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Plant Productivity in Controlled Environments

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To assess the cost and area/volume requirements of a farm in a space station or Lunar or Martian base, a few laboratories in the United States, the Soviet Union, France, and Japan are studying optimum controlled environments for the production of selected crops. Temperature, light, photoperiod, CO₂, humidity, the root-zone environment, and cultivars are the primary factors being manipulated to increase yields and harvest index. Our best wheat yields on a *time* basis (24 g·m⁻²·day⁻¹ of edible biomass) are five times good field yields and twice the world record. Similar yields have been obtained in other laboratories with potatoes and lettuce; soybeans are also promising. These figures suggest that ≈30 m² under continuous production could support an astronaut with sufficient protein and about 2800 kcal·day⁻¹. Scientists under Iosif Gitelson in Krasnoyarsk, Siberia, have lived in a closed system for up to 5 months, producing 80% of their own food. Thirty square meters for crops were allotted to each of the two men taking part in the experiment.

A functional controlled-environment life-support system (CELSS) will require the refined application of several disciplines: controlled-

environment agriculture, food preparation, waste disposal, and control-systems technology, to list only the broadest categories. It has seemed intuitively evident that ways could be found to prepare food, regenerate plant nutrients from wastes, and even control and integrate the several subsystems of a CELSS. But could sufficient food be produced in the limited areas and with the limited energy that might be available? Clearly, detailed studies of food production were necessary.

Soviet scientists have been engaged in such studies for more than a quarter of a century, and NASA supported a limited effort with algae and with higher plants in the early 1960s. NASA-supported studies with higher plants were soon terminated, but the research was reinitiated in the late 1970s. Recent planning for permanent colonies on the moon or Mars and for permanent manned space stations has led to an increased conviction within NASA that such work is essential (8). Related studies are being done in France and in Japan. The discussion here is arbitrarily limited to work with higher plants.

In spite of their recognized importance, only a few token studies have been supported by NASA so far: our own with wheat, studies with potatoes at the Univ. of Wisconsin, lettuce at Purdue Univ., soybeans at the Univ. of North Carolina, and some studies with algae. During the past 5 years, only about 4 million dollars have been allocated to these studies. This seems pitifully small when one

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Table 1. Early growth of wheat at increasing photosynthetic photon flux^a.

PPF ($\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$)	PPF ^b ($\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$)	Total plant growth rate ($\text{g}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$)	PPF use efficiency ($\text{g}\cdot\text{m}^{-2}$ per day per mol)	Leaf area index	Shoot percent dry mass
400	23	30.3	1.32	13.4	10.9
600	35	44.2	1.28	13.5	10.7
800	46	46.1	0.98	14.2	11.2
1000	58	43.9	0.76	15.7	11.2
1400	81	53.9	0.67	15.4	11.7
1700	104	65.5	0.63	18.9	11.8

^aPlants harvested at canopy closure, 24 days after planting; plant density: 2000 plants/m²; cultivar: Yecora Rojo; temperature: 20°C day, 15°C night.

^bUsed a 16-hr photoperiod.

Table 2. The five phases of development in the wheat life cycle.^a

Developmental stage	Day number	Associated morphological change
1) Vegetative	0–12	Germination and early leaf growth
2) Reproductive initiation	13–18	Microscopic change in apical meristem during which ultimate spikelet number is determined
3) Extension	19–30	Further development of floral parts
4) Anthesis	30–35	Pollination and fertilization
5) Grain fill	36–60	Translocation of assimilates into devel- oping seed

^aThe life cycle is about 110 d in the field. The 60-day life cycle shown here is a minimum and occurs only with a 24-hr photoperiod and 27°C temperatures. When the life cycle is increased, the relative lengths of the stages remain about the same.

thinks of the potential importance of such work for future colonization of the moon or Mars or for long-duration space flights. There are so many plants that need to be studied. The amount seems especially meager in the context of the total NASA budget (7 to 8 billion dollars). A single launch of the space shuttle costs about \$200 million, although it is difficult to arrive at an exact figure. Imagine what could be reported in this symposium if the money required for one launch had been allocated to studies in the CELSS program for as long as a decade! Nevertheless, in spite of the limited resources so far allocated to this research, some important results have been forthcoming. It seems clear that plant productivity will not be a fatal limitation to the use of a CELSS in future space exploration. This paper documents this statement by reviewing some of this work.

SOME CALCULATIONS ON THE SIZE OF A CELSS FARM

To gain perspective on the goals of a CELSS plant-production project, we will make a few calculations, beginning with some utopian assumptions and proceeding toward a more realistic situation. The most optimistic, science-fiction achievement that can be imagined is, by some miracle of gene transfer, to make a human being capable of photosynthesis so that the light absorbed by the human epidermis is converted to the chemical bond energy of food. Instead of eating, such a human being would spend most of his or her time standing around in the sun. But would even that work?

The solar constant in the vicinity of the earth's orbit is 1.36 kW·m⁻². About half of that is photosynthetically active radiation (PAR): 0.68 kW·m⁻² or 0.68 kJ·m⁻²·s⁻¹. Assume that our hypothetical, photosynthesizing astronaut requires $\approx 11,700 \text{ kJ}\cdot\text{day}^{-1}$ (2800 kcal·day⁻¹), which is equivalent to 0.135 kJ·s⁻¹ (kW). Divided by the PAR in the solar constant, this value gives an area of $\approx 0.2 \text{ m}^2$ /person. That is, if all the PAR in the solar constant could be converted to food energy all day, an area of only 0.2 m² would be required.

That is clearly impossible, because not even the most efficient plant can convert 100% of absorbed PAR into the chemical bond energy of food. Indeed, a calculated maximum efficiency for photosynthesis is about 25% (based on 8 photons per molecule of fixed CO₂—sometimes achieved with low-irradiance red light and dense algal cultures). An efficiency of 13.5% (15 photons per molecule

of CO₂) is a more realistic figure for higher plants irradiated with more normal light levels. The 25% figure gives an area of 0.8 m², and the 13.5% figure gives an area of 1.5 m², to produce the required 11,700 kJ·day⁻¹.

A human being intercepts a cross-sectional area of sunlight of ≈ 0.5 to 0.9 m² if its rays are from the front or back and normal to the long axis of the body. Hence, even if our hypothetical space traveler wore little or no clothes and stayed in the sun all the time in a position that would intercept nearly all incoming radiation, he or she would nevertheless starve to death. At best, only about half of the energy requirement would be supplied.

Of course, these calculations apply to a space farm as well as to a genetically manipulated space traveler. The smallest space farm using higher plants under continuous irradiance at the solar constant would be $\approx 1.5 \text{ m}^2$ /person. As we consider the more realistic problems of a CELSS, however, this figure gets much larger very quickly.

Few if any plants photosynthesize at a rate approaching 13.5% efficiency under full sunlight. If we reduce the irradiance to half of full sunlight, we will need at least 3.0 m²/person, and if our plants are in the light only about half the time (12 hr/day) the value becomes 6.0 m²/person. If only about half of the biomass produced by the plant can be eaten as food (50% harvest index), the value goes up again to about 12 m²/person. Lastly, if it takes a good portion of the plant's life cycle to establish a solid canopy capable of absorbing most of the light, the value will again increase. Our experience with wheat suggests that the time for canopy development will again double the value to ≈ 24 to 30 m²/person.

What about the energy requirements? They could be low if sunlight is piped to the plants through a fiberoptic system. If, on the other hand, all the light for photosynthesis must be generated electrically, this would require $\approx 600 \text{ W}\cdot\text{m}^{-2}$ if high-pressure sodium (HPS) lamps are used (37.6% efficient) in the most efficient reflectors (90% efficient). This lighting would produce a photosynthetic photon flux (PPF) of 1000 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ or 200 W·m⁻² PAR, which is about half of full sunlight at the earth's surface. To irradiate 24 m² would require 14.4 kW. Of course, additional electrical power would be required to operate the environmental control system plus the various systems for food processing, repair and maintenance of equipment, waste disposal, and mineral nutrient regeneration for the plants.

There is another approach to the calculation, namely to assume some given size for the space farm and then to calculate the nec-

Table 3. Photoperiod/temperature influence on yield components in wheat.

Conditions	Plants/ m ²	Spikes/ m ²	Total seeds per spike	Mass per seed (mg)	Total yield (g·m ⁻²)	Days to harvest	Edible yield (g·m ⁻² ·day ⁻¹)	Harvest index (%)	Edible yield ² (g·m ⁻³ ·day ⁻¹)	Yield efficiency ³ (mg·mol ⁻¹)
Cool temperature (20°C day, 15° night), 14-hr photoperiod	1150	2007	21	29	1154	77	15.1	46	16.3	300
Cool temperature (17°C), 24-hr photoperiod	1076	2387	16	30	1054	66	16.3	35	17.5	189
Significance ⁴	NS	NS	*	NS	NS	*	NS	*	NS	*
Warm temperature (27°C), 14-hr photoperiod	1030	3234	5	27	279	66	4.3	11	4.3	85
Warm temperature (27°C), 24-hr photoperiod	830	2128	10	29	872	61	14.2	29	14.4	164
Significance	*	*	*	NS	*	*	*	*	*	*

²Yield on a volume basis is calculated by adding 0.4 m to the height of the plants to account for the lamps and the hydroponic system.

³Yield efficiency is calculated as milligrams of edible dry biomass per mol of photons required to produce it; supplied photons are totalled for the area over the entire life cycle.

⁴Duncan's least significant difference ($\alpha = 0.05$); * = significantly different; each row of statistical evaluations applies to the differences between the two treatments above it. NS = not significant.

Table 4. Cultivar evaluation—replicated study in controlled environments.

	Spikes/ m ²	Seed per spike (mg)	Mass per seed (g·m ⁻²)	Edible yield	Days to harvest	Edible yield (g·m ⁻² ·day ⁻¹)	Harvest index (%)	Height (cm)	Edible yield ² (g·m ⁻³ ·day ⁻¹)
Yecora Rojo	2130	18	34	1224	67	19	47	56	19.8
BB-19	1771	24	23	987	76	13	46	40	16.2
PCYT-20	2641	15	31	1127	71	16	33	65	15.2
Sonoita	1562	21	32	1067	76	14	50	56	14.6
DLSD ($\alpha = 0.05$)	*	*	*	*	*	*	*	*	*

²Yield on a volume basis is calculated by adding 0.4 m to the height of the plants to account for the lamps and the hydroponic system.

essary productivity of the farm to support a space dweller. To begin with, 100 g of whole-grain, hard-red spring wheat contain about 13 g of water, 14 g of protein, 2.2 g of fat, and 69.1 g of total carbohydrate, including 2.3 g of fiber (13). Bomb calorimeter studies suggest that 100 g of oven-dry wheat could provide 1647 kJ (394 kcal) of food energy, and if we assume that 94% of this energy is digestible and usable by the human being, this would provide 1584 kJ, which we will round to 1500 kJ (370 kcal) of energy. Hence, to provide the 11,700 kJ·day⁻¹ required by a human being, about 780 g·day⁻¹ of oven-dry wheat or its equivalent in other food would be required. If this amount were to be produced in 12 m², yields would have to reach 65 g·m⁻²·day⁻¹; if the production area equaled 30 m², then average daily production must equal 26 g·m⁻²·day⁻¹, a figure that has been closely approached in some of the studies that will be described.

The figure of 30 m²/person seems quite reasonable, even with today's productivity capacities. This is a fairly small area (5 × 6 m, about the size of a good-sized living room). If we double this figure to provide a safety factor and then multiply it by 100 inhabitants of Lunar City, the farm on the moon would occupy an area (6000 m²) a little larger than an American football field, including end zones (5364 m²).

The following sections summarize experience gained so far in attempting to achieve the 26 g·m⁻²·day⁻¹ of edible biomass production that would be necessary for such a CELSS.

RESULTS WITH WHEAT

The foliar environment

At Utah State Univ., we have modified three commercial growth chambers (EGC-13) to create environmental conditions that might be used in space. Each chamber has 1 m² of growing space. High-pressure sodium lamps have been installed in all chambers to in-

crease irradiance levels. In one chamber, 5.2 kW of metal halide and HPS lamps provide 2000 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ PPF (full sunlight at noon). A water filter below the lamps reduces total radiation by 37% without reducing PPF.

We have also designed and built a six-compartment chamber specifically for photoperiod-irradiance studies. Each compartment can experience its own photoperiod and irradiance level, but temperatures in the six compartments remain within 0.2°C of each other. The six lighting systems are exclusively HPS lamps, with the light filtered through 5 cm of chilled water.

We also grow plants in two greenhouse bays that have HPS lamps to raise irradiance, especially during winter, and a layer of water flowing over the greenhouse glass for cooling. We enrich and control CO₂ concentrations in all locations to 1000 μmol of CO₂ per mol of air (ambient = 340 $\mu\text{mol}\cdot\text{mol}^{-1}$). Carbon dioxide from compressed gas cylinders is mixed with filtered air from above the building and introduced into the chambers. In the greenhouse, CO₂ enrichment is achieved by burning natural gas. An infrared gas analyzer continuously monitors CO₂ levels in the chambers and greenhouse bays. We do not use an automatic feedback system because CO₂ levels can easily be maintained manually at 1000 \pm 50 $\mu\text{mol}\cdot\text{mol}^{-1}$. One chamber has been sealed and outfitted with large cooling coils that circulate water at a temperature below the air temperature in the chamber, but above the dew point, so that water vapor does not condense on the coils. In this chamber, the hydroponic root-zone environment has been sealed to isolate it from the foliar environment so that photosynthetic rates of entire canopies of plants in the chamber can be measured by monitoring input gas volumes and input and output CO₂ levels.

The importance of studying canopies instead of individual plants in CELSS research needs to be emphasized. Productivity in a CELSS is not measured as yield per plant, but rather as yield per unit area. Efficient light absorption requires a well-developed canopy, and the behavior of an individual plant is strongly modified by the other

Table 5. Growing conditions.

	Wheat	Potatoes		Lettuce	Soybeans	
		Canopy	Caged plants		Expt 1	Expt 2
Irradiance ($\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$)	1000	475	400	430 (0–11 days) 900 (11–19 days)	700	550
Lamp source	(HPS)	(CWF)	(some CWF side light)	(INC)	(CWF + INC)	
Photoperiod (hours of light)	24	24	24	20	9 ^a	12
Total PAR ($\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$)	86.4	41.0	34.6	30.90 (0–11 days) 64.8 (11–19 days)	22.68	23.76
Temperature ($^{\circ}\text{C}$)	17.5–22.4 (+1 $^{\circ}$ /week)	16	16	25	30/26	26/20
CO ₂ ($\mu\text{mol}\cdot\text{mol}^{-1}$)	1000	365 and 1000	360	360 (0–11 days) 1500 (11–19 days)	400	675
O ₂	Ambient ^b	Ambient	Ambient	Ambient	Ambient	Ambient
N ₂	Ambient ^b	Ambient	Ambient	Ambient	Ambient	Ambient
Relative humidity (%)	60–80	70	70	75 (days) 85 (dark)	75–95	75–95
Plant spacing (m^2/plant)	0.00083	0.21	0.2	0.0125	0.0924	0.0924
Plant density (plants/ m^2)	1200	5	5	80 ^a	10.8	10.8
Air velocity ($\text{m}\cdot\text{s}^{-1}$)	≈ 1.0 (0.1 – 4.0)				0.33	0.33
Cultivar	Yecora Rojo		Norland Early Red	Waldmann's Green		Ransom

^aUntil day 25, “dark” period was interrupted for 3-hr with incandescent lamps (PPF = $69 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$) to inhibit flora initiation.

^bPressure at Logan, Utah equals 85% of sea level pressure.

^cGrowth regulator, TRIA CANTANOL, applied at 10^{-7} g-liter⁻¹ at 4 and 8 days.

Table 6. Nutrient solution compositions for experiments of Table 5 mmol·liter⁻¹. (millimoles per liter)

	Wheat		Potatoes	Lettuce		Soybeans	
	Initial	Make-up		0 – 11 days	11 – 19 days	Expt. 1 (sand culture)	Expt. 2
NH ₄ ⁺	0.0	0.01 ^a	---	---	5.0	---	---
NO ₃ ⁻	15.0	3.75	7.5	15.0	25.0	1.00	3.75
P	0.2	0.5	0.5	1.0	1.0	0.50	0.50
K	3.2	1.00	3.0	6.0	11.0	1.65	1.75
Ca	12.0	1.50	2.5	5.0	5.0	0.50	1.25
Mg	4.0	0.50	1.0	2.0	2.0	1.00	0.50
S	2.0	0.50	1.0	2.0	2.0	1.65	0.50
Cl	16.0	0	0.5		0.018	0.0022	0.25
Fe	0.124	0.0125	0.0899		0.048	0.035	0.022
B	0.080	0.020	0.0227		0.046	0.017	0.012
Mn	0.008	0.002	0.0012		0.0092	0.003	0.0022
Zn	0.0008	0.0002	0.00038		0.00077	0.0003	0.0002
Cu	0.0003	0.000075	0.00016		0.00032	0.0001	0.00008
Mo	0.0001	0.000025	0.00001		0.00011	0.00004	0.00005
Si	0.300	0.075	---		---	---	---
Na	0.600	0.15	0.0005		---	---	0.25

^aNH₄⁺ is added in pH control solution; 0.01 mM is an approximate average concentration.

plants in its vicinity. Plants with vertical leaves (such as wheat) tend to be more efficient in dense canopies than plants with horizontal leaves (5).

Root-zone environment

Our hydroponic system contains four separate, root-zone compartments in each growth chamber, each compartment containing $\approx 0.025 \text{ m}^3$ of nutrient solution. (We are presently reducing this volume to 0.016 m^3 .) The solution is pumped from a single 0.3-m^3 reservoir to the root-zone compartments in all three chambers. It enters each compartment through a distribution manifold at a rate of $80 \text{ mm}^3\cdot\text{s}^{-1}$. This rapid flow rate provides dissolved O₂ and nutrient-solution uniformity between different root-zone compartments. The solution returns to the reservoir by gravity flow, becoming aerated as it cascades back into the reservoir. Measurements show that the solution is never less than 85% saturated with O₂ at all locations.

Each growth chamber typically produces a total dry biomass of $\approx 3 \text{ kg}$, which includes 300 g of mineral elements from the solution. About 0.6 m^3 (600 liters) of water is transpired to produce a 3-kg crop. The water and nutrients are replaced by adding a dilute refill

solution in which concentrations of the nutrients are proportional to their desired concentrations in the plant. The system (made of inert components) is flushed between trials and cleaned by circulating 0.05% sodium hypochlorite and then 0.01 M hydrochloric acid.

The pH of the system is monitored and controlled continuously with an inline pH electrode that opens a solenoid to introduce nitric acid when the pH rises to 5.8. The pH change for young plants is very gradual, and acid is added to maintain the pH between 5.5 and 5.8. As the ratio of plant mass to solution volume increases, the pH changes more rapidly. After 25 days of growth, we use a mixture of ammonium nitrate and nitric acid in the pH adjustment solution. The ammonium ion gradually decreases the pH as it is absorbed. When the ammonium is depleted, the pH gradually rises again until it reaches pH 5.8 and the solenoid admits more control solution.

Wheat plants absorb ammonium from solution more rapidly than any other cation or anion. This absorption occurs throughout their life cycle. Providing ample ammonium along with nitrate nitrogen in nutrient solutions might enhance total nitrogen uptake in short-term studies (3, 6). An increased nitrogen content of foliar plant parts is associated with increased photosynthetic rates, prolonged leaf photosynthetic output, and increased grain protein. The nitrate

Table 7 Yield data for the experiments of Table 5.

Yield component	Wheat	Potatoes			Lettuce	Soybeans	
		Canopy 365 CO ₂	1000 CO ₂	Caged		Expt. 1	Expt. 2
Days to harvest	59	110	110	147	19	97	97
Total dry biomass (g·m ⁻²)	3205	2678	3046	5750	545	2203	3182
Edible dry biomass (g·m ⁻²)	1423	1842	1981	4685	424	938	1077
Harvest index (%)	44.4	68.8	65.0	81.5	78	44	34
Linear growth rate, total biomass (g·m ⁻² ·day ⁻¹)	54.3	24.3	27.7	39.1	28.7	23.6	32.8
Linear growth rate, edible biomass	24.1	16.7	18.0	31.9	22.3	10.3	11.1
Linear growth rate, edible minus seedling time	26.1	19.4	20.9	35.5	---	---	---
Maximum growth rate, total biomass*	100	---	---	81.4	60.4	43.68	---
Edible protein (%)	20	10.2	12.6	10.9	---	43	43
Edible oil (%)	---	---	---	---	---	24	24

*Measured or calculated during the logarithmic growth phase. Net assimilation rates of 125 g·m⁻²·day⁻¹ have been measured for a single day with wheat.

: ammonium ratio also alters uptake of other ions. This ratio is easily controlled in solutions; its long-term effects on wheat growth need to be studied further.

Plant support and plant density

Plant densities well beyond the optimum for field production (≈ 200 to 500 plants/m²) result not only in improved light interception and increased biomass production but also in increased final yields of grain. Seeds are planted in expanded rockwool (Grodan) at densities of up to 10,000 plants/m². The inert rockwool substrate is kept wet during germination and until roots are well-established in the nutrient solution below. Optimum density in a recent experiment was ≈ 2000 plants/m².

Optimizing photosynthetic photon flux: energy, mass, and volume tradeoffs

Energy to power the lighting system for plant growth could be the single largest energy expenditure if electric lamps are used, so significant changes in PPF use efficiency by plants could save more energy than all other CELSS energy inputs combined. If sunlight is used directly, or inexpensive energy is available from a nuclear reactor, a large energy input could be used to reduce the mass and/or volume of the food production system. Initial studies (Table 1) to determine the tradeoffs among energy, mass, and volume reveal that total plant growth rates increase in direct proportion to increases in PPF, but that each additional unit of PPF input is used less efficiently by the plant canopy.

Optimizing plant nutrition in a recirculating hydroponic system

Achieving optimum growth and nutrition from seed imbibition to physiological maturity often requires nutrient solutions that are individually tailored for different species (4). The optimum composition of these solutions can change during the plant's life cycle and may need to be altered for different photosynthesis/transpiration ratios (10). Standard nutrient solutions have produced nutritional deficiencies or imbalances in our rapid growth conditions (2). These imbalances are not always severe, but they can cause such foliar symptoms as necrotic leaf tips. We have observed that foliar symptoms vary with different transpiration rates, which are directly affected by leaf/air vapor-density gradients and by stomatal apertures, which are, in turn, altered by CO₂ levels.

The roles of photoperiod and temperature in yield of grain

The conditions that promote fastest total growth do not lead to the highest yields. This finding represents a major shift in our research approach. We have developed the term *phasic environmental control* to indicate that environmental conditions will need to be different for each phase of plant development. It now appears that maximum yields cannot be achieved without phasic environmental control. Five phases of development in the wheat life cycle can be outlined as in Table 2.

Temperatures above 25°C and long days (including continuous light) promote rapid growth rates and a short life cycle, but they lead to small wheat spikelets and very poor pollination (Table 3). Cool temperatures (20°) cause slightly slower growth rates and lengthen the life cycle but greatly increase spikelet size and seed set. This is a good example of the need for phasic environmental control to obtain the best yields per unit of time.

Testing germplasm and breeding plants for controlled environments

We have tested about 600 cultivars in the greenhouse bays that provide conditions similar to those that promote highest yields in the growth chambers. We also have a group of nine homozygous breeding lines that are short (33 to 50 cm), have excellent head size and seed set, but have below-average mass per seed at harvest. Good head size and seed set are generally more difficult to achieve with environmental modifications than good grain fill, so the potential of these breeding lines is promising. The most significant message from our plant breeding efforts is that additional genetic selection is likely to have major effects on food production in a CELSS.

'Yecora Rojo', 'PCYT 20', and 'Sonoita' are daylength-insensitive, full-dwarf cultivars (50 to 60 cm tall) that consistently have produced high yields (Table 4). Early breeding trials in the greenhouse indicated that line BB-19 (an ultra-dwarf) was the most promising line. Table 4 shows how spikes per square meter, seeds per spike, and seed mass interact in the growth chambers to determine yield. The BB-19 line had significantly more seeds than the other lines, but the mean mass per seed was less than other lines. It is possible that our ultra-dwarf lines have such a large head in relation to their leaf area that the plants have become source-limited, even in our CO₂-enriched, optimizing environments. A high-yielding, short-life-cycle cultivar is ideal for a CELSS. 'Yecora Rojo' was the earliest of the cultivars in this study, and it had the highest yield per unit of time. Ultra-dwarf cultivars seem especially well-suited

for use in a CELSS because their harvest index is higher than taller cultivars, they are much easier to work with in confined spaces, and they do not lodge (fall over) with high nitrogen nutrition.

In research funded as part of our NASA-supported project but operated separately by J. Carman in our department, we are developing techniques to clone wheat from single cells obtained from embryos. Such a process would allow the use of high-yielding hybrids in a CELSS. Because high-density planting could require as much as 5% to 10% of a harvest for planting the next crop, reproduction by cloning would allow that seed to be used as food.

WORK WITH OTHER SPECIES

The projects supported by NASA and noted in the introduction are similar to ours in that each uses the most advanced equipment for monitoring and controlling environment. All have the capacity for CO₂ monitoring and enrichment, for example. There are many interesting differences among these projects, however.

T.W. Tibbitts' project in Wisconsin is carried out largely in the Biotron, where a great variety of conditions and a large support staff are available. The work is done in fairly large controlled-environment rooms. Tibbitts and his postdoctoral co-worker, R. Wheeler (Kennedy Space Center) have spent much time on the problem of tuberization, which, in most cultivars of potato, is encouraged by short days and/or cool temperatures. Tibbitts and Wheeler find, however, that some cultivars tuberize well under continuous light and temperatures of 20°C or below if the irradiance level is high enough. They have not been able to obtain good tuber formation in a purely hydroponic system, but they have developed various media that work well with nutrient solutions. As will become evident, they have been highly successful.

C. Mitchell with his graduate student, S. Knight (and now D. Bubenheim [NASA Ames Research Center, Moffett Field, Calif.], who has just finished his doctoral work with us), have used lettuce as a model plant for production studies. Some of these studies have been carried out in individual units called minitrons, each of which accommodates a small plant canopy (beginning with 36 plants, harvesting six plants at a time up to 19 days). The minitrons are placed in medium-sized, walk-in growth chambers normally illuminated with a combination of high-pressure sodium and metal-halide lamps (Sunbrella units from Environmental Growth Chambers), although the minitrons are usually placed under a water filter with HPS or flood lamps. Mitchell uses a nutrient film technique.

D. Raper and a postdoctoral associate L. Tolley-Henry, at North Carolina State Univ., have devoted much attention to a mathematical model that will describe and predict the growth of a single soybean plant growing in a canopy. They use large walk-in growth chambers illuminated with a combination of fluorescent and incandescent lamps. They use a rapid flowing hydroponic culture system with automatic pH control and frequent monitoring of solution with automated ion chromatography. Solutions are replenished continuously and completely changed every other day; nutrient levels never vary more than 10%. Temperature of the nutrient is controlled within $\pm 0.25^\circ\text{C}$. They have studied nutrient temperatures from 14° to 32°.

Recently, under a different arm of NASA (The Minority Support Program), a study on sweet potatoes has been initiated at the Tuskegee Institute in Alabama. It is to be coordinated with the rest of the NASA CELSS program through W. Knott at the Kennedy Space Center, where the "Breadboard Project", described by J. Bredt, is being initiated. The four projects that are compared in this paper are administered by R. MacElroy at the NASA Ames Research Center, where some plant productivity work has also been done: S. Schwartzkopf has developed a computer-driven glass chamber that accommodates a single plant. Since it does not involve canopies, it is difficult to compare his results with ours. J. Rumel has examined human-bacterial interactions with the plant in Schwartzkopf's chamber and has done some modeling of a functioning CELSS, an activity also carried out by others at various locations.

M. Andre in France has also been studying wheat productivity with the goal of using the plant in a CELSS (1). He continuously monitors gas exchange (photosynthesis and respiration), transpira-

tion, and consumption of nitrogen, phosphorus, and potassium. He and his co-workers have also studied the effects of CO₂ enrichment.

The Japanese are very active in CELSS research (9). They are investigating several gas-recycling systems, the rationale being that gases will have to be purified and stored to control the supply to plants, algae, animals, and humans. Based on the same rationale, they are studying several alternative systems of water recycling and waste disposal. The Japanese have long been interested in algal culture, and some of this work is now being applied to CELSS projects. There is also at least one project on plant production: "...periodical lighting effects on the photosynthesis of plants such as rice plant, mung bean, komatsuna, lettuce, and pimento for obtaining enough data of the gas exchange, the growth rate, and the harvest index. ..." (9). Finally, they are working on a bio-reactor that would use various enzymes to bypass a plant and produce food directly from CO₂.

The "breadboard project" at the Kennedy Space Center has been discussed in this symposium by J. Bredt. It is not a research project but is intended to apply results from crops grown on other NASA-supported projects (at present, wheat) to investigate problems of scaling up the techniques developed in small chambers as well as problems in recycling water and atmospheric gases. As noted by Bredt, the project will eventually also examine food preparation, waste disposal, and regeneration of plant nutrients.

A quarter of a century ago, a CELSS project was initiated in Krasnoyarsk, Siberia. It is called Bios, and its director is I. Gitzelzon. The first bios "space ship", about 20 years ago, enclosed 12 m³. A popular article in Soviet Life (7) provides an excellent summary of the Bios 3 project, which is far-advanced compared with our own work. On 11 Nov. 1983, N. Bugreyev and S. Alexeyev were sealed into the Bios 3 space ship, where they remained for 5 months. They entered with only 20% of the food they would need; all the rest was produced under artificial light (xenon lamps) in an area of 60 m² and a total volume of 315 m³. Air and water were regenerated inside the sealed chamber; only electricity and TV programs were supplied from outside. The two men were under complete medical supervision. The article says that wheat, chufa (a species of sedge bearing edible tubers), peas, dill, kohlrabi, and "many other" plants were grown hydroponically and that there were difficulties with potatoes and tomatoes. The photographs illustrating the article also show turnips, leeks, table beets, cucumbers, and perhaps other plants.

The wheat was only 30 cm tall (an ultra-dwarf) and was bred for Bios. It matured in about 60 days (six crops per year), yielding the equivalent of 80 t·ha⁻¹·year⁻¹ (21.9 g·m⁻²·day⁻¹). It is further stated that "many of our methods of accelerated vegetable cultivation have already been successfully introduced in greenhouses in Norilsk, Yakutsk, and other cities in the Far North."

Excessive oxygen was removed by burning nonedible biomass in a catalytic furnace. When the catalysts went bad, oxides of nitrogen began to build up, but this was noticed because the plants reacted adversely. The catalysts were replaced, and then the air felt "fresher like in the summer in a field after a rain". Lacquers or paints were not used because of toxicity. Earlier versions of Bios space ships used the alga *Chorella* for air purification, but they found it "difficult to cook" and gave it up. Work schedules of the two occupants were out of phase with each other by 12 hr, so only a few hours were spent together each day.

Much was learned in the 5-month experiment, as in previous experiments, and about 20 designs and technologies used in Bios rank as inventions. But the main objective of the experiment was confirmed: "A lengthy stay in space is possible only when all of the biological processes found on Earth are maintained for the entire period." Clearly, we have much to do before we can accumulate the experience of the Soviets.

SOME COMPARITIVE RESULTS WITH FOUR SPECIES

Tibbitts, Mitchell, and Raper have supplied summary information on environmental conditions for representative experiments (Table 5), the recipes of the nutrient solutions that were supplied (Table 6), and harvest data and other results from these experiments (Table 7). As these data were consolidated into the tables, the following observations came to mind: a) The different species require quite different growing

techniques; b) There is a vast number of combinations and permutations of environmental conditions and treatments that can be used to maximize yields; c) The idiosyncrasies of the different investigators and often the equipment that they had available are often highly evident; d) In spite of these differences, yields are in fair agreement with each other and closely approximate the figures arrived at by the calculations near the beginning of this paper.

By emphasizing the diversity, a negative connotation to the variability expressed in the tables is not intended. On the contrary, because there is such a vast range of possibilities, it is important that each investigator sense a great deal of freedom in carrying out his or her project. Creativity must be encouraged in any way possible. Indeed, it would be desirable if many more research teams were investigating these problems.

Study of the tables is revealing. For example, relatively high light levels were used by all investigators, but wheat, with its vertical leaves, is probably best-suited for high irradiance. Soybeans, being short-day plants, were given significantly fewer hours of light each day than the other species. Total light energy provided was highest for wheat and established lettuce plants. Growing temperatures vary from a low of 16°C for potatoes to a high of 30°/26° for soybeans. All but one study with potato plants used enriched CO₂. So far, no attempt has been made to control oxygen and nitrogen, although it is worth noting that the partial pressures of these gases in Logan, Utah, at 1500 m elevation, is 85% of that at sea level, close to the elevation where the other studies were performed.

It is not surprising that there is a considerable difference in plant spacing and plant density. This difference comes about mostly because of the nature of each species, but there is much room for future research on plant density. Potato plants develop into vines when grown in a dense canopy, so in one study individual plants were grown in cages with side lighting.

All have noted that different cultivars of the same species can react quite differently. Wheat yields, for example, can vary as much as three- or four-fold among different cultivars in a single study, and the Wisconsin workers have potato cultivars that grow normally under continuous irradiance and other cultivars that are chlorotic and very stunted under these conditions. The cultivars used in these experiments were chosen because of high yields in previous experiments.

There is considerable variety in the nutrient solutions used in the different studies. Lettuce was given a double ration of nitrogen during the maximum growth phase. Indeed, several elements were especially high in the solutions used for lettuce. Our studies with wheat suggest a high initial requirement for Ca and Mg. We also use considerably more chloride, Fe, and B than the other investigators. There are results suggesting that silicon promotes growth and yield and retards lodging of wheat. Wheat and other plants may also benefit from trace amounts of Na.

The different species require quite different times to mature the crop: from 19 days for lettuce to 147 days for caged potatoes. Thus, the dry biomass harvested, both edible and total, varies considerably. The harvest index was highest for potatoes and lettuce and quite respectable for wheat and soybeans. The linear growth rate expressed as g·m⁻²·day⁻¹ and counting all days from planting to harvest was quite high for wheat and potatoes. Potatoes are especially high when the linear growth rate is based only on edible biomass. Three of the four investigators calculated a linear growth rate on the assumption that several days during germination might use facilities less sophisticated and demanding of energy and space than the growth chambers where the plants mature. Correcting for these assumptions, linear (average) growth rates of edible biomass reach 26.1 g·m⁻²·day⁻¹ for wheat, 35.5 for potatoes, and 60.4 for lettuce. Most of the growth period of lettuce was during the logarithmic phase of growth. The study with wheat, one study with potatoes, and one with soybeans allowed similar calculations and provided the rather spectacular values of 99, 81.4, and 43.6 g·m⁻²·day⁻¹, respectively, for total dry biomass production during logarithmic growth. Our measurements of net assimilation in dense wheat canopies undergoing maximum growth have given yields of 125 g·m⁻²·day⁻¹.

Edible protein, oil, and carbohydrates will be carefully monitored when these crops are used in a CELSS. We were surprised to note high protein in our hydroponically grown wheat (18% with normal values being between 12% and 14%). Note that soybeans would be

an excellent oil crop in a CELSS.

SOME OTHER SPECIES THAT SHOULD BE STUDIED AS CANDIDATES FOR A CELSS

It is imperative that the NASA CELSS program begin to support work with other species besides the four that have so far been emphasized. The study of sweet potatoes at the Tuskegee Institute is a step in the right direction. Cereals besides wheat could be studied. For example, maize is one of the most valuable crops, although its size could be a problem for a CELSS. There are many legumes that might be well-suited for a CELSS (e.g., peanuts and winged beans), and there are many oil crops besides soybeans and peanuts; some might be appropriate for a CELSS (e.g., rapeseed, sesame seed, and linseed). Numerous vegetables should be investigated, including various cabbage relatives, tomatoes, cucurbits (some melons, squashes, etc. are highly productive), onions (for flavor), carrots, etc. Table beets and sugar beets have edible leaves as well as roots. A few small fruits could be grown in a CELSS to provide vitamins and a variety of flavors: strawberries, raspberries, currants, and, perhaps, pineapples.

Exotic crops are often suggested, and some of these should be considered; for example, grain amaranth (*Amaranthus* spp.), oca (*Oxalis tuberosa*, a root crop with many varieties), arracacha (*Arracacia xanthorrhiza*, root crop with edible stalks), quinoa (*Chenopodium quinoa*, a crop with seeds high in protein that has a good amino acid balance), a so-called groundnut (*Apios americana*, formally an important tuber crop of the Amercian indians), and many others (12). It is time to proceed with the work.

Note added in proof: Since submitting this manuscript, we have successfully combined the factors discussed here to achieve grain yields of 60 g·m⁻²·d⁻¹ at the highest irradiation levels (2000 μmol·m⁻²·s⁻¹, 144 μmol·m⁻²·d⁻¹). This is over twice the highest yields reported in this paper. At high CO₂ levels and high irradiance, key factors appear to be high plant densities, optimized nutrients, and relatively low temperatures (20°C).

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