

**STUDIES ON MAXIMUM YIELD OF WHEAT
FOR THE CONTROLLED ENVIRONMENTS OF SPACE**

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The economic feasibility of using food-producing crop plants in a Controlled-Environment Life-Support System (CELSS) will ultimately depend on the energy and area (or volume) required to provide the nutritional requirements for each person. Energy and area requirements are, to some extent, inversely related; that is, an increased energy input results in a decreased area requirement and vice versa.

A major goal of our research effort is to determine the controlled-environment food-production efficiency of wheat per unit area, per unit time, and per unit energy input. We have studied wheat for the following reasons:

(1) Its grain can be processed into a wide variety of food products that can supply a major portion of dietary carbohydrates and protein. Certain other crops (e.g., lettuce) can supply only a small portion of dietary calories before toxic levels of vitamins or secondary products are consumed.

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(2) Wheat, rice, and maize (in that order) are the major food crops of the world. Much is known about wheat physiology, and this knowledge can be rapidly adapted to new environments.

(3) Much is also known about wheat genetics, so it is possible to quickly select and breed new cultivars for a new environment.

(4) Wheat forms flowers in response to long days (i.e., it is a long-day plant) and grows well in continuous light, which results in a maximum use efficiency per unit mass of the lighting system. Short-day crop plants such as rice have an obligate requirement for a dark period (about 8 to 12 hours, depending on species and cultivar) before they initiate seed production. Tomatoes cannot grow under continuous light, which causes their leaves to become chlorotic (yellow) and eventually die.

(5) The vertical leaf orientation allows wheat to efficiently absorb high levels of photosynthetically active radiation (400 to 700 nm) and convert this energy into a high grain yield per unit area. Crop plants with horizontal leaves efficiently absorb low levels of radiation but generally are less efficient when radiation levels are high (Gar-

dner et. al. 1985; Leopold and Kriedemann, 1975).

Based on our productivity findings from the past few years, we can now calculate the size and energy requirements for each person in a CELSS. First, however, it is useful to compare our findings with theoretically achievable limits, and then with more realistic potentially achievable productivities.

THE THEORETICAL MINIMUM SIZE OF A CELSS

At the CO₂ concentrations present in the earth's atmosphere, species with C₄ photosynthesis (e.g., maize, sugarcane) are often more efficient than species with C₃ photosynthesis, which include wheat and most crops (summary in Salisbury and Ross, 1985). At elevated CO₂ levels, however, C₃ plants are significantly more efficient than C₄ plants. C₃ crop plants are therefore an excellent choice for a CELSS or a lunar station, where CO₂ levels are expected to be elevated. From the stoichiometry of electron transport in photosynthesis and a proton requirement of three for ATP synthesis (Handgarter and Good, 1982), a theoretical minimum of 9 moles of photons are required to fix 1 mole of CO₂ into carbohydrates in C₃ species. This is known as a quantum requirement of 9 or a quantum yield (reciprocal of quantum requirement) of 0.111. The theoretical quantum requirement

of C₄ species is 15 (quantum yield of 0.067).

At the whole plant level, however, some energy is required for nitrate reduction, some is lost to fluorescence, some is absorbed by nonphotosynthetic pigments and reradiated as heat, and some is used in the respiratory synthesis of complex molecules, so the best achievable quantum yield is 0.083 (quantum requirement = 12). This has been achieved only at low irradiance levels and in the absence of photorespiration (Ehleringer and Pearcy, 1983; Osborne and Garrett, 1983). This quantum yield is close to the conversion efficiencies achieved with algae.

If we could achieve a continuous quantum yield of 0.083 from a photosynthetic photon flux (PPF) of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (about one half full sunlight at the earth's surface), we could theoretically produce 216 $\text{g m}^{-2} \text{d}^{-1}$ of carbohydrates. (Calculations: $1000 \mu\text{mol m}^{-2} \text{s}^{-1} \times 86,400 \text{ s d}^{-1} \times 0.083 = 7.2 \text{ mol CO}_2 \text{ m}^{-2} \text{d}^{-1} \times 30 \text{ g (mol CH}_2\text{O)}^{-1} = 216 \text{ g m}^{-2} \text{d}^{-1}$.) Assuming 4 kcalories per gram of carbohydrates and a requirement of 2600 kcal person⁻¹ day⁻¹, then we can calculate $(216 \text{ g m}^{-2} \text{d}^{-1} \times 4 \text{ kcal g}^{-1} \text{ divided into } 2600 \text{ kcal person}^{-1})$ a minimum continuous-food-production area of only 3 m^2 per person.

THEORETICAL ENERGY REQUIREMENTS

McCree (1972) calculates that 5 μmol of photons s^{-1} produced by high-pressure sodium lamps in the photosynthetic part of the spectrum (400 to 700 nm) represent almost exactly one watt of energy. Thus, if high-pressure sodium lamps can be made 40 percent efficient at producing photosynthetic energy (efficiency of 37.6% is noted below), an input of 500 W m^{-2} could produce 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. If 3 m^2 were required per person, the energy input could be as low as 1.5 kW per person. This is the highest possible efficiency that could be achieved by any plant species.

POTENTIALLY ACHIEVABLE SIZE AND ENERGY REQUIREMENTS

This analysis of theoretical size and energy requirements is highly simplified. The following factors reduce the achievable productivity of higher plants below the theoretical maximum.

1. Light Absorption.

Plant leaves never absorb all the incident radiation. We have found that, under ideal conditions, 5 percent of the photosynthetically active radiation is reflected, and 1 percent is transmitted, even by a dense canopy with vertical leaves. It is unlikely that absorbed energy will ever exceed 95 percent of incident photosynthetic energy.

A more significant absorption problem occurs during the early stages of growth when small plants do not cover the surface area and consequently cannot intercept all the incident irradiation. We grow wheat at densities up to 1500 plants m^{-2} ($6.7\text{ cm}^2\text{ plant}^{-1}$, 2.6 cm between plants). This is 3 to 6 times normal planting densities in the field, but plant leaves absorb only 50 percent of the irradiance when they are 14 days old and 90 percent when 18 days old. After day 18, light interception continues to be excellent until harvest at day 60. The germinating seeds do not require light until emergence on day 3, but absorption efficiency is low from day 3 to about day 18. In our current system, this loss is about 20 percent of the total area and energy required to grow the crop. A mechanical system or transplanting to alter plant spacing during early growth (so plants are moved apart as they mature) could eliminate some of this loss. Such systems are being used in commercial controlled-environment food production.

Increasing plant densities even beyond those we have used would also improve early interception of radiation before day 30, but this approach has two problems, one engineering and one biological: (1) We have not yet designed a system to support ultra high densities of plants above a hydroponic root-zone environment. (2) Interplant competi-

tion for light quickly becomes considerable at high plant densities. Little is known about the effects of this low-light stress on young plants, but field studies indicate that high densities decrease seed yield before total plant growth is reduced (see discussion in Gardner et al., 1985).

2. Harvest Index.

The most significant limitation to food production is that not all the biomass produced by the plants is edible. The edible divided by total biomass (both dry) is called the harvest index. A lettuce crop has about 80 percent edible leaves and 20 percent inedible stem and roots. Potatoes can have a harvest index of edible tubers of 80 percent of the total biomass, and wheat can reach 60 percent edible grain on a dry-mass basis. Under the best conditions, there is a 20 to 40 percent loss from inedible plant parts.

Many authors have suggested crops with edible roots, leaves, and reproductive structures. Sweet potato and sugar beet are examples. In most cases, however, only the young leaves are edible, although it is the mature tubers, roots, fruits, or seeds of such plants that are normally harvested. Unusual food crops should be considered for a CELSS, but claims of high productivity and high harvest index often cannot be substantiated.

3. Digestible energy per unit edible biomass.

When the energy content of oven dry wheat grain is determined by combustion in a bomb calorimeter, values as high as 3.94 kcal g⁻¹ are obtained, but the digestible energy is only about 3.7 kcal (Table I). This relationship also holds for other food commodities.

Table I

**DIGESTIBLE ENERGY CONTENT OF
HARD RED SPRING WHEAT GRAIN**

	As Harvested (%)	Oven Dry %	kcal g ⁻¹	Kcal g ⁻¹ In Bomb Calorimeter
Carbohydrates	66.8	76.8	x 4	= 3.07
Protein	14.0	16.1	x 4	= 0.64
Fat	2.2	2.5	x 9	= 0.23
Fiber	2.3	2.6	0	--
Ash	1.7	2.0	0	--
Moisture	13.0	0.0		--
	<u>100.0</u>	<u>100.0</u>		<u>3.94</u>

Net Usable Digestible Energy Varies from about 90 to 95% of the 3.94 Kcal g⁻¹ (See FAO publication 24. 1970. Amino Acid content of Foods and Biological Data on Proteins.)

Assuming 94% digestibility:

$$\begin{array}{rcl}
 & 3.94 & \\
 \times & .94 & \\
 \hline
 & 3.70 & \text{kcal g}^{-1} \\
 \times & 4.18 & \text{joules Kcal} \\
 \hline
 & 15.0 & \text{joules g}^{-1}
 \end{array}$$

4. Energy conversion.

High-pressure sodium lamps produce 376 W of energy between 400 and 700 nm per 1000 watts input power. This makes them 37.6% efficient (personal communication: Chris Mpelkas, Sylvania Test and Measurements Lab, Danvers, MA). Their output, however, must be reflected down onto the plants. The best reflectors are about 90 percent efficient. This makes the overall efficiency of the system 33.8 percent. Efficiencies of 27.4 percent have been achieved on a commercial scale. The Phytofarm in Dekalb, Illinois, has an energy input of 219 W m^{-2} from high-pressure sodium lamps and a photon output of $300 \mu\text{mol m}^{-2} \text{ s}^{-1}$ or 60 W m^{-2} of photosynthetic irradiance (Maynard Bates, personal communication).

5. Respiration.

Respiration provides the energy to synthesize complex molecules from the initial products of photosynthesis. It occurs at the same rate in wheat leaves in both the light and the dark (Azcon-Bieto and Osmond, 1983). When wheat is grown in continuous irradiation, all the respiratory synthesis of compounds must occur in the light. This respiratory evolution of CO_2 decreases the quantum yield and may be part of the reason a quantum yield of 0.111 has not been achieved in plant leaves.

Assuming that all respiration takes place in the light and that we can continuously achieve a quantum yield of 0.083, there is still a loss of fixed carbon to root system respiration. This loss is proportional to the biomass of the root system. Field grown crop plants typically invest 20 to 30% of their biomass in roots, but our hydroponically grown wheat plants invest only about 10% of total biomass in roots.

Carbon dioxide evolution during photosynthesis from "dark" respiration is taken into account in our calculations by assuming a quantum yield of 0.083 rather than 0.111.

Considering these factors, the potentially achievable size and energy requirements can be calculated as follows:

Theoretical (with $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF)	216 g $\text{m}^{-2} \text{d}^{-1}$
95% light absorption over life cycle	205 g $\text{m}^{-2} \text{d}^{-1}$
80% harvest index	164 g $\text{m}^{-2} \text{d}^{-1}$
Multiplied by 3.7 kcal g^{-1} (94% digestible)	607 kcal m^{-2}
Assume 3000 kcal per person per day:	5 $\text{m}^2 \text{ person}^{-1}$

Energy requirement:

$1000 \mu\text{mol m}^{-2} \text{s}^{-1} =$	200 W m^{-2}
200 W m^{-2} divided by 0.338 efficiency =	592 W m^{-2}
$592 \text{ W m}^{-2} \times 5 \text{ m}^2 = 3552 \text{ W person}^{-1} =$	3.6 kW person^{-1}

These theoretical efficiencies will be very difficult to achieve, but they represent a long term goal. They will be extremely difficult to achieve with a crop plant (like strawberries) that is chosen for its asthetic qualities and flavor rather than for its productivity. Nonetheless, research will need to be done on all species grown in a CELSS to optimize their edible productivity.

CURRENTLY ACHIEVABLE PRODUCTIVITIES WITH WHEAT

During the past year, after spending much time on designing and building research chambers to create optimum environmental conditions for studies on wheat productivity, we have obtained reproducible production data that can be used to estimate the size of a CELSS. We have been highly successful in converting photosynthetic irradiance into biomass but less successful in converting total biomass into edible yield.

Quantum Yield and Short-Term Photosynthesis

We measure short-term rates of carbon fixation in wheat canopies with a gas exchange system that includes a pressurized growth chamber. A canopy of 0.8 m^2 is grown in this chamber with the roots in a sealed, recirculating, hydroponic system. A photosynthetic photon flux of $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in an atmosphere enriched to $1700 \mu\text{mol CO}_2 (\text{mol air})^{-1}$ has re-

sulted in photosynthetic rates as high as $58 \mu\text{mol m}^{-2} \text{s}^{-1}$ of carbon dioxide absorbed per unit horizontal area. Ninety-four percent of the photon flux was absorbed, resulting in a quantum requirement of 16.2. This can be compared to the theoretically achievable quantum requirement of 9 and potentially achievable requirement of 12.

If we subtract for root respiration and multiply by the photoperiod each day, this figure can be converted into a daily growth rate. Root biomass in our hydroponic systems is typically only 10 percent of the total (20 to 30% in the field). Subtracting this estimated 10 percent respiratory loss and assuming continuous light, this photosynthetic rate should result in a growth rate of $135 \text{ g m}^{-2} \text{d}^{-1}$. This compares well with the theoretically achievable growth rate of $205 \text{ g m}^{-2} \text{d}^{-1}$ (at 95% light absorption).

Measured Growth Rates.

We measure actual growth rates at weekly intervals by removing a 0.2 m^2 section of plants (about 200 plants in a rigid support), blotting the roots dry, weighing the section, and returning it to the hydroponic solution. A few plants are destructively harvested and dried to determine percent dry mass, from which dry-mass growth rates can be calculated. We have measured growth rates of $875 \text{ g m}^{-2} \text{week}^{-1}$ or 125

$\text{g m}^{-2} \text{ d}^{-1}$. This growth rate serves as a validation of the short-term photosynthesis measurements. Unfortunately, it takes about 22 days for a group of plants to reach this growth rate, and the rate gradually decreases as the plants mature. These factors combine to make a best-achievable growth rate of $89 \text{ g m}^{-2} \text{ d}^{-1}$ averaged over a 60-day life cycle.

The production of $89 \text{ g m}^{-2} \text{ d}^{-1}$ total biomass is truly remarkable by conventional agricultural standards. Typical field productivities are less than $10 \text{ g m}^{-2} \text{ d}^{-1}$, and $20 \text{ g m}^{-2} \text{ d}^{-1}$ is exceptional (Table II). Wheat is obviously stressed even in the best field conditions. The stress factors could be low carbon dioxide and/or low light, neither of which would be economical to change in the field.

Yield and Harvest Index.

These high growth rates are the good news. The bad news is that we have not yet been able to cause wheat growing at high rates to partition a normal percentage (40 to 50%) of its total biomass into edible grain. A crop producing $89 \text{ g m}^{-2} \text{ d}^{-1}$ should have a grain yield of 35 to 45 $\text{g m}^{-2} \text{ d}^{-1}$; our best yield has been only $21.4 \text{ g m}^{-2} \text{ d}^{-1}$. At $21.4 \text{ g m}^{-2} \text{ d}^{-1}$, 30 m^2 and 15 kW person⁻¹ would be required. This is our currently achievable productivity. Table III indicates some of the growth parameters associated with this yield.

Table II
A COMPARISON OF WHEAT
PRODUCTIVITIES IN DIFFERENT
ENVIRONMENTS

	Absolute Seed Yield g m ⁻²	Life Cycle days	Yield Per Day g m ⁻² d ⁻¹	Total Biomass g m ⁻²	Biomass Per Day g m ⁻² d ⁻¹	Harvest Index %
Field Production	300-700	90-130	3-7	700-1800	7-18	45
World Record in Field*	1450	120	12.1	3200	27	45
CELSS Project	1200	56	21.4	5000	89	24
Russian Study**	1000	56	17.9	2860	51	35

*Winter Wheat (sown in autumn; actually in the field about 270 days).

**Achieved with 50% of CELSS project energy input (Gitel'zon, 1977).

Table III
HIGHEST CURRENTLY ACHIEVABLE YIELDS

Cultivar	Total Biomass g m ⁻² d ⁻¹	Edible Biomass g m ⁻² d ⁻¹	Days In Growth Chamber	Harvest Index %	Plants Per m ²
Fremont	89.0	21.4	56	24.0	715
Anza	69.0	21.4	60	31.0	450

Plants harvested from a 400 x 500-mm experimental plot area (0.2 m²)
guard rows not included in calculation.

The problem of low harvest index is caused by low seed number per head. A comparison of our yield components with field production data clearly indicates the problem, as shown in Table IV.

Table IV
YIELDS IN CONTROLLED ENVIRONMENTS AND IN THE FIELD

	Life cycle days	Seed yield g m ⁻²	Harvest index percent	Heads per m ²	Seeds per head	Mass per seed mg
Controlled environment	60	1300	25%	3000	15	29
High yield from field	120	800	45%	800	30	33

Continuous light and a constant high temperature (27°C) are principle factors responsible for shortening the life cycle from 120 to 60 days. These same two factors may also be responsible for the low seed number per head. Low seed number per head is the combined result of two factors: (1) fewer spikelets formed on the head (spike) during the floral induction phase (days 4 to 13) and (2) poor pollination during anthesis (days 25 to 35).

There is evidence that long photoperiods result in the production of fewer spikelets per spike during floral induc-

tion (Rawson, 1970; Lucas, 1972). David Bubenheim, a graduate student, is now conducting studies to quantify the effect of photoperiods as long as 24 hours on rate of reproductive development in wheat. The most significant of his preliminary findings are as follows (Bubenheim and Salisbury, 1985):

(1) The length of the vegetative phase is extremely short in continuous light. In one cultivar, reproductive development began 48 hours after germination.

(2) The length of the initiation phase, during which spikelet number is determined, is inversely proportional to photoperiod between 12 and 24 hours. A short initiation phase results in fewer spikelets per spike (head) and fewer potential seeds per head.

(3) Development of daylength-insensitive cultivars (from Mexico) is faster in long photoperiods during the vegetative and initiation phases, but the stem elongation phase is greatly retarded by long photoperiods. These two effects offset each other, making the cultivars appear insensitive to photoperiod.

A second problem is poor pollination and seed set in existing florets. Wheat is self-pollinated, and the anthers

(male flower parts) either do not form or do not grow normally after pollination in our conditions. Microscopic examination has indicated that pollen is often aborted before it accumulates starch, while embryo sac (female flower part) development is completely normal.

We are just beginning to study the problem. Our environmental conditions are very different from those in which wheat evolved, so many environmentally induced factors could be contributing to cause poor seed set. Two parameters, however, are associated with pollen sterility: nutrient (especially boron) deficiency and high temperatures. Boron and calcium are passively absorbed and translocated in the transpiration stream to foliar plant parts. The foliar concentrations of these elements are therefore determined by their concentration in the root zone and by the ratio of transpiration to photosynthesis. In the field this ratio is typically about 200 to 250 grams of water transpired per gram of biomass produced. The high CO₂ levels in our controlled environments cause photosynthesis to increase, but, by causing stomates to close, transpiration is decreased. Transpiration/photosynthesis ratios can be as low as 50:1. Calcium and boron concentrations in leaf tissue are decreased accordingly.

We compensate for the reduction by using 2.5 times normal calcium and boron concentrations in the initial hydroponic solutions of young plants. This change results in tissue concentrations of these elements that are similar to those found in field-grown wheat leaves, but the nutrient imbalance caused by high CO₂ may not be completely alleviated in all plant parts. Foliar applications of boron have increased fruit set in prune trees that had adequate foliar levels (Hanson and Breen, 1985). The amount of calcium and boron is typically low in wheat heads, and it is especially low in developing heads just previous to emergence from the leaf sheath. One of the classic symptoms of boron deficiency is poor pollen viability (Kirkby and Mengel, 1983). We therefore analyzed the concentrations of 13 elements in wheat heads before and after emergence in 12, 18, and 24-hour photoperiods with 700 $\mu\text{mol mol}^{-1}$ CO₂ environment. Photoperiod had little effect on the amount of any element in the heads; indeed, with the exception of calcium, magnesium, and boron there was almost no effect of developmental stage on nutrient composition. The changes in these 3 elements are shown in Table V.

The concentration of these elements is low in postemergence heads and extremely low before emergence, but these data do not necessarily indicate a deficiency of these ele-

ments. We are currently analyzing additional normal head samples to determine adequate levels of these elements.

Table V
CONCENTRATIONS OF THREE ELEMENTS IN WHEAT HEADS
(Mean \pm STD. Deviation)

Stage of Head Development	Ca	Mg	B
	-----%-----	-----	$\mu\text{g g}^{-1}$
Preemergence (Day 27)	0.05 \pm .02	0.09 \pm .02	4.6 \pm 1.6
Postemergence (Day 50)	0.34 \pm .10	0.27 \pm .03	9.3 \pm 1.2

High temperatures are also associated with pollen sterility in wheat. A recent report indicates that cool night temperatures might be especially beneficial (Carlson and Williams, 1985). We have begun studies in shorter photoperiods, but we have not yet provided particularly cool night temperatures (27°C day, 25°C night). It may be important to provide cool dark periods during the week of anthesis.

Within the next year, we expect to solve the harvest index barrier to high yields. Finding the solution could rapidly increase our currently achievable yields. Meanwhile, we have examined several cultural, environmental, and genetic approaches to yield optimization.

The Effect of CO₂ Concentration on Growth and Yield.

Table VI summarizes data from the first of two carbon-dioxide-enrichment studies conducted in the fall of 1984. The trial compared responses of dwarf (50-cm tall) and semi-dwarf (80-cm tall) wheat cultivars grown at three CO₂ concentrations: 350 $\mu\text{mol mol}^{-1}$ (ambient), 700 $\mu\text{mol mol}^{-1}$, and 1800 $\mu\text{mol mol}^{-1}$.

Table VI

THE EFFECT OF CO₂ CONCENTRATION
ON TOTAL AND EDIBLE
BIOMASS OF WHEAT*

CO ₂ Concentration $\mu\text{mol mol}^{-1}$	Vegetative Fresh Mass On Day 28 g	Total Biomass** $\text{g m}^{-2} \text{d}^{-1}$	Edible Biomass** $\text{g m}^{-2} \text{d}^{-1}$	Harvest Index %	Root Mass %	Seeds Per Head
350	1218	47.5	15.8	33.3	7.5	18.7
700	1966	70.0	19.8	28.3	8.8	16.0
1800	2066	56.1	13.6	24.2	15.3	12.0

*Each value represents the mean of 4 replicate plots of 0.2 m² each.

**These values do not include a 7-day germination period in the greenhouse.

Table VII shows responses of three of these cultivars plus another one in the greenhouse. Although sunlight in the greenhouse was supplemented with light from high-pressure-sodium lamps (24 h d⁻¹), the total irradiance was lower than

Table VII Part A

RESPONSE OF CERTAIN WHEAT CULTIVARS TO
ENRICHED CARBON DIOXIDE IN THE ATMOSPHERE
(October, 1984, trial)

Location CO ₂ Concentration ($\mu\text{mol mol}^{-1}$)	Cultivar	Total Grain Yield g m ⁻²	Days to Matu- rity	Grain Yield Per Day (oven dry) g m ⁻² d ⁻¹	Plants m ⁻²	Heads per m ²	Seeds per Head	Harvest Index %
Greenhouse 700	Fremont	681	59	11.5	450	1729	17.3	39
	Fremont*	701	60	11.7	450	1318	24.3	36
	PCYT 20	584	60	9.7	450	1187	18.6	41
	Y. ROJO	427	56	7.6	450	1654	13.7	36
Chamber 2 350	FMT	842	57	14.8	450	1290	23.3	32
	FMT HD**	931	57	16.3	715	1786	20.5	34
	Anza	957	60	15.9	450	1730	17.8	35
	PCYT 20	528	60	8.8	450	1540	13.1	32
Chamber 3 700	FMT	1079	63	17.1	450	2355	16.5	25
	FMT HD	1196	63	18.9	715	2893	15.5	24
	Anza	1284	67	19.2	450	2019	18.1	31
	PCYT 20	1041	67	15.5	450	2262	14.0	33
Chamber 1 1800	FMT	850	59	14.4	450	1832	18.8	37
	FMT HD	942	59	15.9	715	2125	17.3	26
	Sonoita	594	59	10.1	450	2495	7.2	20
	PCYT 20	492	63	7.8	450	3224	4.7	14

*Two replicate plots of Fremont (FMT) were grown in the greenhouse; the differences between the plots represent experimental error.

**HD = high density (715 plants m⁻²; all other treatments included 450 plants m⁻²)

Table VII Part B

Location; CO ₂ Concentration $\mu\text{mol mol}^{-1}$	Cultivar	Root Mass %***	Plant Height cm	Vegetative Growth (grams fresh mass)		
				Day 17	Day 23	Day 28
Greenhouse	Fremont*	12	73	260	612	1035
	Fremont*	11	65	196	508	936
	PCYT 20	12	50	175	450	823
	Y. ROJO	9	45	249	627	956
Chamber 2 350	FMT	7	65	226	601	1161
	FMT HD**	8	70	387	899	1526
	ANZA	9	79	215	649	1287
	PCYT 20	6	47	227	506	896
Chamber 3 700	FMT	11	81	372	1338	2223
	FMT HD	8	82	573	1798	2901
	Anza	8	85	304	865	1581
	PCYT 20	8	58	221	586	1160
Chamber 1 1800	FMT	20	77	423	1186	1912
	FMT HD	13	77	-	1710	2435
	Sonoita	13	50	573	1421	2153
	PCYT 20	15	57	329	1004	1762

*Two replicate plots of Fremont (FMT) were grown in the greenhouse; the differences between the plots represent experimental error.

**HD = high density

***Figures for root mass indicate percent of total plant dry mass.

it was in the three chambers. It varied during the life cycle from 400 to 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, whereas irradiance in the three chambers was held at 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

For the trials, a new system was devised to hold the plants. Instead of styrofoam lids with foam plug inserts, U-

shaped metal bars were placed side by side and held together with long bolts. Seedlings are held in closed-cell foam rubber (weather stripping) between the bars. Transplanting is faster in this system, and it allows us to use much higher plant populations. The distance between rows is fixed at either 30 or 38 mm, but the spacing within rows can be varied to achieve a wide range of plant densities. The dimensions of the lids are 400 x 500 mm.

A second replicate trial confirmed the findings of the first carbon-dioxide-enrichment study. In both studies total plant biomass was considerably increased by CO₂ enrichment, but grain yield and harvest index were higher at 700 $\mu\text{mol mol}^{-1}$ CO₂ than at 1800 $\mu\text{mol mol}^{-1}$ CO₂. These data suggest that the highest CO₂ concentration may be too high for maximum yields, but if high CO₂ is inducing a secondary effect, such as nutrient deficiency, then adjustment of other environmental parameters would lead to increasing yields even at the highest CO₂ level. The stomatal closure induced by high CO₂ greatly reduces transpiration, but reducing humidity increases transpiration, which may increase nutrient uptake and ultimate yield. We have preliminary data suggesting that reduced humidity increases nutrient uptake in high CO₂ conditions. Reducing transpiration with high carbon dioxide and high humidity might save energy (that required to evaporate

water) in a CELSS.

Table VIII quantifies the effect of CO₂ enrichment on the ratio of grams of water given off in transpiration to grams carbohydrates fixed in photosynthesis.

Table VIII
TRANSPIRATION/PHOTOSYNTHESIS RATIO
(g H₂O/g CH₂O)

CO ₂ μmol mol ⁻¹	PPF 900 μmol m ⁻² s ⁻¹	PPF 2100 μmol m ⁻² s ⁻¹
350	177	90
700	122	65
1800	60	49

Typical field values are 200 to 250

These transpiration rates are very low, but they do not appear to be an inherent problem. Transpiration is important for cooling plant leaves, but even the lowest transpiration rates provide adequate cooling in our conditions, and low transpiration rates still provide ample purified water for a life support system. The limiting factor may be nutrient uptake, but nutrients could be applied as foliar sprays.

THE EFFECT OF INCREASED PHOTOSYNTHETIC PHOTON FLUXES ON PHOTOSYNTHESIS

Plant growth research in controlled environments is typically conducted at photosynthetic photon fluxes between 300 and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Photosynthesis of single leaves of C_3 crops light saturate in this range, but leaves in crop canopies complete for available light so that dense communities of vigorous crop plants often do not light saturate even in full sunlight (2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$). If increased energy inputs lead to increased productivity, the size of a CELSS food production facility can be reduced accordingly. It is not yet known whether energy or volume will be the more limiting constraint.

Growth and yield over a range of energy inputs should provide valuable design information. We have obtained short term (7-day) photosynthetic responses to PPF levels of up to 2,100 $\mu\text{mol m}^{-2} \text{s}^{-1}$. These measurements were made in an open gas exchange system that utilizes a sealed growth chamber as the assimilation chamber. The design of this system is discussed in Sestak, Catsky, and Jarvis (1971). Photosynthetic calculations are described in Nobel (1983). These results are shown in Figures 1 and 2. It is apparent that photosynthetic rate in a CO_2 enriched environment is light limited even in the highest naturally occurring light levels.

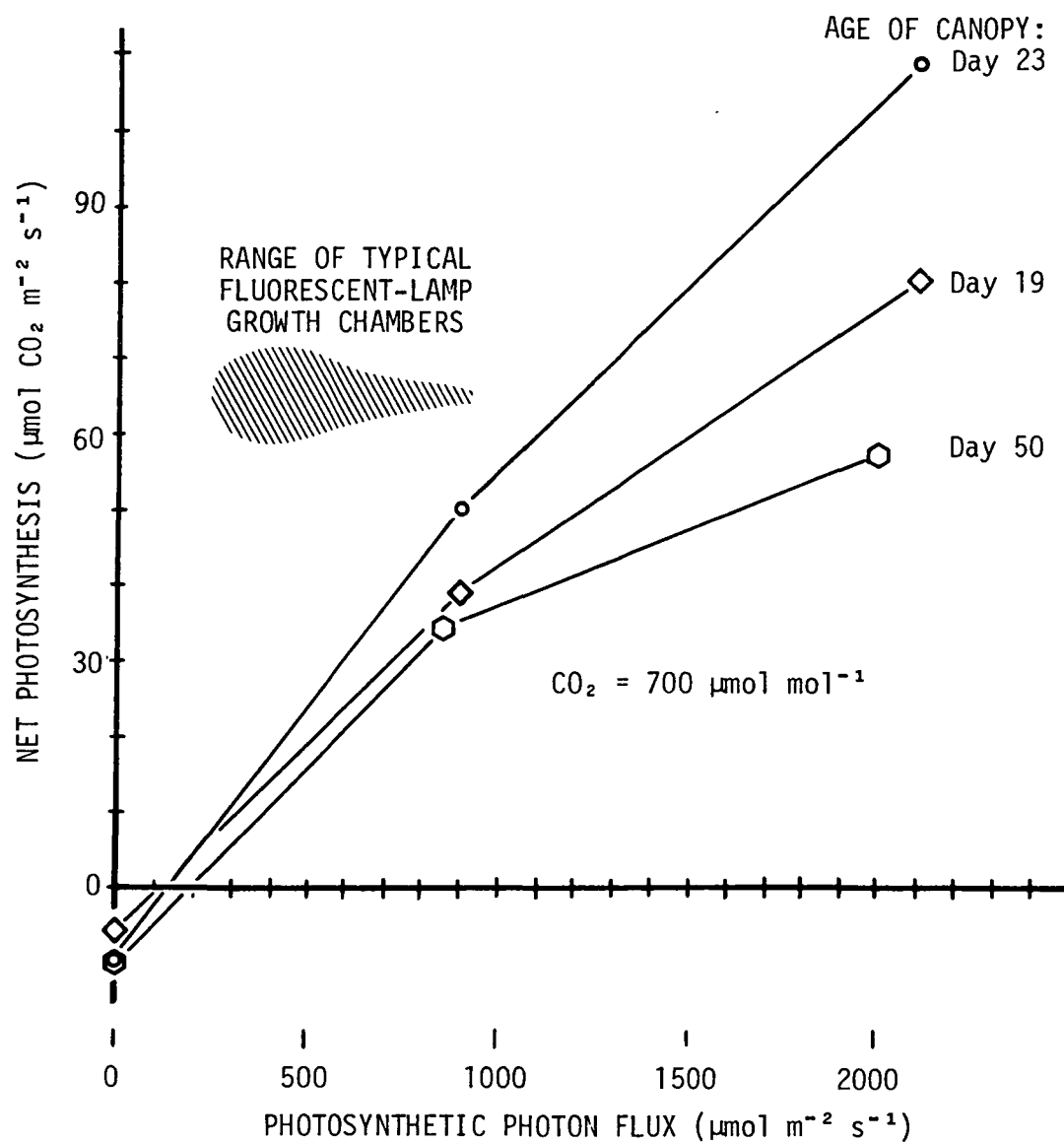


Figure 1 Net photosynthesis as a function of irradiance level. Note that photosynthesis of a dense canopy increases with increasing light at least up to the level of sunlight. Note also that most growth chambers in use today (which use fluorescent plus incandescent lamps; PPF about 250 to 900 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) are just above the light compensation point. At such a light level, doubling the irradiance more than doubles net photosynthesis.

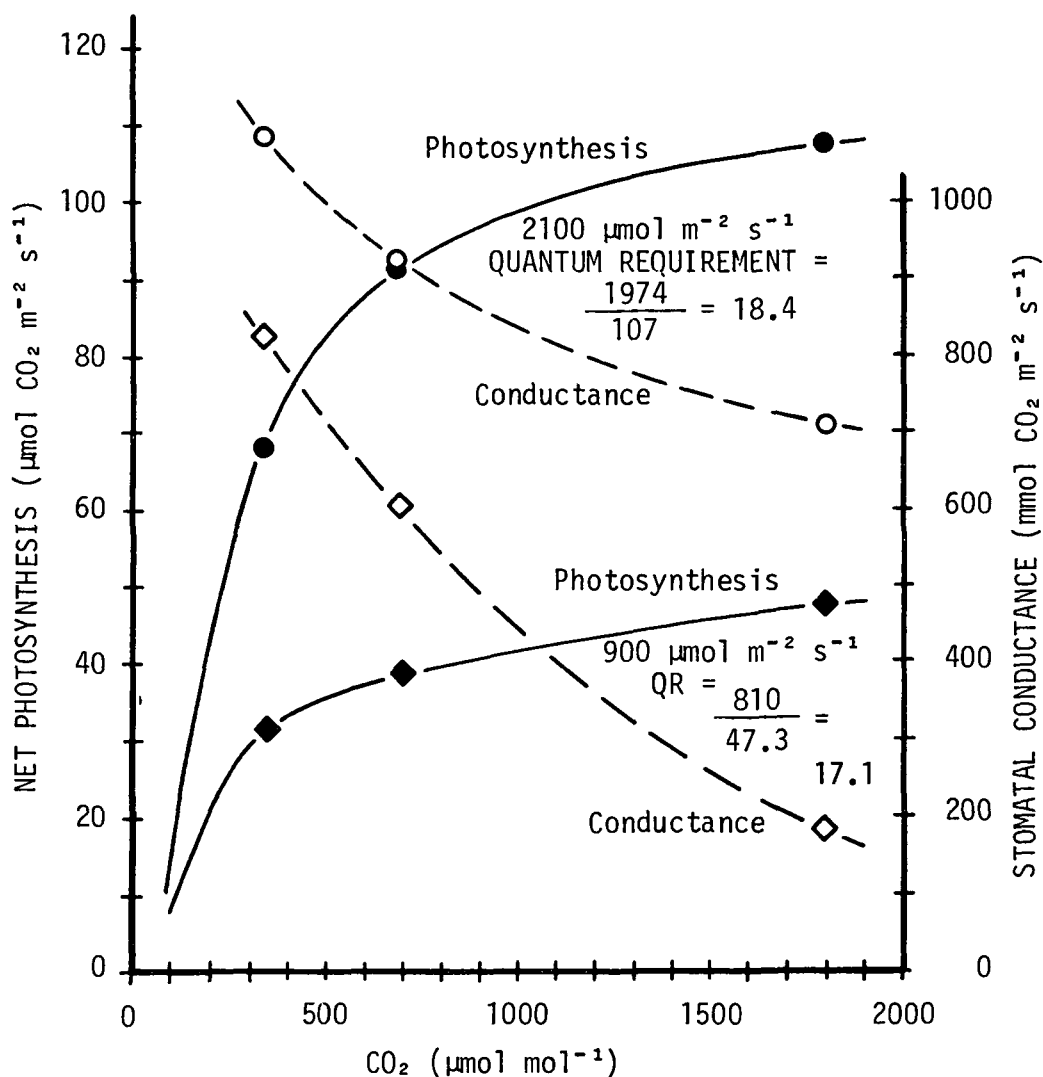


Figure 2 Net photosynthesis and stomatal conductance as a function of carbon-dioxide concentration at two irradiance (PPF) levels. Note that conductance decreases sharply as CO_2 increases, indicating stomatal closure. Photosynthesis increases with increasing CO_2 , but the increase with increasing light is much more striking. Higher light levels also induce stomatal opening, increasing conductance. (Curves for photosynthesis are extrapolated to an approximate CO_2 compensation point of 100)

We studied the longer term effects of high irradiance by exposing a plant canopy to $2100 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 24 h d^{-1} for 7 days. No change in CO_2 uptake was observed during this period. We also examined the initial photosynthetic rate after a 4-hour dark period, during which assimilates could be unloaded and exported from the leaves. Again, no change in net photosynthesis was observed. These results suggest that feedback inhibition of photosynthesis is not a serious problem even in continuous light. If these rapid growth rates can be translated into edible productivity, the option of substituting energy for volume over a wide range will be available to CELSS system designers.

The Effect of Planting Density on Growth and Yield

As discussed earlier, poor light absorption during early growth considerably reduces energy efficiency. When ample nutrients, water, and oxygen are available in the root zone, high plant populations should lead to enhanced early growth, which might also lead to higher yields. This hypothesis was tested using our newly designed plant support lids (discussed earlier). A very rapid circulation rate in our hydroponic solution minimizes any root zone deficiencies so that competition for light is the primary limiting factor. Table IX shows the results of an initial study with a 24 h d^{-1} photoperiod and with a PPF of $700 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Table IX

**THE EFFECT OF PLANTING DENSITY
ON GROWTH AND YIELD**

Plant Density m ⁻²	Vegetative Fresh Mass Day 22	Total Biomass At Harvest g m ⁻² d ⁻¹	Edible Biomass At Harvest g m ⁻² d ⁻¹	Heads m ⁻²
380	368	39.2	9.1	2000
680	585	41.0	7.6	2800
1060	722	38.2	9.2	2900
1320	855	48.8	15.7	3700
High Intensity Field Production:				
400	—	20.0	8.0	800

The growth parameters at each density represent one 400 x 500 mm block of plants with the guard rows removed.

Higher plant densities are clearly associated with increased vegetative fresh mass for the first 22 days of growth. Growth parameters at harvest show an inconsistent, but generally positive response to high densities. Additional tests need to be conducted.

BREEDING A CULTIVAR FOR CELSS

The production of multiple heads per plant, known as tillering, is a desirable phenomena in field production, but it decreases plant uniformity and harvest index and is thus

undesirable in controlled environments where unicum cultivars can be planted at high densities.

We now have cultivars that do not tiller in the field. In our enriched controlled environment conditions, however, they tiller almost as much as control plants. Elevated levels of nutrients (especially nitrogen), water, CO₂, and light are all known to promote tillering. The combination of these factors has prevented us from testing the unicum concept in our studies. Theory continues to predict that uniculms would perform better in high production environments, but the germplasm is not yet available.

We have had considerable success in breeding ultradwarf (less than 50-cm) cultivars. The results of a replicated yield trial are shown in Table X.

Yields tend to be slightly less than our highest yielding dwarf lines, Sonoita, Yecora Rojo, and PCYT 20, but plant height has been reduced considerably. Consequently, yield per m³ has been improved. Harvest index should also be increased, but the immediate advantage is that ultradwarf lines are much easier to work with in confined, controlled environmental areas. The difficulties of providing a uniform environment increase exponentially with plant height.

Table X
YIELD PERFORMANCE OF BEST
ULTRADWARF ADVANCED BREEDING LINES

Cultivar	Height cm	Yield g m ⁻²	Yield g m ⁻³
39-1-1	29	49.2	170
40-1-3	34	49.2	145
44-3-2	44	54.8	125
50-1-1	37	53.6	145
Commercial full dwarf wheats			
Sonoita	44	51.0	116
Yecora Rojo	46	65.9	143
PCYT 20	52	69.9	134
Olesen's Dwarf*	27	40.5	150
Semidwarf wheat	90		
Full size wheat	150		

*Olesen's Dwarf was the source of dwarfing genes for these breeding lines.

Last spring we selected 121 lines from the CIMMYT germ-plasm collection in Mexico. One of these cultivars is less than 20 cm tall, and several others show great promise for genetic yield enhancement. We continue to evaluate new material in both the field and in a hydroponic greenhouse section that is enriched with CO₂ and supplemented with high-pressure-sodium light.

FOOD PRODUCTION IN SIMULATED MICROGRAVITY

Microgravity may be more important to high productivity than any other environmental parameter, yet we have no information on the long term responses of crop plants to microgravity conditions, and only a few long term studies have been attempted with plants in the simulated microgravity environment of clinostats.

The gravity compensation environment of clinostats may or may not be an accurate simulation of true weightlessness for plants. This question will remain unanswered until more data from spaceflight experiments are available for comparison. In the meantime, we are attempting to obtain information on long-term crop-plant responses to weightlessness by using clinostat simulation.

Eliminating inadvertent environmental stress while providing gravity compensation on a clinostat is a challenging task, but minimizing stress is especially important with crop plants. Crop plants have been bred for rapid growth when environmental conditions are favorable, and they are generally more sensitive to stress than noncrop species. Our objective has been to design a clinostat to minimize mechanical stress and provide the favorable environmental conditions that allow crop plants to express their full growth

potential.

A clinostat was constructed to provide high intensity radiation from "above" the plants at all times. Thirty-four pots were placed on the inside of a 1.4-m diameter cylinder so that plant tops were directed at the axis of rotation. The cylinder is divided vertically (right angles to the axis of rotation) with plywood painted white. One 400-W metal halide lamp (Sylvania Super Metal Arc) is placed at the axis of rotation on each side of the plywood. The lamps were protected by glass cylinders, which were ventilated with small fans so that radiant heating of plant leaves could be minimized. The rotation rate of the clinostat is controlled by a variable speed, DC electric motor, which is connected to the central axis by a gear-reduction chain drive. The rotation rate for all experiments was 0.6 rpm, which resulted in a gravitational acceleration of 2.8×10^{-4} g at the outside edge of the clinostat. This is well below the threshold g response for shoots and at or below the threshold response for roots.

A capillary-tube, drip-irrigation system was used to provide nutrient solution as the plants moved past the bottom on each revolution. Fiberglass window screen was stretched over the top of each pot to hold the soilless media (1:1:1 ratio, peat:perlite:vermiculite) in place during rotation.

Table XI
WHEAT YIELD COMPONENTS AS
AFFECTED BY MICROGRAVITY SIMULATION

	total bio- mass g	total seed mass g	harvest index %	heads per plant	seeds per head	mass per seed mg
CONTROL	9.4	3.8	40	10	18.4	20.4
CLINOSTAT	9.8	2.6	27	7	20.0	19.6

Results are preliminary, but Table XI summarizes our findings with wheat. We can now draw the following conclusions (Bugbee and Salisbury, 1985).

- (1) Peas, soybeans, and wheat are capable of producing viable seed while being continuously grown on a clinostat.
- (2) Plant growth rates are not necessarily affected by clinostating.
- (3) Structural support of foliar plant parts on clinostats may be helpful, although the contact with the support could itself be stressful (Jaffe, 1976).
- (4) Irradiation from "above" the plants may be necessary to eliminate a photocompensation effect.
- (5) Plants on this clinostat do not consistently bend in the direction of rotation (Hoshizaki and Hamner, 1982; Tibbitts and Hertzberg, 1978).

PLANT TISSUE CULTURE FOR RAPID REGENERATION OF HYBRID WHEAT

(John G. Carman)

Our primary goal in the tissue culture of wheat is to consistently regenerate 1000 or more uniform, high-yielding hybrid plants from the callus initiated from either a 4-mm slice of young inflorescence tissue or an individual wheat embryo. We are optimistic that we can reach this goal within two years. Our short range objectives are to:

- (1) Identify wheat cultivars that show promise for tissue culture regimes.
- (2) Optimize the culture medium for callus induction, somatic (asexual) embryoid proliferation, and somatic embryoid germination on agar-solidified medium.
- (3) Optimize culture conditions and growth regulator concentrations for somatic embryoid proliferation in cell suspension cultures.

Our accomplishments to date include:

- (1) Identification of a winter wheat that infrequently produces, in callus culture, somatic embryoids that are identical in appearance and germination properties to sexually formed embryos.
- (2) Identification of two spring wheat cultivars that

undergo extensive somatic embryogenesis in callus culture. Unfortunately, the embryoids produced are not as well formed as those produced in the winter wheat cultivar.

- (3) Continued optimization of culture medium variables such that a 2-fold increase has been realized for some wheat cultivars in frequency of somatic embryoid formation over former culture media used for wheat tissue culture as currently reported in the literature.

As we develop suspension culture systems for wheat tissue cultures, we hope to be able to achieve our goal of 1000 plants per explant. Recently, such systems that have been developed for rice have yielded far greater numbers of plants, with theoretical projections of 126,000 plants per explant within a six-month culture regime.

CONCLUSIONS

The data in this paper provide many reasons to be optimistic about enhancing our current productivities. We now have the research equipment and instrumentation to study physiological responses to unusual environmental conditions, and we especially look forward to data from CELSS experiments in space. We are also interested in the problems created by nearly complete closure of a ground-based facility.

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