Approaching the photosynthetic limits of crop productivity

by Frank B. Salisbury, Ph.D.

An address by Frank B. Salisbury, Professor of Plant Physiology, Department of Plant Science, Utah State University at Logan, and member, NASA Life Sciences Advisory Committee, to the "Food for Peace" founding conference, Sept. 5, 1988, Chicago:

Just how much could a crop produce if all the environmental parameters were set at optimal levels so productivity was limited only by the plant's genetic potential? This question has interested plant physiologists, agriculturists, and ecologists almost from the time these sciences came into being. Although no one has tried to answer the complete question, agricultural productivity has increased tremendously during the past century as parts of the question were at least partially answered.

Almost a century and a half ago, Justus von Liebig propounded his "law of the minimum" or (as it was later called) "the law of limiting factors." This principle stated that plant growth was limited by the one factor that was presented to it in the most limiting amount. Thus, it might not help to add phosphorus fertilizer if there was not enough nitrogen fertilizer available in the soil. This principle led to incredible advances as crop physiologists looked for the limiting factors and then supplied them so they were no longer limiting. On a world basis, water is probably the most important limiting factor, but the level of carbon dioxide in the atmosphere also limits yield, and nitrogen fertilizers are limiting on a worldwide basis. Liebig's law had to be modified in several important ways (for example, it is common for more than one factor to be limiting), but its impact was immense.

To find out how much productivity could be achieved if all limiting factors were eliminated (by converting them to optimum levels) requires application of the most modern technologies of environmental control. Radiation (light), carbon dixoide (and other atmospheric gases), water, and mineral nutrients must all be carefully controlled. Such other factors as humidity, wind velocity, acidity, and aeration of the root medium, which often indirectly influence radiation, carbon dioxide, water, and mineral nutrients must also be controlled and set at optimum levels. Once this is done, the plant can grow in a *stress-free environment*. Plant physiologists define stress factors as those environmental parameters that in any way limit yield below genetic potential. Clearly, the technological challenges are complex, so complex that no one has attempted to consider all of them at once until recently.

The impetus for finally trying to develop stress-free environments for plant growth was the developing space program. After our initial manned forays into near-Earth orbit and even to the Moon, planners of space exploration began to speak of extended trips such as a manned voyage to Mars or exploration of the asteroids and of permanent human colonies on the Moon and even on Mars.

Such projects would almost certainly require production of food in the spacecraft or the lunar or Martian colonies. This would be expensive, since totally artificial environments for the growth of plants would have to be produced and maintained, but the expense of resupply from Earth might be even greater. In the early 1960s, NASA, as well as Soviet space scientists, initiated research programs to achieve maximum crop yields in controlled environments. The Soviets have continued their program to the present, but NASA dropped theirs until the late 1970s.

In 1981, four projects were funded to study questions of maximum yield. One of these, at the University of Wisconsin, uses potatoes as its crop; another at Purdue University studied lettuce (and now several other crops including oilseed crops); a project at North Carolina State University investigates soy beans; and we at Utah State University examine wheat. There are two or three other related or supporting projects, including a rather recent one on sweet potatoes at the Tuskegee Institute in Alabama. This discussion is based on some of our results with wheat, which proved to be ideally suited for this kind of work because the nearly vertical leaves of wheat plants are capable of highly efficient absorption of light and thus can achieve extremely high productivity.

How can we know when we are approaching the plant's genetic potential? The key to answering this question is the knowledge that the basic function of plants is to convert light energy to chemical bond energy in the process of photosynthesis, and the chemical bond energy (plant yield) can never exceed the light energy that is absorbed by the plant. Actually, it can never exceed some maximum conversion efficiency. Plant physiologists have been studying photosynthesis for many decades, and we now know enough to set some limits on the efficiency of the photosynthetic process. On this basis, it is possible to calculate the maximum possible crop productivity for a crop irradiated with some known amount of light. This calculated maximum productivity can be compared with the observed productivity to see how close the genetic potential has been approached.

Calculating maximum productivity

There are several ways to calculate theoretical maximum productivity. Here is one approach: In photosynthesis, light energy is absorbed as individual packets called *photons* or *quanta*. The unit of measurement for these photons is the *mole,* which is a specific number of photons or other atomic or molecular particles. (The number, called Avogadro's number, in a gram molecular weight of the substance is very large: 6×10^{23} particles per mole.) The energy in a mole of photons of white light, which is effective in photosynthesis, is approximately 217 kilojoules per mole (kJ/mol), depending on the exact spectral composition of the light.

The chemical bond energies in protein, carbohydrate, and fat vary, but we have used an average value for carbohydrates of approximately 510 kJ/mol. Research on photosynthesis suggests that it takes about 12 moles of photons to produce one mole of carbohydrate, so we can calculate an efficiency of 19.6%, which says that if photosynthesis were functioning at an optimum efficiency, about 19.6% of the absorbed light energy could be converted to the chemical-bond energy of carbohydrate.

But there is more to consider. To begin with, some of the light energy will be reflected or transmitted by the leaves and thus not used in photosynthesis. In our system, 98% of the light energy is absorbed, so this reduces the maximum efficiency only to 19.2%. A more important consideration is the fact that the plant is not only making carbohydrate and other compounds in the process of photosynthesis; it is also using them up in the process of respiration, a process that is essential to maintain the plant and keep it functioning. Exactly how much is used up in respiration will depend upon several factors such as temperature, but a good average number is 20-30%. Taking the most optimistic value of 20%, we reduce the maximum possible efficiency of the plant to about 15.4%. So, considering real plants that are respiring as well as photosynthesizing, about the best we can ever hope to achieve is about 15% of the light energy converted to the chemical-bond energy of food.

Actual efficiencies have been measured in the field by many workers. Typically, the efficiencies are less than 1%, but world records for crops that photosynthesize by the C_3 pathway (wheat, rice, legumes, virtually all fruits and vegetables, etc.) have reached 7.4% for the short period of maximum growth, but only about 2% for the entire life cycle. A few plants photosynthesize by the C_4 pathway (maize, sorghum, sugar cane, other tropical grasses, and so on), which is somewhat more efficient when carbon dioxide levels are as low as they are in the Earth's atmosphere and when water is limiting. These have reached 10.2% for the maximum growth phase and 3.7% for the entire life cycle. It is reasonable to imagine that factors other than light are responsible for the differences between the observed efficiencies and the calculated ones.

TABLE 1

Some summary figures on wheat yields as a function of light levels

Light levels (photosynthetic photon flux) (in moles/meter²/day)	32	86	144
Potential yield based on 15.4% efficiency (grams/meter²/day)	60	162	272
Life-cycle yield (grams/meter²/day)	43	95	137
Yield efficiency	11%	9%	7.8%
Short-term yield (grams/meter²/day)			150
Yield efficiency			13.4%

Original data in Bruce G. Bugbee and Frank B. Salisbury, 1988, "Exploring the Limits of Crop Productivity: I. Photosynthetic Efficiency of Wheat in High Irradiance Environments," *Plant Physiology*, in press.

TABLE 2

Dependence of space-farm size on irradiance

Irradiance (mol/meter²/day)	Grain (grams/meter²/day)	Farm size (meter²/person)	Power (kW/person)
32	18	43	10.3
86	41	19	11.4
144	60	13	15.6

The wheat experiments

To see if we could do better than has been done in the field, we have purchased and modified three plant growth chambers in which it is possible to produce light levels equal to sunlight at noon on June 21 and to control such other factors as carbon dioxide, water, and mineral nutrients. The nutrients are provided in solution in a hydroponic system. The solution circulates rapidly around the roots so that it always contains ample oxygen, and its exact composition is the best that we know how to concoct (although it is reasonable to think that we can improve it with further research). We have other facilities that we use in these studies, including a greenhouse bay that provides environmental control almost as good as that produced in our growth chambers.

High-pressure sodium and metal halide lamps provide the key to controlled-environment studies such as ours by making it possible to produce high light levels. (These lamps are commonly used for street lighting.) Until these came into use a few years ago, growth chambers could only produce about a fourth of solar light levels.

In one of our most successful experiments, plants were grown at a temperature of 20°C day/15°C night with 20 hours of light per day, providing, at the highest light level, about two and one half times as many photons per day as could be achieved with natural sunlight anywhere on Earth. Carbon dioxide was elevated to 1,200 micromoles per mole of air, which is three to four times the carbon dioxide levels in the Earth's atmosphere during the past century. (In earlier studies, we had determined this to be an optimum carbon dioxide level.)

Water and mineral nutrients were provided as noted above, and humidity and air velocity were also controlled. We used the wheat cultivar Yecora rojo, which had performed the best in many previous trials; different wheat cultivars respond quite differently in our optimized conditions. We planted 2,000 wheat plants per square meter, which is 5-10 times as many plants per square meter as are normally planted in the field. We have gone as high as 6,000 plants per square meter in some experiments! We used six different light levels, two in each of three chambers.

We found that total biomass (roots, stems, leaves, and wheat grains) increased with increasing light levels all the way up to the highest light level that we used; there was no sign of leveling off at the highest light level. The efficiency of conversion of light energy to chemical bond energy was highest at the lowest light level; about 11%, which is higher than anything ever observed in the field and not very far below the calculated maximum efficiency discussed above. At the highest light level, efficiency dropped to about 7%.

The harvest index

From the standpoint of food production, the *harvest index* is extremely important. This is the percentage of total biomass that can be used as food. Harvest index increased in our study from about 40% at the lowest light level to about 45% at the highest light level. The calculated efficiencies are based on the entire life cycle, and thus will necessarily be lower than the potential efficiency, because it takes time to develop the canopy before light is absorbed efficiently. Based on photosynthesis measurements that we made during the period of maximum growth after the canopy had developed, we achieved efficiencies of 13.4%, which is getting amazingly close to the calculated maximum efficiency of 15%.

Say that a person requires 11,700 kJ of food energy per day (2,800 kilocalories). One hundred grams of oven dry wheat (or equivalent food) contains about 1,500 kJ of food energy. Thus 780 grams of oven dry wheat or equivalent would be required each day for each person. If this food is produced in a space farm with the maximum light level used in our experiment (60 grams per square meter per day of edible wheat), only 13 square meters would be required to produce food continuously for one individual. That is an area about the size of my office (a little over 3 by 4 meters, or 10 by 14 feet). Such a farm, producing a crop in 79 days at which time another crop would immediately be planted, would grow enough wheat to provide the necessary 780 grams per day.

One of the growing chambers for the experiment described by Salisbury. His co-researcher, Dr. Bruce Bugbee, here lifts up the rock wool base of the plant-support system to show the dense root system of the 18-day-old plants. The inside walls of the chamber have mirror surfaces to maximize reflection of light, and at left is the reflection in the open door of the growing chamber.

I for one would hate to be dependent for my life's food on a farm that size that had to produce at maximum efficiency with no foul-ups! Thus, a lunar farm will probably be quite a bit larger to provide a margin of safety and to allow the use of lower light levels, not to mention the growth of several crops besides wheat, many of which will not be as efficient as wheat. Table 2 shows some figures for productivities at different light levels based upon our experiment. At the lowest light level, 43 square meters would be required to feed a single person. Assume an intermediate light level at which 20 meters per person would be sufficient, and consider a farm about the size of an American football field (5,000 square meters). Such a farm could provide food for about 250 people. A farm that size, operating at the average present efficiency for all the world's crops could support only one or two people, to give some idea of the difference between everyday Earth farming and an ultimate, controlled agriculture in a lunar colony.

These studies have provided at least partial answers to the original questions, and most important for NASA, they have shown that space farming is an achievable and worthy goal. Do they contribute anything to Earth-based agriculture? So far, we haven't given much thought to such contributions, but we have every reason to believe that consideration of our experimental results and their implications should indeed contribute to the solution of some of the problems discussed at this conference.