux (PPF), carefully managed hydroponic culture, and very high planting densities.

3. Because of the vast genetic diversity of wheat we have been able to study genetic/environment interactions and then use this data to select and develop appropriate lines for controlled environments. We now have a large collection of wheat genotypes.

4. We have studied closure of the root-zone environment by using recirculating hydroponic culture. Water and nutrients are added to replace what the plants remove but nothing is discarded.

MAXIMUM PRODUCTIVITY

Our accomplishments to date are best summarized as a maximum productivity curve (Figure 1). It appears that productivity is limited by PPF at even the highest PPF level. Potential productivity and field productivity are included in this Figure for comparison. The assumptions that are necessary to determine potential productivity are discussed in detail in two recent papers (1, 2). World record field yields are also reviewed in these papers.
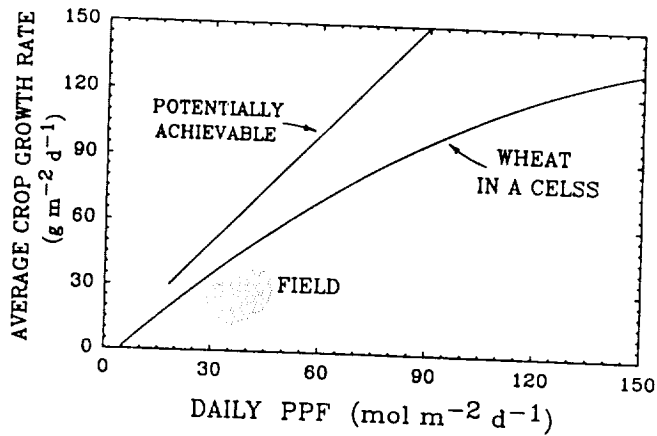
Figure 1. A comparison of measured growth rates (total biomass) in a CELSS with potentially achievable growth rates. The shaded area represents the range of record yields in the field. Note that the CELSS growth rate approaches the potentially achievable growth rate at low PPF levels and that the growth rate does not saturate at high PPF levels.

ENERGY EFFICIENCY

Figure 2 includes the same data for crop growth rate as Figure 1, but indicates the energy efficiency associated with different PPF levels. Efficiency is measured as percent by assuming 217 kJ per mole of photosynthetic photons and 17.8 kJ per g of dry biomass (average of seeds and stems). Efficiency does not reach a maximum until about 30 mol m^{-2} d^{-1} and then gradually decreases.
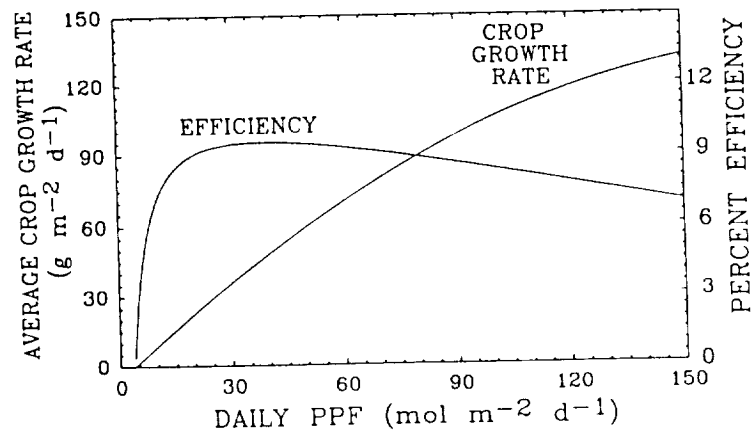
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Figure 2. The effect of daily PPF on PPF utilization efficiency. The crop growth rate curve is the same as in Figure 1.

REPRODUCIBILITY

How reproducible is the yield curve in Figures 1 and 2? Figure 3 shows the overall mean from eight separate studies and compares this mean with the yield from our best single study. The 8 studies include different environmental conditions (photoperiod, temperature); different cultivars (Yecora Rojo and Veery 10); and different cultural conditions (planting densities, etc.). The studies were also conducted in different types of growth chambers. About half of the scatter in the data is the result of parameters other than PPF, but much of the scatter is from unidentified causes (experimental error). Reproducibility is critical in a CELSS, but variability is inherent in biology.

As we identify the causes of low yields, we improve our ability to accurately predict yields.

Figure 3 also indicates the lack of data at low and high PPF levels. Additional research at low PPF levels would help to identify the peak energy efficiency. Studies at higher PPF levels would help to determine the peak efficiency per unit volume. Studies at all PPF levels are important because PPF interacts with other environmental, cultural and genetic factors.
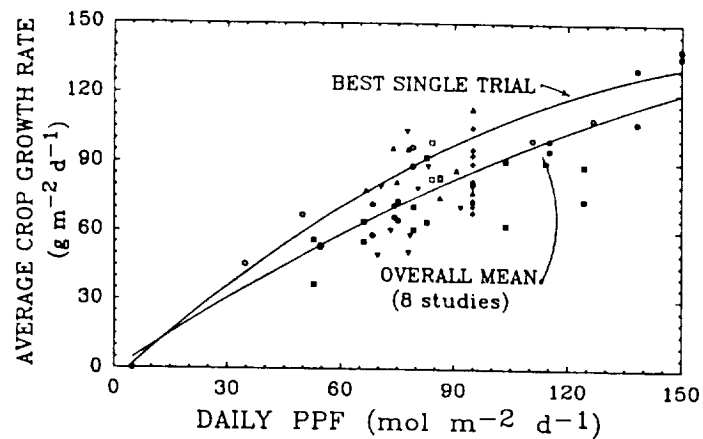
Figure 3. Reproducibility in a CELSS: A comparison of our best single trial with the overall mean of 8 different trials. Symbols represent different studies.

A MODEL TO EVALUATE PROGRESS

Crop physiologists have used correlation analysis to identify factors associated with high yields, but as we learn more about crop plant communities it has become useful to identify and separately analyze the constituent processes that determine yield. The model outlined here consists of the PPF input and the four, primary plant processes that determine yield.

This type of analysis is not unique and has been used by several other investigators to analyze field productivity (3, 6, 7, and 8). The four constituent plant processes are:

1. Percent PPF absorption by photosynthetic tissue

2. Photosynthetic efficiency (moles of CO_2 fixed per mole of photons absorbed).

3. Respiratory efficiency (net carbon fixed in biomass per unit carbon fixed in photosynthesis).

4. Harvest Index (edible biomass / total biomass).

Considerable research has been done on each of these processes so it is possible to determine theoretical maximum, and potentially achievable values for each factor (Table 1). A detailed analysis of the derivation of each of these values is presented in Bugbee and Salisbury (2).

	THEORETICAL	POTENTIALLY ACHIEVABLE	WHEAT IN A CELSS
ABSORPTION	100 %	98	90
PHOTOSYNTHETIC EFFICIENCY	34	18	16
RESPIRATION EFFICIENCY	82	75	70
HARVEST INDEX	100	90	44
TOTAL	27.5	11.9	4.4

Table 1. Values for the four constituent physiological processes that determine yield. All values are in percent. The total at the bottom is the result of successive multiplication. Values for wheat in a CELSS are average values over the life cycle. Higher instantaneous values have been measured, but cannot be sustained.

PERCENT PPF ABSORPTION

Measurements of PPF absorption over the life cycle are shown
in Figure 4. A maximum absorption of 98% is possible about 15
days after emergence (emergence occurs 48 to 72 hours after
germination). The high plant densities necessary to obtain high
yields in a CELSS cause very rapid PPF absorption. Senescence
during the last part of the life cycle reduces absorption. High
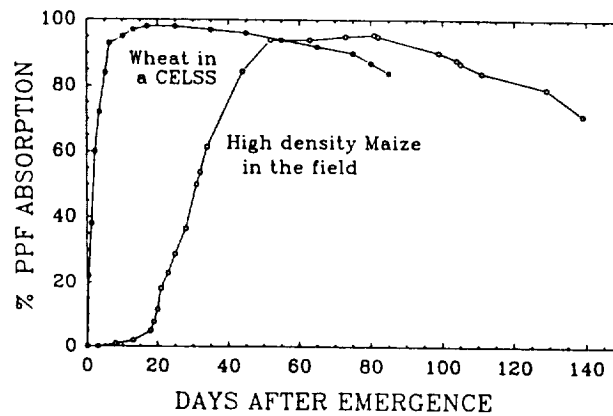density maize from the field is included as a comparison.

Figure 4. A comparison of PPF absorption of wheat in a
CELSS with maize in the field. Complete data were not
available for field grown wheat, but field wheat absorbs
significant amounts of PPF up to 5 days sooner during early
growth than maize.

PHOTOSYNTHETIC AND RESPIRATION EFFICIENCY

We have used a sealed growth chamber as a cuvette to measure
canopy photosynthesis and a smaller cuvette to measure
photosynthesis of individual leaves in the canopy. All of the
measurements in the following figures were made with CO_2
enrichment. Figure 5 indicates the photosynthetic capacity of

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single leaves at two different temperatures. The response of
these wheat leaves is considerably different than typical field
curves. The assimilation rate of 45 μmol m^{-2} s^{-1} is very high,
but these leaves had ample nitrogen and high CO_2. Single leaves
at ambient CO_2 typically reach a maximum photosynthetic rate at a
PPF of about 600 μmol m^{-2} s^{-1}, at 25°C these leaves did not reach
a maximum at a PPF of 1000 μmol m^{-2} s^{-1}. A temperature of 17°C is
too low for maximum photosynthesis, but note that dark
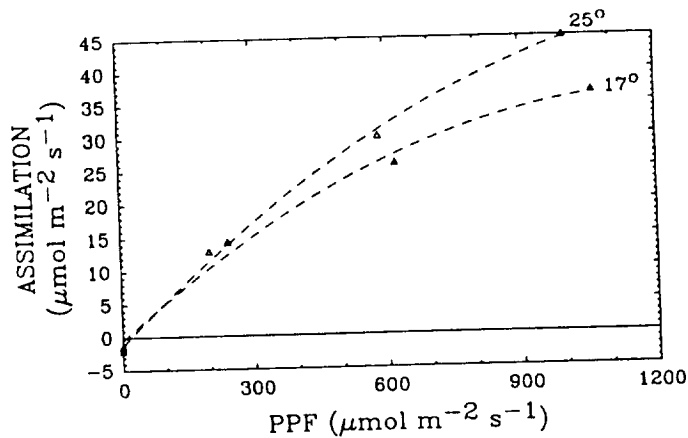respiration at 17°C was slightly lower than at 25°C.

Figure 5. Single leaf photosynthesis a function of PPF
level at 17 and 25°C. These leaves were part of a canopy,
grown in a CO_2 enriched CELSS environment.

Figure 6 compares gross assimilation of single leaves and a
canopy. The gross assimilation data in this figure do not
include dark respiration. They indicate only the photosynthetic
response to PPF. The response of the canopy to PPF is almost
perfectly linear. The single leaf data indicate that the top
leaf layer (LAI=1) is responsible for all of the canopy
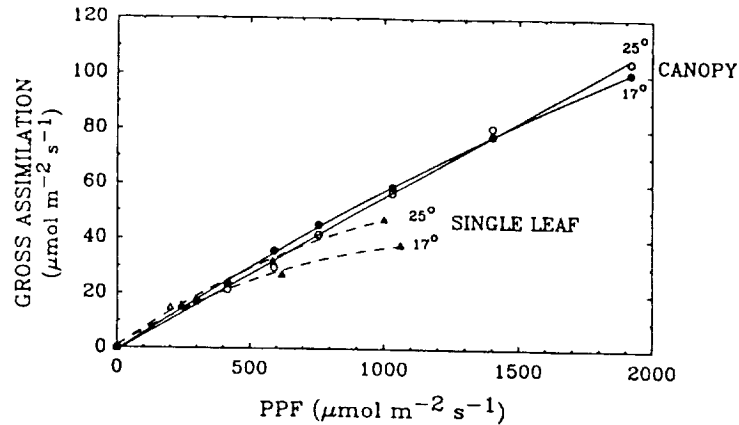photosynthesis up to a PPF of about 400 μmol m^{-2} s^{-1}.

Figure 6. The effect of PPF level on gross assimilation at two temperatures.

QUANTUM REQUIREMENT

The dimensionless ratio of moles of photons absorbed to moles of CO_2 fixed is called the quantum requirement. (The inverse of this ratio, moles of CO_2 fixed per mole of photons absorbed, is sometimes used and is called the quantum yield). The best quantum requirement that has been measured in a single leaf has been about 12.5, and this was with 2% oxygen, which almost completely eliminated photorespiration (4). Figure 7 indicates the apparent quantum requirement for single leaves and canopies at different PPF levels. This figure is developed directly from the data in Figure 6. It is necessary to use the term "apparent" quantum requirement because we measured incident PPF and not absorbed PPF. The difference between apparent and actual quantum requirements is about 10% for single leaves and 2 to 4% for the canopy. If we had made these measurements with 2% oxygen and measured absorbed photons, it is likely that the quantum requirement would have approached 13 (below 200 μmol m^{-2}

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s^{-1} PPF) in both single leaves and the canopy.

The most striking aspect of Figure 7 is that the quantum requirement for canopies remains very low as the PPF increases to full sunlight!
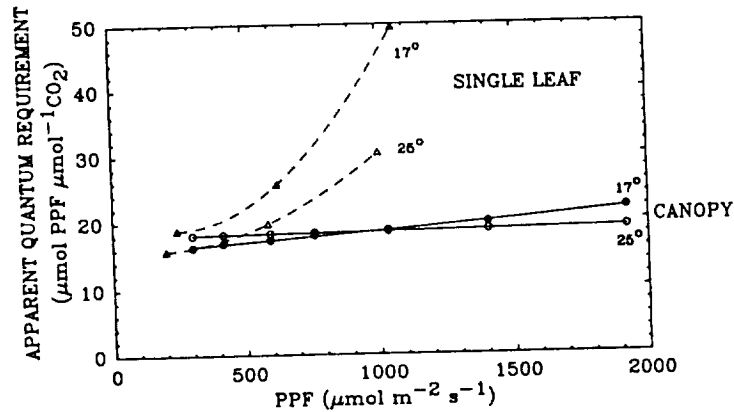

Figure 7. The apparent quantum requirement for single leaves and a canopy at two different temperatures.

NET PHOTOSYNTHESIS

Photosynthesis cannot be measured in the absence of dark respiration, but the standard assumption is that dark respiration occurs at the same rate in the light as in the dark. This assumption may not be perfectly accurate (see discussion in 2), but it is necessary to estimate gross photosynthesis. Figure 8 shows what was actually measured to get the data in Figure 6. Although 25°C is optimum for photosynthesis, far less dark respiration occurs at 17°C resulting in a higher rate of net photosynthesis at all PPF levels. The high respiration rates in the canopy are the result of an excessively high leaf area index (about LAI=30). Most of these leaf layers are in a very low PPF environment and contribute almost nothing to photosynthesis. The

top layer of leaves, as indicated by the single leaf
measurements, is responsible for almost all of the photosynthesis
at the lower PPF levels. The high LAI results in a high
respiration rate, which causes the respiration efficiency to be
low. Note that the PPF compensation point (point at which
assimilation is zero) is 300 μmol m^{-2} s^{-1} at 17°C and 600 μmol m^{-2}
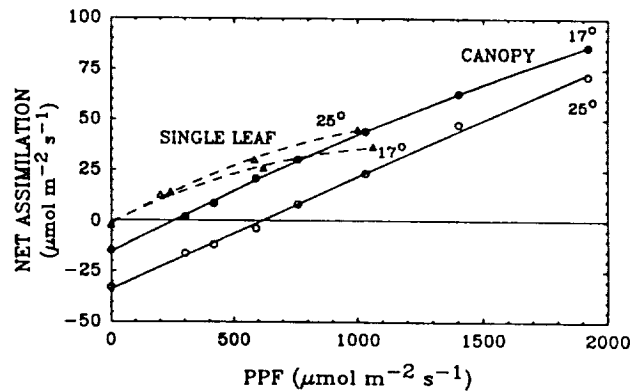s^{-1} at 25°C.

Figure 8. Net assimilation (photosynthesis) in single
leaves and a canopy at 17 and 25°C.

THE RELATIONSHIP BETWEEN LAI AND PPF ABSORPTION

An LAI of about 10 is adequate to absorb 95% of the PPF
(Figure 9). Canopies, grown in a CELSS environment, reach this
LAI at 10 to 15 days after emergence. The LAI continues to
rapidly increase to a maximum of about 40 and then begins to
decrease because the lower leaves senesce. LAI continues to
decrease until it reaches an LAI of about 10 at harvest. This
would seem to be a strong argument against the use of high plant
densities, but tillering causes even plants grown at low
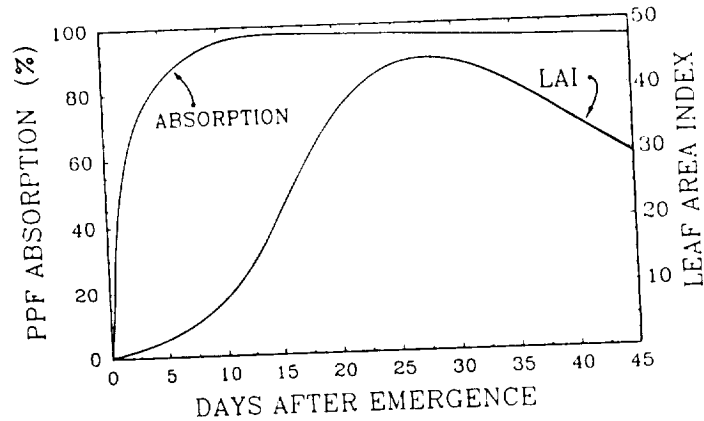densities to reach the same high LAI's.

Figure 9. The relationship between leaf area index and PPF absorption. Head emergence is at about day 40. An LAI of 10 is sufficient to absorb over 95% of the PPF.

EXCESSIVE TILLERING

Wheat plants form more tillers in response to favorable environmental conditions. Tillering is usually beneficial in the field, but optimal conditions in a CELSS cause excessive tillering and result in an excessive LAI. Figure 10 indicates culm formation at two planting densities. More culms are formed than can be supported by the PPF levels. Late forming culms are at lower levels in the canopy and do not have sufficient PPF for maintenance respiration after the canopy fills in. After about day 15 they begin to senesce until the number of culms is reduced to a level that can be maintained. This represents a large waste of resources that cannot be alleviated by reducing the planting density. High density planting results in slightly more culms (heads) per unit area on day 45 than the low density planting. This increase in head number is typically associated with increased grain yields at harvest.
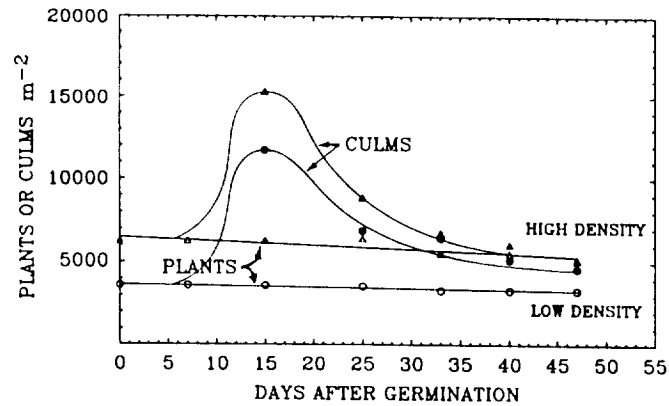
Figure 10. The effect of plant density on culm number from germination to 45 days old. Excessive culm formation (tillering) occurs, followed by senescence.

HARVEST INDEX

Unlike the other components of yield, our harvest indexes (seed mass divided by total plant mass) have not exceeded those in the field (40 to 55%). In fact, many of our early studies resulted in harvest indexes of 25 to 35%. Recent refinements have helped us achieve harvest indexes of over 50% and we are confident harvest indexes of 55% or even 60% will ultimately become routine. Harvest index appears to be particularly sensitive to environmental conditions in the final two weeks before harvest.

Harvest index is reduced considerably by late forming tillers. Figure 11 indicates the effect of primary, secondary, and tertiary tillers on harvest index (data from 1). Note that the mean harvest index was 40 to 43% in this study, but that the harvest index of primary and secondary tillers was 47 to 52%. This is another important reason to try to eliminate late forming

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tillers.

The elimination of tillering has long been a goal of this
project. We developed 20 wheat lines that do not tiller in the
field but in optimal controlled environments form 2 to 4 tillers
per plant. Genetic alterations do not appear to provide an easy
solution, but altering the red/far-red radiation ratio might be
very effective. This ratio directly alters the phytochrome
equilibria in plant tissue, which in turn regulates tillering
(see discussion in 2). We hypothesize that a high level of far-
red radiation during the first 10 to 20 days of growth may be
sufficient to eliminate late forming tillers. The red/far-red
ratio appears to be sensed at the base of the wheat plant so the
canopy itself becomes a biological far-red filter after canopy
closure. As indicated in Figure 10, culms are initiated a few
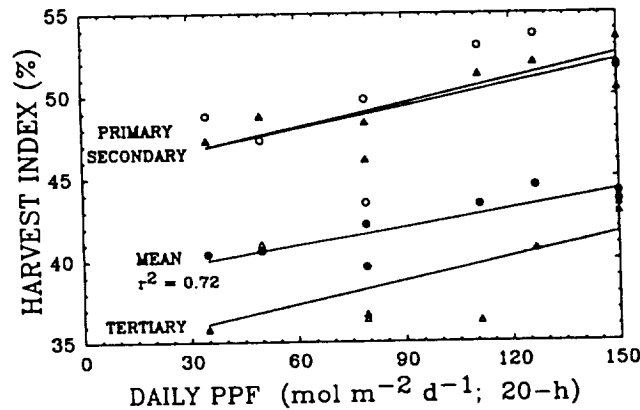days after emergence and reach a peak at day 15.

Figure 11. The harvest index of three different tiller
categories as affected by PPF level. The photoperiod in
this study was 20-h.

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PHOTOPERIOD

When daily PPF is the same, low PPF levels and long photoperiods usually result in better growth than high PPF levels and short photoperiods. Wheat is a long-day plant for reproductive initiation and thus does not have an obligate need for a daily dark period. Wheat plants yield well and appear healthy in continuous light, but continuous light might reduce efficiency per photon. Three recent studies with 16, 20, and 24-h photoperiods have indicated that wheat plants do not need, or benefit from, a daily dark period. Crop growth rate and yield per photon were nearly identical in all photoperiods. Photoperiod has large effects on plant height and length of the life cycle, however. Compared to a 16-h photoperiod, continuous light shortened the life cycle by 30% and shortened plant height by 25%. Both of these effects would be beneficial in a CELSS.

CARBON DIOXIDE CONCENTRATION

Based on an extensive literature of CO_2 research we have used CO_2 enrichment in all of our studies. Some of our early studies on optimum CO_2 levels indicated a possible detrimental effect of very high CO_2 concentrations on growth and yield. Other studies have also found toxic effects of CO_2 concentrations above about 1500 $\mu mol\ mol^{-1}$ (5). Because of the evidence for CO_2 toxicity, we have elevated CO_2 levels only to 1200 $\mu mol\ mol^{-1}$. We have recently begun to investigate the effects of higher levels. High CO_2 levels increase photosynthesis on a short term (hours) basis in single leaves and we have also found that they increase short-term canopy photosynthesis (Figure 12).
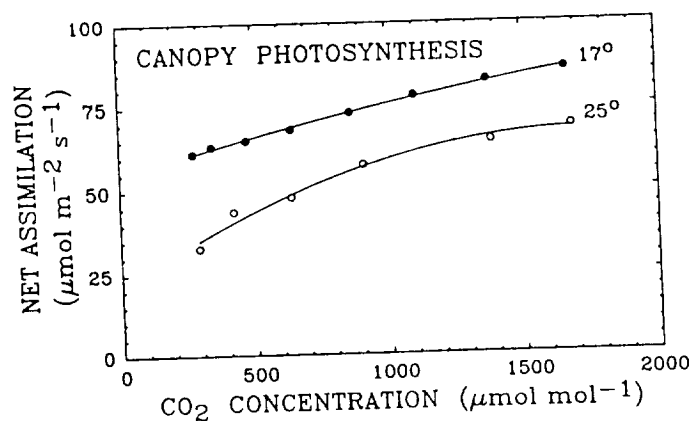
Figure 12. The effect of CO_2 concentration on canopy photosynthesis at 17 and 25°C.

We have modified six, plexiglass cylinders to allow the evaluation of different foliar environments in a common hydroponic root-zone environment. A preliminary study was conducted with two replicate cylinders at each of three CO_2 concentrations (340, 1200, and 2400 μmol mol^{-1}). Carbon dioxide enrichment to 1200 μmol mol^{-1} resulted in a 20% increase in total biomass (crop growth rate; Figure 13) and a 15% increase in seed yield (Figure 14). Enrichment to 2400 μmol mol^{-1} resulted in decreased growth and a larger decrease in yield. Elevated CO_2 levels appear to have an inhibitory effect on harvest index (Figure 15). This reduction in harvest index may be caused by a decrease in seed set (Figure 16). The seeds that were set in the highest CO_2 treatment were exceptionally large (75 mg per seed) but this increase did not overcome the effects of poor seed set. A replicate trial is in progress. If inhibition of seed set is reproducible we need to examine the casual factors. One

hypothesis is low boron concentrations in the emerging heads. High CO_2 levels close stomates and dramatically reduce transpiration. Boron (and calcium) are passively absorbed and delivered to the top of plants in the transpiration stream. Elevated CO_2 reduces these elements in foliar plant parts and boron is essential for good pollen formation. Low boron levels in emerging wheat heads might be ameliorated by increasing the concentration of boron in the nutrient solution or with the application of foliar sprays of boron.
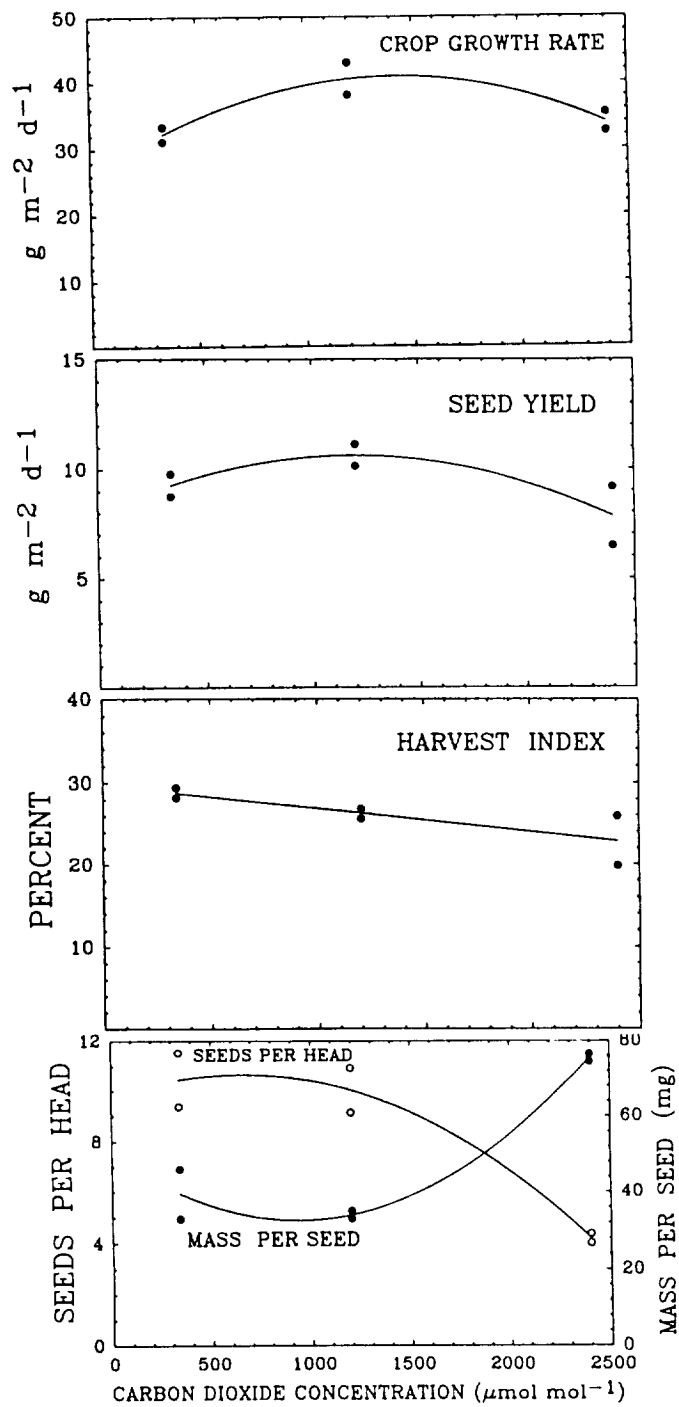
Figures 13, 14, 15, and 16. Crop growth rate, seed yield, harvest index, seeds per head and mass per seed as affected by CO_2 concentration.

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NITRATE CONCENTRATION IN HYDROPONIC SOLUTION

Nitrate concentrations of about 0.5 mM in nutrient solutions are sufficient to allow maximum nitrogen uptake by small seedlings and isolated root pieces. Concentrations of up to 30 times higher than necessary (15 mM) are often used in hydroponic solutions to insure adequate nitrogen nutrition. If the nitrate concentration is maintained above 0.5 mM and if the solution flow rates are sufficiently rapid to deliver the nitrogen to all parts of the root-zone, then low nitrogen concentrations should result in maximum nitrogen uptake and growth rates. We tested this hypothesis in two recent studies. Nitrate concentrations were maintained at 1, 5, and 15 mM in each of three, identical hydroponic systems. Each hydroponic system delivered solution to four, 0.2-m plots arranged in a completely random design (12 total plots). An initial trial indicated that there may be an interaction between nitrate concentration and iron nutrition of wheat plants.

In a second trial, the iron deficiencies were alleviated by changing the iron chelate in solution. Results of the second trial are shown in Figure 17. There was no statistical difference in growth rates among any of the three treatments at any time. One mM nitrate resulted in a slightly higher growth rate at the end of the life cycle, but there was insufficient replication to associate this increase with statistical significance.
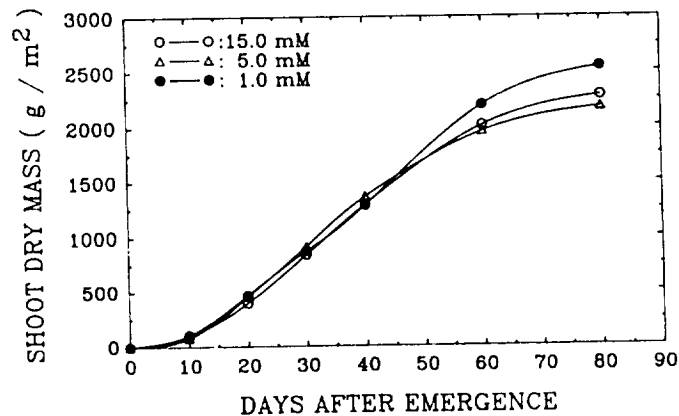
Figure 17. The effect of solution nitrate concentration on crop growth rate.

There were no differences in seed or leaf protein among the treatments. There were also no significant differences in tissue nitrate concentration, indicating that wheat may be able to regulate the translocation of nitrate to foliar plant parts even at high nitrate levels in solution.

A small amount of the nitrate that reaches foliar plant parts is effluxed through stomata as ammonium gas. This concentration is usually less than 5% of the total nitrogen in the plant. Figure 18 indicates the nitrate removal from two of the 3 systems. The 5 mM treatment was in between the 1 and 15 mM treatments and has been left out of this figure for clarity. About 10% more nitrate disappeared from the 15 mM treatment than the 1 mM treatment. If this went into the plant, it should have resulted in a higher nitrogen concentration in the plant tissue.

If it was lost to the atmosphere, it suggests an important incentive to use low nitrogen concentrations in a CELSS. We are currently replicating this study to more accurately measure the fate of nitrogen added to the solution.
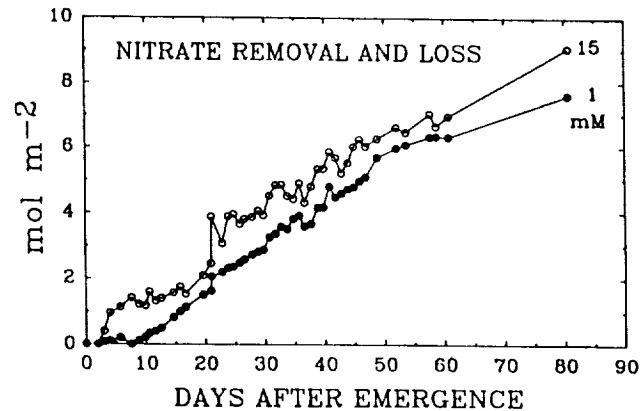

Figure 18. Nitrate removal from hydroponic solution as a function of two nitrate concentrations in hydroponic solution.

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