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# The Limits of Crop Productivity

*Validating theoretical estimates and determining the factors that limit crop yields in optimal environments*

Bruce Bugbee and Oscar Monje

Plant scientists have sought to maximize the yield of food crops since the beginning of agriculture. There are numerous reports of record food and biomass yields (per unit area) in all major crop plants, but many of the record yield reports are in error because they exceed the maximal theoretical rates of the component processes. In this article, we review the component processes that govern yield limits and describe how each process can be individually measured. This procedure has helped us validate theoretical estimates and determine what factors limit yields in optimal environments.

Productivity studies are expensive to conduct and are subject to measurement error. In field studies, side lighting of small experimental plots or sampling error from multiple destructive harvests has frequently resulted in unrealistically high estimates of biomass productivity (Gifford 1974, Loomis and Gerakis 1975, Monteith 1978).

In controlled, hydroponic environments, it is possible to double record yields from reliable field studies by diminishing the limitations of temperature, CO<sub>2</sub>, water, and nutrients. Under these conditions, growth is limited by the incoming radiation. For

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## **Biomass allocation to edible products is the yield component with the greatest potential for improvement**

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example, increasing daily inputs of photosynthetic radiation to four times summer sunlight in the field increased biomass productivity of wheat to four times that achieved in the field (130 versus 30 g m<sup>-2</sup> d<sup>-1</sup> of biomass; Bugbee and Salisbury 1988). These findings encouraged us to examine the theoretical limits of crop productivity.

We have considered experimental results in the context of models based on well-characterized, component biological processes. Many models have been developed to analyze productivity in the field. Because it is difficult to predict a plant's biological response to stress conditions (Loomis and Williams 1963), we focus on crop response in near-optimal controlled environments.

## **Component processes and energy efficiency**

The model we have used separates yield into five component parts: incident photosynthetic radiation, radiation absorption, carbon fixation in photosynthesis, carbon utilization in respiration, and biomass allocation to

edible products. Separating yield into these processes has several advantages: theoretically maximal rates are characterized for each process; maximal rates have been measured in vitro and in individual plant organs; each of the processes can be measured on plant communities in sealed environments; and the efficiency of the system is determined by successive multiplication of the efficiency of each process.

The model makes it possible to relate theoretically maximal rates of processes to measured crop productivity. Variations of this model have been used to calculate potential productivity in the field; however, verification is difficult because daily carbon fluxes must be measured accurately (Charles-Edwards 1982, Loomis and Williams 1963, Monteith 1972).

The photosynthetic photon flux (PPF; moles of photons—400 to 700 nm—per unit area per unit time) is the primary input to all plant production systems. All other environmental factors (e.g., temperature, water, and nutrients) influence growth and yield by altering the efficiency of PPF utilization. Water stress, for example, decreases leaf expansion, which decreases radiation absorption. Other environmental factors (e.g., light quality) can reduce PPF use efficiency by affecting biomass allocation to edible products (yield).

## **Absorption of photosynthetic radiation by green tissue**

Photosynthesis can occur only when photons are absorbed by green leaves.

Many studies indicate that percent PPF absorption is the parameter most highly correlated with final yield (Gifford et al. 1984, Hay and Walker 1989, Shibles and Weber 1965).

Absorbed PPF is measured by subtracting reflected and transmitted PPF from incoming PPF (Gallo and Daughtry 1986, Hall and Kanemasu 1990). PPF is not uniform over a horizontal area in a growth chamber, and several measurements must be taken to accurately determine the average PPF level. Transmitted PPF also varies and must be averaged over a large area. It is much easier to determine PPF absorption in a growth chamber than in the field, however, because the sun is constantly changing position in the field.

A single leaf typically transmits approximately 4% of the incident PPF, reflects an additional 6%, and absorbs 90% of the PPF (Nobel 1991). Multiple layers of leaves in a fully developed canopy reduce PPF transmission to approximately 0.2% in an optimal environment, and vertical leaves (typical of grasses) reflect less PPF than do horizontal leaves. We typically measure less than 2% reflected PPF from healthy wheat canopies, for an absorption of 98%. To optimize yields, the challenge is to reach quickly and maintain this level of absorption until harvest.

Although absorption is 98% at full canopy development, an average PPF absorption over the wheat life cycle is 90% (Figure 1). Due to high planting densities, which are an important component of high yields in favorable environments, PPF absorption can exceed 90% a few days after emergence. PPF absorption is reduced by leaf senescence during the last part of the life cycle.

### Carbon-fixation efficiency in photosynthesis

In calculations of carbon-fixation efficiency, net gains of photosynthetically fixed carbon are usually combined with respiratory losses of carbon; the sum of the two processes can be estimated by measurements of plant dry mass. Net photosynthesis and respiration can be separated by measuring carbon fluxes in sealed, controlled environments.

The procedures for measurement of

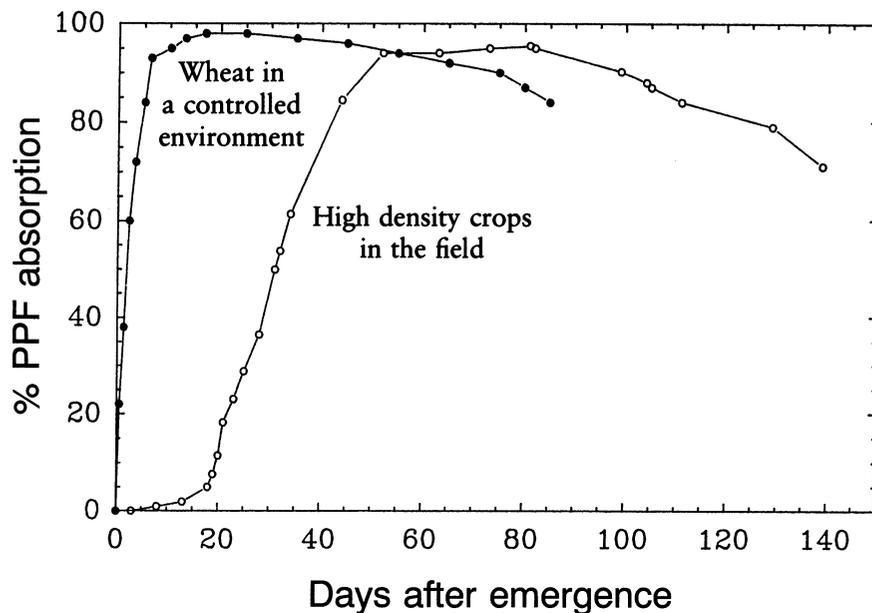


Figure 1. A comparison of percent absorption of the photosynthetic photon flux (PPF) by a high-density wheat canopy in a controlled environment and field data from maize (Gallo and Daughtry 1986). The maize data are typical of high-density crops in the field, including wheat. Average PPF absorption over the life cycle was 90% for the controlled-environment wheat canopy and approximately 50% for the maize field crop. Thus, a primary reason for increased yields in controlled environments is the increased absorption of light. During senescence, absorption decreases in both environments.

CO<sub>2</sub> fluxes (i.e., gas exchange) have been well developed for small chambers with single leaves (Field et al. 1989) or whole plants (McCree 1986), and we adapted these procedures to measure communities of plants in growth chambers. In a sealed growth chamber containing a community of wheat plants, we determined net photosynthesis from the disappearance of CO<sub>2</sub> and respiration from the efflux of CO<sub>2</sub> from the plants. Measurement of CO<sub>2</sub> fluxes required the simultaneous, rigorous measurement of CO<sub>2</sub> and H<sub>2</sub>O vapor, mass flow of air, temperature, pressure, and PPF (Bugbee in press).

Photosynthesis, photorespiration, and dark respiration occur simultaneously in the light and are not easily separated (Azcon-Bieto and Osmond 1983, McCree 1986). In our calculation, we combined photosynthesis and photorespiration, which reduces photosynthetic efficiency (defined as moles of carbon fixed per mole of photons absorbed). We calculated carbon fixed and photons absorbed per unit ground area and averaged over the duration of the light period (canopy quantum yield). In our calculation of daily gross photosynthesis,

we assumed that the rate of dark respiration in the light is the same as it is in the dark (Azcon-Bieto and Osmond 1983, McCree 1986), although the many studies of respiration have been unable to demonstrate conclusively whether they are equivalent (Johnson 1987, Lambers 1985).

The theoretically maximal photosynthetic efficiency can be calculated from plants' underlying biochemistry. One photon is required to excite one electron (Stark-Einstein law), four electrons are required to split each water molecule (both photosystems must be excited), and two molecules of water are required to reduce each molecule of CO<sub>2</sub>; thus, a minimum of eight photons is necessary to fix CO<sub>2</sub> into a simple carbohydrate (CH<sub>2</sub>O; Nobel 1991).

Photons of red light (exactly 700 nm) have the lowest possible energy to excite electrons in photosynthesis, but, because of the Emerson enhancement effect (cooperation of the two photosystems), it is more appropriate to assume that photons have an average wavelength of 680 nm. At 680 nm, photons contain 176 kJ mol<sup>-1</sup> (from  $E = hc/\lambda$ ), so eight moles of photons contain 1408 kJ. The energy

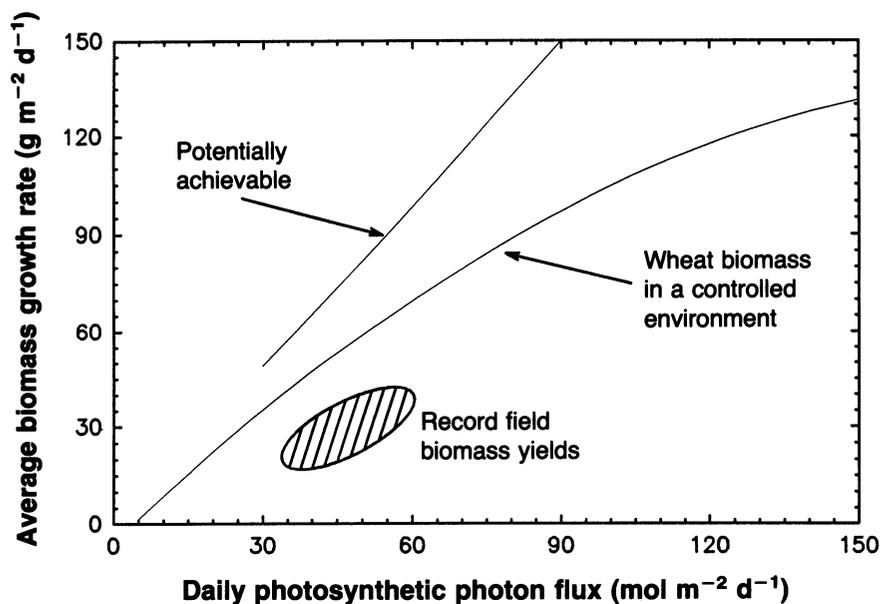


Figure 2. A comparison of potentially achievable yield, yield in a near-optimal controlled environment, and the range of record yields in the field for all major crop plants (shaded area). All data are for total dry biomass. The potentially achievable yield was calculated by assuming that photosynthetic photon flux (PPF) is the only limiting factor. The controlled-environment wheat yield is from Bugbee and Salisbury (1988). Maximal field yields are from studies in the literature. Summer PPF in the field is 30 to 60 mol m<sup>-2</sup> d<sup>-1</sup>.

in a mole of carbon in sucrose, a simple carbohydrate, is 479 kJ mol<sup>-1</sup>. Thus, the theoretical maximum energy efficiency of photosynthesis is 34% (479/1408).

The number of moles of CO<sub>2</sub> fixed, or O<sub>2</sub> evolved, per mole of photons absorbed is known as the quantum yield. Because eight photons are required to fix each molecule of CO<sub>2</sub>, the theoretical maximum quantum yield is 1/8, or 0.125. Björkman and Demmig (1987) measured a variety of vascular plants in the laboratory and found an average quantum yield of 0.111 for O<sub>2</sub> evolution, which is close to the theoretical maximum. This result suggests that the light reactions of photosynthesis, which are measured as O<sub>2</sub> evolution, can operate at near theoretical efficiency. Not all of the energy trapped by the light reactions is used to fix CO<sub>2</sub> into carbohydrate, however, and the highest quantum yield for CO<sub>2</sub> fixation measured in a single leaf (at a PPF level below 200 μmol m<sup>-2</sup> s<sup>-1</sup>) is 0.09 moles of photons per mole of CO<sub>2</sub> fixed (Ehleringer and Björkman 1977, Ehleringer and Pearcy 1983, Long and Drake 1991, Osborne and Garrett 1983).

Photosynthetic photons from sun-

light have an average wavelength of 550 nm (McCartney 1978) and thus contain 217 kJ mol<sup>-1</sup> of photons. Because the average wavelength of fluorescent and metal halide lamps (and the energy content of photosynthetic photons) is similar to that of sunlight (Campbell et al. 1975), a more realistic calculation for the energy conversion efficiency of photosynthesis is 19.9% (470/217 kJ per photon times a quantum yield of 0.09). Because maximal photosynthetic efficiency occurs only at PPF levels below 200 μmol m<sup>-2</sup> s<sup>-1</sup>, the challenge is to obtain high photosynthetic efficiency in a plant canopy at high PPF levels.

### Carbon use efficiency in respiration

Plants consist of more than simple carbohydrates; additional energy is required to synthesize structural carbohydrates, proteins, and lipids. This energy comes from respiration. Much progress has been made in coupling models of respiration with other physiological processes (Amthor 1991). Respiration efficiency has not been as well studied in plants as in microorganisms and animals; thus, a

large theoretical and empirical foundation can be applied to studies of plant respiration. Carbon-use efficiency is defined here as the net carbon gain per day divided by the total carbon fixed per day in photosynthesis (daily net photosynthesis divided by gross photosynthesis).

It is useful to divide respiration into growth (biosynthesis) and maintenance components (Amthor 1991, Hay and Walker 1989, Lambers et al. 1983). The theoretically minimal amount of nonstructural carbohydrate (sucrose or glucose) required to synthesize structural carbohydrates, proteins, and lipids in higher plants has been analyzed. Structural carbohydrates (cellulose and hemicellulose) can be made from hexose sugars with approximately 86% recovery of mass; amino acids can be synthesized with 70% recovery of mass (from ammonia); and lipids with 36% mass recovery (DeWit et al. 1978, Penning de Vries et al. 1974).

It is more appropriate to analyze respiration efficiency, however, on an energy basis. McDermitt and Loomis (1981) found that energy recovery in the products of respiration was high and nearly constant over a broad range of plant materials. Specifically, energy recovery in biosynthesis was 91% for cellulose and hemicellulose, 88% for lignin, 89% for lipids, and 83% for proteins. The energy recovery in seed formation was also remarkably constant at 88.4 ± 1% over a wide range of seed types, including high lipid (rape seed), high protein (soybean), and high carbohydrate (wheat).

Other workers have confirmed and extended these findings. Energy recovery in some types of plant tissue can be as high as 95% (Lafitte and Loomis 1988, Williams et al. 1987). If the costs of growth-related processes, such as substrate transport, are included, the efficiency factor is reduced only by approximately 2% (Williams et al. 1987). The energy efficiency of respiratory biosynthesis (growth respiration) is thus close to 90%, excluding the energy used in maintenance respiration.

Additional energy derived from respiration is required for plant maintenance to support essential functions such as resynthesis of substances that undergo renewal, maintenance of ion

gradients and metabolites, and for physiological adaptation to a changing environment (Amthor 1984, Lambers 1985). It is more difficult to estimate the energy required for maintenance respiration because more information is needed about turnover and replacement of compounds. However, Penning de Vries (1975) calculated that maintenance requires 1.5 to 2.5% of plant dry mass per day; these values are close to measured values (Amthor 1989).

PPF absorption and photosynthetic efficiency of higher plants can equal that of dense algal cultures, but the increased structural complexity of higher plants (nonphotosynthetic stems and roots) increases their maintenance requirements (Geider and Osborne 1989). For this reason, it is likely that biomass productivity in higher plants will always be slightly less than algae. However, it is unlikely that algae can replace current crops because they do not partition biomass to highly edible products.

Maintenance requirements may be reduced in favorable environments because a rapid growth rate and short life cycle result in less standing biomass to maintain (Johnson 1987). The advantage of rapid growth rates may be offset, however, by the increased rate of protein turnover. A constant environment (e.g., temperature, light, wind, and water potential) might reduce protein and lipid turnover, because the plants do not need to adapt to changing conditions. Another factor is root respiration per unit mass, which is typically several times higher than in shoot tissue. However, in an optimal, flowing hydroponic system, the relative size of the root system is usually much smaller than in field-grown plants. A small, active root system may require less total carbon than the larger, but less active, root systems of plants in the field (Bugbee and Salisbury 1989).

Some models have assumed that maintenance respiration requirements were constant throughout the life cycle (McCree and Van Bavel 1977), but because stem tissue is less metabolically active and because seeds have a low maintenance requirement (Winzeler et al. 1976), maintenance requirements per unit mass typically decrease during plant ontogeny. Maintenance requirements can de-

crease to 0.5% of total biomass during grain fill (McCree 1983, Stahl and McCree 1988). Simulation models indicate that yield is sensitive to changes in the magnitude of the maintenance requirement (McCree 1988). Our calculations indicate that 80% of the energy in the initial products of photosynthesis can be recovered in plant tissue if maintenance requirements are reduced to 0.5% during grain fill.

The potentially achievable biomass energy conversion efficiency, within the constraints discussed above, is approximately 15.6% ( $0.98 \times 0.199 \times 0.8$ ). The biomass growth rate that would result from this efficiency is shown in Figure 2.

### Biomass allocation to edible products

Biomass allocation is measured as the harvest index, which is the ratio of dry mass of edible product divided by the total dry mass of plant tissue. Harvest index has been widely studied in crop plants and is responsible for most of the yield increases in the field during the past 50 years (Hay and Walker 1989).

Crop plants vary widely in their

harvest indexes. Potatoes and lettuce grown in an optimal environment often have harvest indexes of 80% (Knight and Mitchell 1988, Wheeler and Tibbitts 1987), but most crop plants have harvest indexes ranging from 35 to 50%. The harvest index of lettuce is high because only the stem base and roots are inedible. The harvest index of potatoes may be high because the structural carbohydrate in leaves and stems is respired and lost as  $\text{CO}_2$  before harvest. Therefore, harvest index increases even though edible biomass does not increase because total biomass decreases.

Genetically modifying crop plants for optimal, controlled environments might increase harvest index because less leaf area is necessary in high- $\text{CO}_2$ , high-light environments. Profuse vegetative growth (great height and large leaves) increases a plant's competitive ability; however, this competitive ability is neither necessary nor desirable in optimal environments because it decreases harvest index. For example, full-dwarf wheat cultivars (less than 40 cm tall) are less competitive with weeds than are semidwarf cultivars (80 cm tall), and the full-dwarf cultivars have lower yields in the field. Many full-dwarf

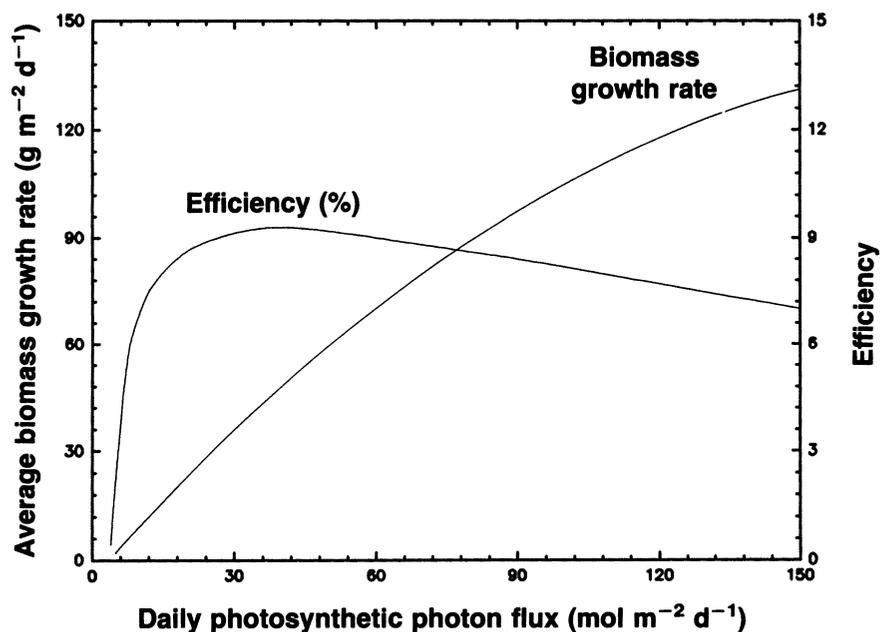


Figure 3. The tradeoff between energy conversion efficiency and yield in controlled environments. Percent efficiency is calculated as energy in dry biomass divided by the energy in the photosynthetic photons. The peak efficiency (9.4%) occurred at 30–40  $\text{mol m}^{-2} \text{d}^{-1}$ , and then efficiency slowly decreased. The biomass growth-rate data is taken from Figure 2.

cultivars outyield semidwarf cultivars in controlled environments, however, because their reduced stem mass increases harvest index.

Environmental manipulations might also increase biomass allocation to edible products in low harvest-index crops (less than 50% edible). For example, elevated temperatures during the vegetative growth of wheat decrease the duration and the size of vegetative plant parts; reduced temperatures during reproductive growth increase the duration and thus the size of edible, reproductive plant parts.

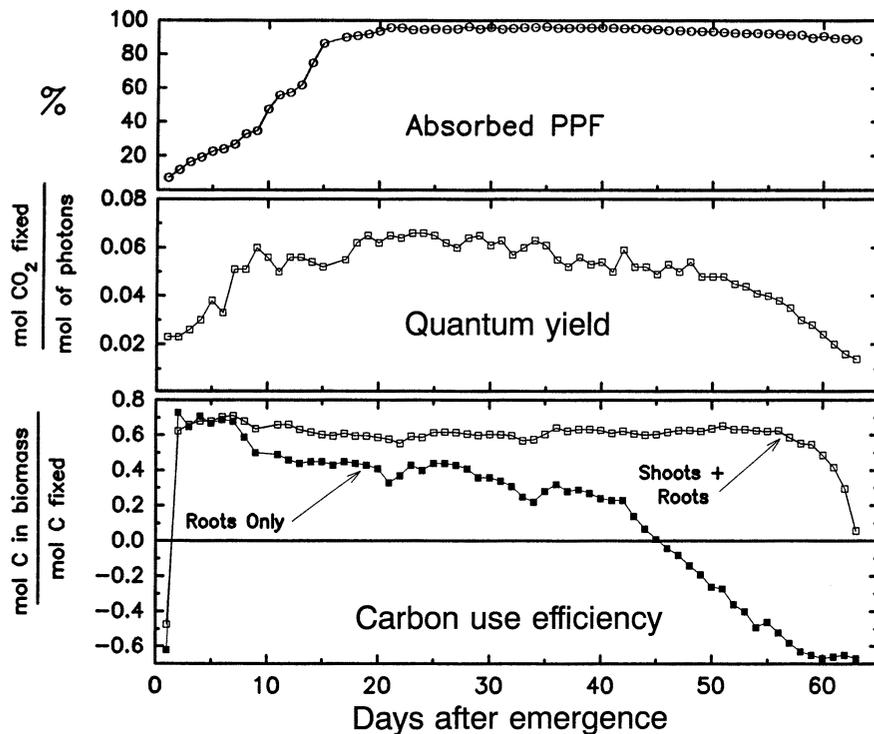
Vegetative growth stops after anthesis in wheat, and all photosynthates are translocated to the developing grain. A harvest index of 67% would be possible if the rate of carbon fixation was constant over the life cycle, vegetative growth occurred for 30 days, and grain fill occurred for the next 60 days. The harvest index

could be even higher if some of the stored carbon in leaves and stems was remobilized to grain before harvest.

We have found that seed size does not limit yield, provided that an adequate number of heads with fertilized embryos are present after anthesis. Average seed size can increase from approximately 30 mg to 80 mg per seed to accommodate extra photosynthate.<sup>1</sup>

Because little of the material in most plant leaves, stems, and roots is digestible, a harvest index of 100% would be possible only if cellulose, hemicellulose, and lignin could be processed and converted to digestible compounds. A harvest index of 80% might be achieved in several crop plants with appropriate genetic and environmental manipulations.

<sup>1</sup>B. Bugbee and O. Monje, 1992, unpublished results.



**Figure 4.** Daily measurements of the three determinants of biomass yield during the life cycle of a wheat canopy grown at saturating  $\text{CO}_2$  ( $1200 \mu\text{mol mol}^{-1}$ ) and high photosynthetic photon flux (PPF) ( $1400 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). The canopy quantum yield was low during the first 15 days, probably because individual leaves were PPF saturated. After canopy closure (percent absorption more than 95%), the canopy quantum yield increased. Carbon use efficiency was low during the first few days, because of seed respiration, and declined during the final days before harvest. Canopy carbon use efficiency of shoots and roots was surprisingly constant over most of the life cycle and did not change during the transition from vegetative growth (first 33 days) to grain fill (final 33 days). Root carbon-use efficiency became negative on day 45 because the root mass was decreasing.

## Currently achievable efficiency

Several years of research on genetic, cultural, and environmental parameters associated with optimal yield culminated in a series of controlled environment studies (called the Utah State University Wheat Project) that demonstrated high yield potential at harvest (Bugbee and Salisbury 1988). When the calculated energy in the harvested biomass (Leith 1968) was divided by the energy in the incident PPF, the energy recovery reached a maximum of 9.5% at a daily PPF of approximately  $30 \text{ mol m}^{-2} \text{ d}^{-1}$  and declined at higher PPF levels (Figure 3).

The average daily PPF in the field ranges from 35 to  $60 \text{ mol m}^{-2} \text{ d}^{-1}$  during the summer months in different geographical areas. Increasing PPF to approximately three times field PPF levels resulted in increased yields, but energy recovery in grain decreased to approximately 7% (Figure 3). The shape of the efficiency curve for edible biomass is nearly identical to that for total biomass because harvest index changes only slightly with daily PPF. We have since developed the instrumentation to enable us to measure separately the individual determinants of yield.

## Photosynthetic efficiency

Careful measurements with our canopy gas-exchange system at high  $\text{CO}_2$  levels indicated that canopy quantum yields can approach maximal values during the middle of the life cycle (Figure 4; quantum yield = 0.07). Photosynthetic energy-conversion efficiencies of more than 15% are thus possible in plant canopies at high PPF and  $\text{CO}_2$  levels. At lower PPF levels, the short-term photosynthetic efficiency increased to 17%. Leaf senescence during the final stages of the life cycle reduced photosynthetic efficiency and thus reduced the average efficiency over the life cycle to approximately 12% at high PPF and 14% at lower PPF levels.

## Respiration efficiency

We have not attempted to separate respiration requirements into growth and maintenance components because doing so would require long dark periods or low light levels, which quickly alter the canopy growth characteristics

(Lambers et al. 1983). It is relatively easy, however, to integrate growth and maintenance measurements. Integrated measurements indicate that respiration efficiency averages approximately 65% on a mass basis (Figure 4); this level is slightly higher than values measured in other crops in controlled environments (Stahl and McCree 1988). The respiratory energy efficiency (averaged over the life cycle) was approximately 75%, assuming a typical composition of 88% carbohydrate, 2% lipid, and 10% protein in total plant biomass of wheat at harvest.

Our highest efficiency for total biomass production was approximately 9.5% (Figure 3). We estimate that the components of this efficiency were 90% PPF absorption, 14% average photosynthetic efficiency, and 75% average respiratory energy efficiency ( $0.9 \times 0.14 \times 0.75 = 0.095$ ).

### Biomass allocation to edible grain

Our harvest indexes of 40–45% have not exceeded those measured in the field (Bugbee and Salisbury 1988). High CO<sub>2</sub> concentrations and a continuous supply of nitrogen in the root zone promote vegetative growth and may thus reduce the harvest index.

Wheat forms secondary branches or shoots, called tillers, when environmental conditions are favorable. High PPF and elevated CO<sub>2</sub> also cause excessive tillering. Late-forming tillers have a 10% lower harvest index (Figure 5). Eliminating late (tertiary) tillers may increase the mean harvest index to more than 50%. Experiments in field environments have genetically selected for reduced tillering, but lines that do not tiller in the field still form multiple tillers in controlled environments. Although genetic selection has not eliminated tillering, we have reduced tillering by altering the red/far-red radiation ratio (Barnes and Bugbee 1991). This ratio controls phytochrome equilibrium in plant tissue, which in turn regulates tillering. We are now preparing to examine the effect of reduced tillering on harvest index and yield.

### Continuous nondestructive measurement of growth rates

Different environmental factors can limit plant growth at different stages

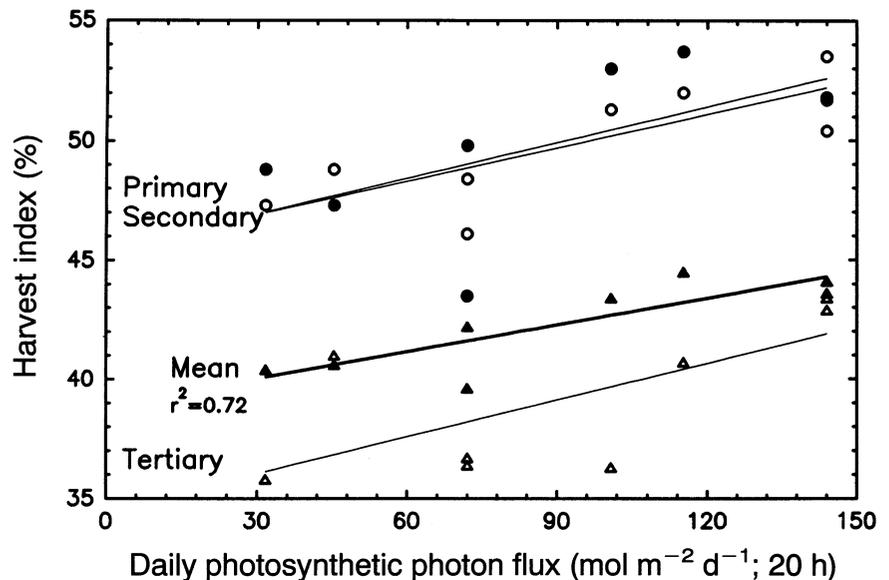


Figure 5. The effect of daily photosynthetic flux (PPF) on harvest index (ratio of edible to total biomass). Note that early forming tillers—primary (○) and secondary (●)—have a much higher harvest index than late-forming tillers—tertiary (△). The harvest index increased slightly with increasing PPF. The root dry mass is included with the total plant biomass in these data. Root mass is not typically included in harvest index calculations in the field, so these data are approximately 3% lower than field values. Tertiary tillers were still showing some green color at harvest. ▲, mean of all tillers.

of the life cycle. For example, mild water stress reduces leaf expansion and PPF absorption during early growth, but it has almost no effect on canopy photosynthesis after canopy closure.

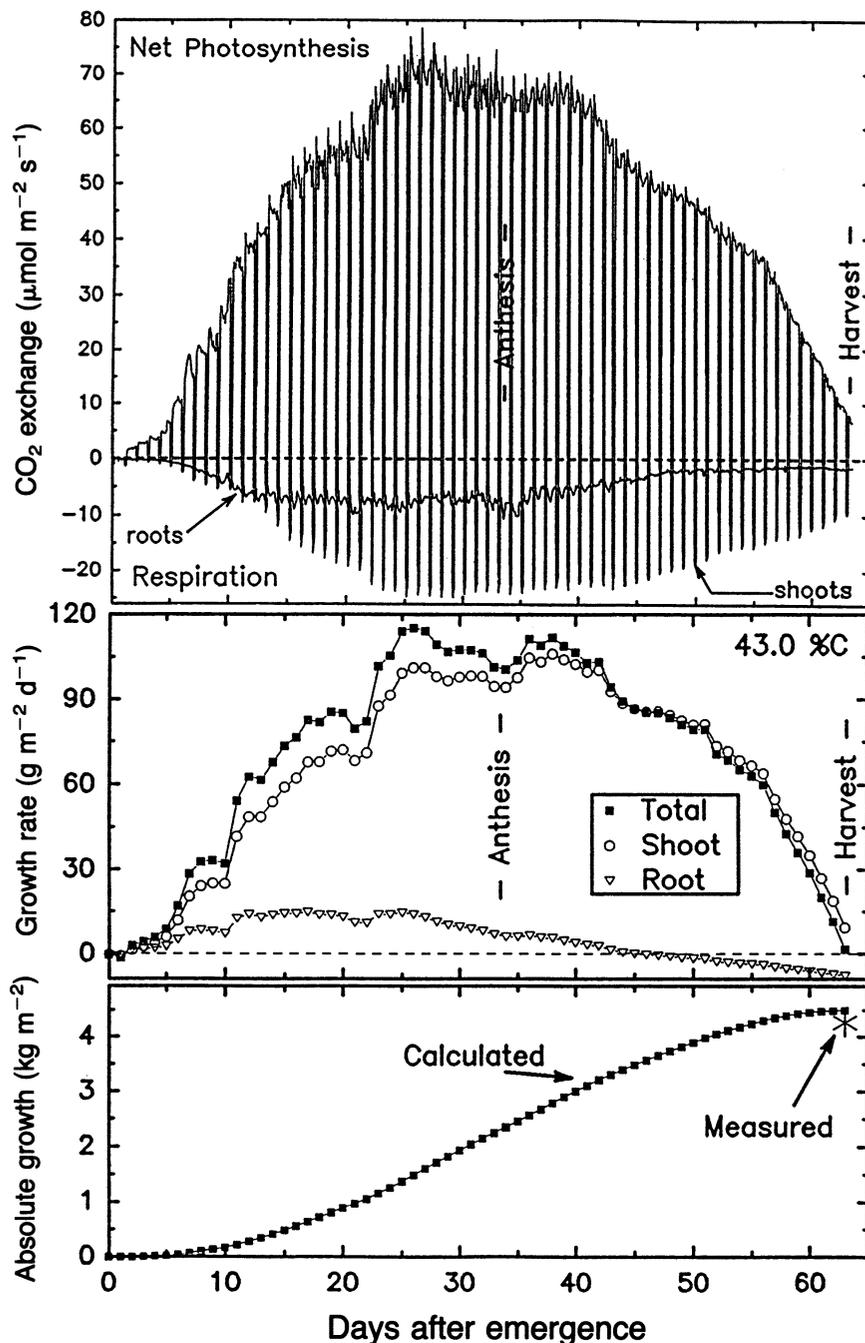
Plant growth curves are invaluable in assessing the effects of these limiting factors. Plant growth rates are typically estimated from a series of sequential, destructive harvests in which it is assumed that the harvested plant material is representative of the entire crop (Hunt 1982). Regression analysis is then used to fit the data and to estimate growth rates. This technique has often been applied in the field, where large areas of plant material can be harvested at consecutive time intervals. We have used sequential harvests and regression analysis in growth chambers, but the limited sample size often does not allow the harvested area to represent the entire crop, and it is difficult to develop representative growth curves.

Continuously monitoring and integrating CO<sub>2</sub> fluxes in growth chambers may provide a much better measure of canopy growth rates. This process is nondestructive, so it can be used to measure net CO<sub>2</sub> fixation in

the entire canopy each day. Plant dry mass at harvest can be derived if CO<sub>2</sub> fluxes are measured accurately and integrated over the entire growth period and if the percentage of carbon in the plant dry mass is accurately measured.

It is often difficult to measure CO<sub>2</sub> fluxes accurately. Carbon dioxide exchange is based on several measurements and requires sophisticated instruments that must be frequently calibrated (McCree 1986). Adsorption and desorption of CO<sub>2</sub> by materials used in the construction of growth chambers can also cause errors (Bloom et al. 1980). Carbon dioxide fluxes from the chamber itself must be well characterized before plant growth rates can be predicted. Correction must be made for water vapor fluxes (from transpiration) that interfere with the analysis of CO<sub>2</sub> fluxes (Bugbee in press).

Since Bate and Calvin (1971) first estimated plant dry mass from CO<sub>2</sub> fluxes, there have been enormous improvements in infrared gas analysis for CO<sub>2</sub>, and we have a much better understanding of the factors that affect the carbon/dry matter ratio in plant material (Ho 1976). When Dutton et al. (1988) reexamined the



**Figure 6.** Canopy net photosynthesis, shoot dark respiration, and root-zone respiration of a wheat crop from seedling emergence until harvest (top). The erratic rate of net photosynthesis during the light period each day was caused by fluctuating photosynthetic photon flux (PPF) levels due to fluctuating line voltage. During a four-hour dark period each day, photosynthesis abruptly stopped and allowed the measurement of shoot respiration. Root respiration was continuously measured and is superimposed on the shoot respiration. Total respiration (not shown on graph) is the sum of shoot and root respiration. Daily growth rate (middle) and absolute growth (bottom) were calculated from the measured  $\text{CO}_2$  fluxes. Short-term changes in growth rate were directly correlated with small, daily changes in PPF levels from the electric lamps. Measured dry mass at harvest (bottom) agreed within 5% of the dry mass calculated from gas-exchange data. The harvested dry mass contained 43.0% carbon. The data in this figure were calculated from the data in Figure 4.

estimated plant dry mass from  $\text{CO}_2$  fluxes for six growth chambers, the average error ranged from 1% to 7%. Part of the error was attribut-

able to failure to collect all of the dead and abscised plant parts no longer attached to the plant (i.e., plant dry mass was not accurately measured).

Reddy et al. (1989) reviewed the literature on the relationship between  $\text{CO}_2$  exchange and plant dry mass and confirmed the findings of Dutton et al. (1988). They stressed the importance of accurately measuring the percentage of carbon in biomass.

Previous growth estimates based on carbon flux data involved only short time intervals (hours to days). A comparison of plant dry matter and carbon exchange data at the end of each growth cycle determine the accuracy of measurement, as is shown in Figure 6. We measured 43.0% carbon in the harvested biomass, and the gas-exchange measurements of  $\text{CO}_2$  uptake were within 5% of the carbon in the harvested dry mass.

Carbon flux can be measured and averaged over short time intervals, for example five-minute intervals from plant emergence to harvest (Figure 6). These data were used to calculate the biomass growth curves. The erratic fluctuations in photosynthetic rate were due largely to changes in the output of the high-intensity discharge lamps as the line voltage changed. We are currently investigating ways to stabilize the light output.

Root-zone carbon efflux is usually combined with the carbon fluxes in the foliar environment, but separately measuring root respiration can provide new insights to crop productivity. For example, we can estimate the carbon-use efficiency of roots (Figure 4), estimate oxygen demand of the root system, and determine how closely root metabolic activity is coupled to shoot growth. Procedures for measuring root respiration are discussed in Bugbee (in press). The carbon-use efficiency of the roots became negative during the last 20 days of the life cycle because the total root biomass was decreasing (Figure 4).

### Optimal wheat productivity in the field

The record wheat yield in the field was measured on a one-hectare field of the winter wheat cultivar Gaines in Washington State (Wittwer 1975).

Winter wheat usually produces the record wheat yields, partly because it is in the field for approximately nine months during the winter, compared with spring wheat, which is grown for only four months in the spring and summer. This makes it difficult to realistically estimate yield per day from winter wheat because growth is slow during the winter months.

We estimated total yield per day by dividing the total grain yield (1450 g m<sup>-2</sup>; 216 bushels/acre). We assumed a 100-day period of active growth, which probably overestimated the yield per day because growth occurs after planting in the fall and in the early spring, and these days are not included in the 100-day active growth period. When combined with average daily PPF data for Washington State, the calculated total PPF efficiency (energy in the harvested grain divided by the energy in the photosynthetic photons) was 2.2%.

## Conclusions

Because of environmental limitations, crops do not achieve their genetic yield potential in even the best field conditions. In hydroponic, high-CO<sub>2</sub>, controlled environments, yields are limited by the photosynthetic photon flux even at daily PPF levels that are three times higher than full summer sunlight. Biomass productivity and edible yield, however, are still well below the calculated potentially achievable yield in these environments.

We use photosynthetic gas-exchange techniques in crop monoculture communities to measure daily photosynthetic and carbon-use efficiencies throughout the life cycle in controlled environments. These data are being used to assess short- and long-term environmental effects on biomass productivity.

Biomass allocation to edible products is the yield component with the greatest potential for improvement. This research should ultimately increase understanding of the factors that limit yield in the field.

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AFBS announces the

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### Criteria

The fellowship program is open to all biologists holding an earned doctorate in the life sciences who can demonstrate exceptional competence in a relevant biological discipline; who have established leadership in areas of community service and concern; and who have a strong commitment to and experience in applying biological knowledge to the improvement of public policy in the United States. Further details are given in the application materials.

### Award

For the 1993–1994 fellowship year (1 September 1993 – 31 August 1994), one-half sabbatical support or a comparable postdoctoral stipend (up to \$30,000) is planned for one fellow. If awarded, the fellowship will be administered by AFBS directly. Deadline for receipt of complete application materials, including letters of reference, at AFBS is 1 February 1993.

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