tries. The world population–food problem makes increasing stress on U.S. soils inevitable in the foreseeable future. Adequate protection against excessive loss of productive topsoil requires that the level of publicly supported soil conservation activities be promptly adjusted to this circumstance.

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Increasing Crop Production Through More Controlled Photosynthesis

Can photosynthetic and biosynthetic mechanisms be used to increase productivity in green plants?

James A. Bassham

Everyone is affected by the balance between world food supply and population. For people in more prosperous countries, insufficient or more costly food production results in higher food prices, diminished ability to buy other goods and services, and sometimes, for those lowest on the economic ladder, malnutrition. In less developed countries (LDC's) the people may have to depend on largess from wealthier nations when shortages occur in food production. Port facilities and internal distribution systems in such countries are often inadequate for the job of handling greatly increased imports, and relief sometimes comes too late. The plight of LDC's has been exacerbated by rapidly rising energy costs, which have led to a diminished capacity to use energy in agriculture—for example, in fertilizer production. There has been famine and starvation in some areas.

That many more such tragedies were averted was due to the green revolution, wherein food production was greatly increased in developing countries by the selection of improved plant varieties through breeding for desirable characteristics; by the application of fertilizers, pesticides, and herbicides; and by better methods of tilling, irrigation, and harvesting. Limitations are becoming apparent, however, particularly as the cost of fixed nitrogen fertilizers rises with the cost of gas and petroleum. Some high-yielding strains of cereals produced by extensive breeding programs may prove to be especially susceptible to diseases and pests. Plant breeding methods can be used to make resistant strains in time, but a large portion of one or more seasons' crops could be lost. Nearly complete establishment of high-yielding but vulnerable strains over large areas where the population is critically dependent on a single crop could lead to disaster. Other concerns include the possible adverse ecological effects of pesticides and herbicides, and even of excessive amounts of nitrogen fertilizers. New worries stem from predictions of a worsening weather pattern for agriculture on a global scale—predictions that seem more alarming in view of recent weather in the Northern Hemisphere.

Inextricably linked to the food problem is the energy problem: we need to find new supplies of energy and organic materials to replace the rapidly dwindling supply of the most useful fossil fuels, petroleum and natural gas. We will have to find ways to make more and better use of coal and oil shale, but the economic and environmental costs of developing and processing those stores are high. Alternative sources of organic compounds and even energy that were previously uneconomic are likely to become economic, particularly when environmental costs are considered.

An obvious source to turn to for these alternative supplies is green plants. In Brazil, ethyl alcohol from the fermentation of wastes in sugar processing is already being added to gasoline for auto-

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mobiles. There will probably be a return to greater use of natural fiber as oil and gas become scarcer. Alcohols, terpenes, and other natural oils and hydrocarbons derivable from plants can serve as feedstocks for synthetics. The use of cellulose, the most abundant of plant materials, as a starting point for organic materials has probably not been fully explored.

Throughout history we have used wood and straw combustion for energy, and nuclear power surpassed wood combustion in importance as an energy source in the United States only in the last 15 years. The energy needs of an industrialized nation such as the United States are enormous, however, and the efficiency with which green plants convert solar energy to combustible materials is limited to a few percent, so we are not likely to meet the major part of our energy requirements that way. It is possible, nevertheless, to foresee significant contributions to our energy needs from green plants. Regional impacts (for example, in the U.S. Southwest) could be very important. In underdeveloped nations, where life-styles in rural areas require much smaller amounts of energy, the contributions made by energy from plants could greatly improve the standard of living. One often mentioned example is the conversion of animal wastes to gas for cooking and heating in India. The amount of animal wastes depends, of course, on the productivity of plants consumed by the animals.

How Can We Increase Plant Productivity?

Plant productivity is thus of vital importance not only for food production but also for materials and energy production. The question is how the rapidly growing knowledge of plant biochemistry and physiology can be used to increase plant productivity. The great advances in agricultural efficiency in developed countries and the green revolution in developing countries must be credited mainly to agricultural scientists such as plant breeders and organic chemists who synthesize pesticides for industry. Detailed information about plant mechanisms of photosynthesis and biosynthesis (which together constitute phytosynthesis) has been acquired at an accelerating rate over the past 30 years, but has not yet been put to extensive practical use.

From about 1967 on, and lately with greater frequency, there have been a number of national and international meetings of plant physiologists with agricultural scientists to discuss ways to apply our knowledge toward obtaining higher crop yields (*1–5*). Other groups, usually including a few plant scientists along with engineers and chemists, have been meeting to talk about the possibilities of obtaining energy and materials from agriculture. These discussions are about two possibilities: useful conversion of municipal and agricultural wastes, and "energy farming"—that is, growing plants specifically for energy (*6*, *7*).

Plant productivity enters into considerations of using agricultural wastes: more productivity means more wastes in a unit area, hence lower collection costs. For energy farming, high productivity is even more important since energy as a "crop" does not have a high economic value compared to most conventional crops, even at today's energy costs. Of course, use of marginal land for energy crops may be possible, and considering the growing need for food, such land may be the only choice for energy farming. Some proposals envisage farming of aquatic plants, in either freshwater [water hyacinths are popular (*8*)] or the ocean [for example, kelp attached to wire racks (*9*)]. Special considerations for aquatic plants include the high cost of harvesting, carbon dioxide supply, arrangements for light absorption, and mineral supply. The remainder of this discussion will be limited to land plants.

Maximum Photosynthetic Efficiency

The total dry mass of organic material produced by a land plant and, to a variable and lesser extent, the yield of the harvested organ (such as the seed, root, or fruit) are related to the efficiency with which the plant uses the energy of sunlight to drive the conversion of carbon dioxide, water, and minerals to oxygen and organic compounds—the process of photosynthesis.

While there is general agreement that increased photosynthesis is helpful in most cases in increasing the yield of harvested organs, such increases do not necessarily translate linearly into increased yields. The total plant material produced, however, does depend linearly on the difference between total photosynthesis and total respiration. The actual weight and caloric value of the plant material also depend on the nature of the end products made from photosynthate by biosynthesis. If the crop is all of the plant above ground, harvested while the plant is still growing rapidly (which is sometimes the case for alfalfa, for example), the yield can be expected to be roughly proportional to the integrated daily photosynthetic rate, provided both the rate of respiration and the amount of root material are approximately in proportion to the leaf and stem mass. Before discussing possible ways to increase productivity by increasing photosynthesis, it is useful to consider what maximum efficiency of solar energy conversion could be expected from land plants (*10–12*).

The photosynthetic process takes place entirely in the chloroplasts of green cells. Chloroplasts have an outer double membrane. Inside there is a complex organization of membranes and soluble enzymes. These inner membranes contain the light-absorbing pigments—chlorophyll a, chlorophyll b, and carotenes—as well as various electron carriers, membrane-bound enzymes, and so on. All are required for the conversion of light energy to chemical energy. The membranes form very thin hollow disks (thylakoids).

As a result of photochemistry in the inner membranes, water is oxidized inside the thylakoids, releasing protons and molecular oxygen. The electrons are carried through the membranes and bring about the reduction of a soluble, low-molecular-weight protein called ferredoxin, which contains iron bound to sulfhydryl groups of the protein. The oxidation of two water molecules requires the transfer of four electrons to ferredoxin (Fd) molecules. Each electron following this course must be transferred through a number of steps, two of which are photochemical reactions. In each of these two light reactions a photon of light is used to transfer one electron with a quantum efficiency of 1.0. The light requirement for the transfer of four electrons is thus eight photons

$$2H_2O + 4Fd^{3+} \xrightarrow[\text{photons}]{\text{eight}} 4H^+ + O_2 + 4Fd^{2+}$$

This equation does not give the entire result of what happens in the thylakoids. Concurrent with the electron transfer, there is conversion of adenosine diphosphate (ADP) and inorganic phosphate (P_i) to the biological acid anhydride, adenosine triphosphate (ATP). About three ATP molecules are formed for each four electrons transferred, so the approximate complete equation becomes

$$2H_2O + 4Fd^{3+} + 3ADP^{3-} + 3P_i^{2-} \xrightarrow[\text{photons}]{\text{eight}} H^+ + 3ATP^{4-} + 4Fd^{2+} + O_2$$

The important point is that the utilization of 8 einsteins (moles of photons) by the thylakoid photochemical apparatus produces 4 moles of reduced ferredoxin and about 3 moles of ATP. These are the amounts of reduced ferredoxin and ATP needed to bring about the reduction of 1 mole of carbon dioxide to sugar in the "dark" reactions that follow. This reduction of carbon dioxide occurs in the stroma region of the chloroplasts, outside the thylakoids. Photosynthesis is usually considered complete when carbon dioxide has been converted to the glucose moiety as starch, a major storage product in chloroplasts. By considering only 1/6 mole of such a glucose moiety, one can write a simplified equation for the entire process of photosynthesis

$$CO_2 + H_2O \xrightarrow[\text{photons}]{\text{eight}} (CH_2O) + O_2$$

where (CH_2O) denotes one-sixth of a glucose moiety. The free energy stored by this reaction is about 114 kilocalories per mole of carbon dioxide reduced to starch. (There is a bit more energy stored per carbon in starch than in free glucose.)

Green plants use only light with wavelengths from 400 to 700 nanometers. This photosynthetically active radiation (PAR) constitutes about 43 percent of the total solar radiation at the earth's surface. All this light is used as if it were 700-nm light, but the energy input between 400 and 700 nm at the earth's surface is equivalent to that of monochromatic light at 575 nm. One einstein of light has an energy content, E, given by Avogadro's number times $h\nu$, where h is Planck's constant and ν is the frequency of the light. With the appropriate units, E (kcal/einstein) = $28{,}600/\lambda$, where the wavelength $\lambda = c/\nu$ in nanometers (c is the velocity of light). One einstein of 575-nm light contains 49.74 kcal. The theoretical maximum energy efficiency for the photosynthetic reduction of carbon dioxide to starch glucose moieties with white light is $114/(8 \times 49.74) = 0.286$.

For total solar energy conversion, it is necessary to multiply by the ratio of PAR to total energy, 0.43, giving an efficiency of $0.286 \times 0.43 = 0.123$. This figure is sometimes quoted as the maximum for aquatic plants (for example, unicellular algae) when it is assumed that there is total light absorption and no dark respiration.

Table 1. Solar energy at the earth's surface in the United States.

Region	Energy			
	Btu $foot^{-2}$ day^{-1}	cal cm^{-2} day^{-1}	kcal m^{-2} day^{-1}	watt m^{-2}
U.S. average (annual basis)	1450	393	3930	190
U.S. Southwest (annual basis)	1700	461	4610	223
U.S. Southwest (summer)	2500	678	6775	329

Table 2. Maximum photosynthetic productivity and measured maximum yields in selected plants. Figures given are for total dry matter. Values in parentheses are calculated on an annual basis from maximum growing habits.

Region or plant	Yield			Efficiency (%)
	g m^{-2} day^{-1}	ton $acre^{-1}$ $year^{-1}$	metric ton ha^{-1} $year^{-1}$	
	Theoretical maxima			
U.S. average annual	61	100	224	
U.S. Southwest, annual basis	72	117	263	
U.S. Southwest, summer	106	172	387	
	Measured maxima			
C-4 plants				
Sugarcane	38	(62)	(138)	2.4
Napier grass	39	(64)	(139)	2.4
Sudan grass (*Sorghum*)	51	(83)	(186)	3.2
Corn (*Zea mays*)	52	(85)	(190)	3.2
C-3 plants				
Sugar beet	31	(51)	(113)	1.9
Alfalfa	23	(37)	(84)	1.4
Chlorella	28	(46)	(102)	1.7
	Annual yield			
C-4 plants				
Sugarcane	31	50	112	2.8
Sudan grass (*Sorghum*)	10	16	36	0.9
C-3 plants				
Alfalfa	8	13	29	0.7
Eucalyptus	15	24	54	1.3
Sugar beet	9	15	33	0.8
Algae*	24	39	87	2.2

*Aquatic plant—may be with CO_2 enrichment.

The establishment of theoretical limits to the efficiency of conversion of light absorbed is fairly precise, since the constraints are universal for land plants. There are two additional efficiency factors to be considered before the overall upper limit to be expected from a plant under growing conditions is reached. These are far less precise, being subject to great variation depending on plant species, stage of growth, plant spacing, and a host of other factors. One of the efficiency factors is the fraction of received energy the plant can actually absorb. This depends on the leaf canopy, reflectance, and other factors. The upper limit has been estimated as 0.80 (*10, 11*). Obviously, such a high value could only be achieved when the plants have reached a stage of growth where the leaf canopy completely covers the ground.

The other factor is respiration. Plant cells use up stored energy when not photosynthesizing. This occurs at night, or in the day for plant tissues that are shaded or are not green, such as roots, stems, and fruit. There is some trade-off with the canopy factor, since a dense canopy is likely to include shaded or dimly illuminated leaves. The actual value of the respiration correction varies widely, and the value used here, 0.667, may be considered as only an estimate.

Multiplying these two factors by the previous ones gives a value for the efficiency expected as the upper limit for land plants during the maximum growing season of $0.286 \times 0.43 \times 0.80 \times 0.67 = 0.066$ (*13*).

Maximum Dry Matter Production of Field Crops

The solar energy incident at the earth's surface, averaged over 24 hours per day and 365 days per year, is 3390 kilocalories per square meter per day for the United States as a whole (average) and 4610 kcal m^{-2} day^{-1} for the U.S. Southwest (Table 1). The amount of energy that could be stored by a land plant growing year-round under optimal conditions of temperature, water, fertilizer, and leaf canopy would be $0.066 \times 4610 = 304.3$ kcal m^{-2} day^{-1}. This would give $304.3/114 = 2.67$ moles of CO_2 reduced to (CH_2O) (*14*). Since starch or cellulose formation results in the loss of one H_2O (molecular weight, 18) per glucose moiety (molecular weight, 180), the actual weight added per CO_2 reduced is

$(180 - 18)/6 = 27$, so $2.67 \times 27 = 72$ grams of cellulose or starch are formed per square meter per day. This corresponds to 263 metric tons per hectare per year (Table 2). Other values of daily solar energy in kilocalories per square meter per day may be converted to expected maximum dry weight stored in metric tons per hectare per year by multiplying them by 0.057.

Doubtless this theoretical upper limit is unobtainable under any present or projected growing conditions. What are the actual maximum rates that have been obtained? Reports from a variety of sources (Table 2) (*15*) give values for both the maximum growing season and the annual production. The highest values during the maximum growing season for corn and sorghum are about half the theoretical maximum for the U.S. Southwest summer. On an annual basis sugarcane, the highest, is slightly less than half the theoretical maximum. These measurements were all made in the United States in the temperate zone, where winter temperatures severely restrict growth for even plants such as sugarcane that grow year-round. The maxima lend credibility to the proposition that under year-round optimal conditions of temperature and growth, yields corresponding to energy conversion efficiencies of 4 to 5 percent would be achievable.

Photosynthetic Carbon Reduction Pathways

The terms C-4 plants and C-3 plants encountered in Table 2 refer to important characteristics of photosynthetic carbon metabolism. All known green plants and algae capable of oxidation of water to oxygen employ the reductive pentose phosphate (RPP) cycle (*16, 17*). This cycle begins with the carboxylation of a five-carbon sugar diphosphate, ribulose 1,5-diphosphate (RuDP) (Fig. 1). The six-carbon proposed intermediate is not seen, but is hydrolytically split with internal oxidation and reduction, giving two molecules of the three-carbon product, 3-phosphoglycerate (PGA). With ATP from the light reactions, PGA is converted to phosphoryl PGA, which in turn is reduced by NADPH to the three-carbon sugar phosphate, 3-phosphoglyceraldehyde (Gal3P). The reduced two-electron carrier, NADPH, is regenerated by the reaction of the oxidized form, $NADP^+$, with two molecules of reduced ferredoxin, also produced by the light reactions in the thylakoid membranes. Five molecules of triose phosphate are converted to three molecules of the pentose monophosphate, ribulose 5-phosphate (Ru5P) by a series of condensations, isomerizations, and chain length dismutations. Finally, the Ru5P molecules are converted with ATP to the carbon dioxide acceptor RuDP, completing the cycle.

When the three RuDP molecules are carboxylated to give six PGA molecules, and these are in turn reduced to six Gal3P molecules, there is a net gain of one triose phosphate molecule, equivalent to the three CO_2 molecules taken up. This net Gal3P molecule can either be converted to glucose 6-phosphate (G6P) and then to starch, or it can be exported from the chloroplasts to the cytoplasm. Once there, it is reoxidized to PGA, yielding in addition ATP and NADH, which thus become available to the nonphotosynthetic part of the cell for biosynthesis. Some of this exported carbon and reducing power may be used to make sucrose, a sugar which can then be translocated from the photosynthetic cell into the vascular system of higher plants, through which it can move to other parts of the plant such as the growing tip, seeds, roots, or other sinks. Alternatively, in an expanding leaf, the material exported from the chloroplasts may stay in the cell and be used in the synthesis of new cellular material, leading to cell division.

Plants that have only the RPP cycle for CO_2 fixation and reduction are termed C-3 plants, since the primary carboxylation product is a three-carbon acid. Certain plants of supposed tropical origin—including but not restricted to a number of tropical grasses such as sugarcane, corn, crabgrass, and sorghum—have, in addition to the RPP cycle, another CO_2 fixation cycle (*18–20*). In this cycle (Fig. 2) CO_2 is first fixed by carboxylation of phosphoenolpyruvate (PEP) to give a four-carbon acid, oxaloacetate, which is then reduced with NADPH to give malate (or in some cases the amino acid aspartate).

The malic or aspartic acids are be-

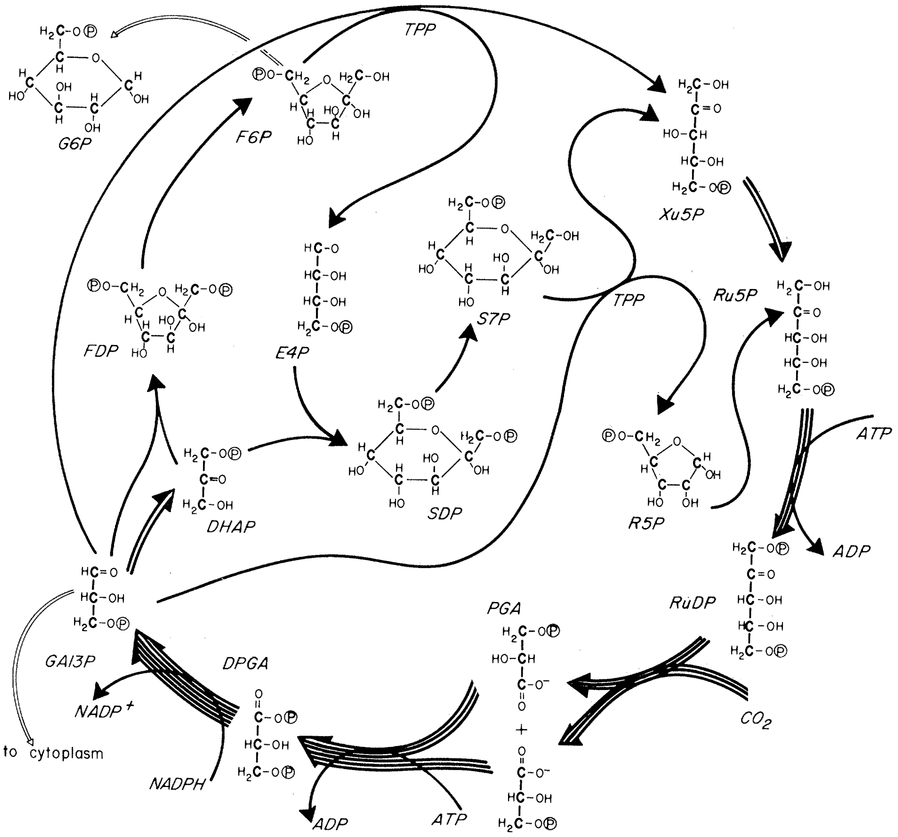

Fig. 1. The reductive pentose phosphate cycle. The heavy lines indicate reactions of the RPP cycle; the faint lines indicate removal of intermediate compounds of the cycle for biosynthesis. The number of heavy lines in each arrow equals the number of times that step in the cycle occurs for one complete turn of the cycle, in which three molecules of CO_2 are converted to one molecule of GAl3P. Abbreviations: *RuDP*, ribulose 1,5-diphosphate; *PGA*, 3-phosphoglycerate; *DPGA*, 1,3 diphosphoglycerate; *NADPH* and $NADP^+$, reduced and oxidized nicotinamide-adenine dinucleotide phosphate, respectively; *GAl3P*, 3-phosphoglyceraldehyde; *DHAP*, dihydroxyacetone phosphate; *FDP*, fructose 1,6-diphosphate; *F6P*, fructose 6-phosphate; *G6P*, glucose 6-phosphate; *E4P*, erythrose 4-phosphate; *SDP*, sedoheptulose 1,7-diphosphate; *S7P*, sedoheptulose 7-phosphate; *Xu5P*, xylulose 5-phosphate; *R5P*, ribose 5-phosphate; *Ru5P*, ribulose 5-phosphate; and *TPP*, thiamine pyrophosphate.

lieved to be translocated into chloroplasts of the bundle sheath cells (cells near the vascular system of the leaf), which contain the enzymes and compounds of the RPP cycle. There these acids are oxidatively decarboxylated, yielding CO_2, NADPH, and pyruvate which is translocated back out of the vascular bundle sheath chloroplasts. Finally, the pyruvate is converted by reactions which use up two ATP molecules to reform the PEP. Plants with this cycle are called C-4 plants because the first compounds formed when CO_2 is incorporated are four-carbon acids. The site of the conversion of pyruvate back to PEP appears to be in specialized mesophyll cells whose chloroplasts do not contain a complete RPP cycle (RuDP carboxylase is missing). The exact sites of various reactions of the C-4 cycle and the possible intracellular transport of metabolites remain subjects of some controversy.

The net result of the C-4 cycle appears to be fixation of CO_2 in the mesophyll cells and translocation of the product into the bundle sheath chloroplasts, followed by release of CO_2 close to RuDP carboxylase and the other RPP-cycle enzymes located there. The cost is two ATP molecules per CO_2 molecule transported. While at first glance this complex mechanism may appear to be hardly worth the trouble (after all, C-3 plants do without it), it turns out that the C-4 cycle performs an extremely valuable function. One reflection of its value is the higher productivity of C-4 plants seen in Table 2. The C-4 plants are in general capable of higher rates of net photosynthesis in air under bright sunlight than the most active C-3 plants.

Photorespiration

The reason for the photosynthetic advantage of C-4 plants lies in the virtual abolition of photorespiration in these plants. The C-3 plants, in air under bright sunlight, and especially on a warm day where growing conditions should be very favorable, lose a certain part of the sugar phosphates formed in their chloroplasts by photosynthetic fixation through reoxidation to CO_2. Apparently the energy and reducing power liberated by this oxidation are not conserved and the process is energetically wasteful. As light intensity and temperature increase, an increase in photosynthetic CO_2 uptake is partly negated by increased photorespiration. Net photosynthesis, the difference between the two processes, does not increase as rapidly for C-3 plants as for C-4 plants. The limiting effect on C-3 plants can be removed by reducing the level of O_2 in the atmosphere to 2 percent or by elevating the CO_2 pressure, but plants in the field must live with the natural atmosphere, which contains 0.033 percent CO_2 and 20 percent O_2 (*21*).

There is still some controversy surrounding the detailed mechanism of photorespiration, but much evidence supports the role of glycolic acid as the key intermediate compound (*21*). It is produced in the chloroplasts by oxidation of sugar phosphate and then oxidized outside the chloroplasts to give photorespiratory CO_2. Production of glycolate is favored in C-3 plants by high light intensities, atmospheric or higher O_2 pressure, low CO_2 pressures, and elevated temperatures. Its formation is inhibited by elevated CO_2 pressures, although there is reported to be some glycolate formation insensitive to CO_2 pressure inside the chloroplasts where the C-3 cycle is operating (*22*). It is thought that glycolate formation from sugar phosphates is minimized in C-4 plants (*21*). Some glycolate is produced even in C-4 plants, so that a further effect of the C-4 cycle may be due to the ability of PEP carboxylation in the other parts of the leaf to recapture CO_2.

Can Photorespiration Be Reduced in C-3 Plants?

In any event, the virtual absence of photorespiration in C-4 plants has stimulated plant scientists to try to endow C-3 plants with C-4 characteristics. A reading of recent symposia on carbon dioxide metabolism and plant productivity suggests that there is not much optimism that this can be done in the near future (*23*). The C-4 plants are characterized not only by an additional biochemical pathway, but also by a distinctive morphology (Kranz anatomy) and differing biochemical capabilities between their two main classes of photosynthetic cells. Giving C-3 plants all the necessary genetic information would require some very sophisticated genetic engineering, yet would not necessarily result in diminished photorespiration if the new information were not compatible with the native system.

Another approach would be to cut off photorespiration at the beginning by eliminating the oxidative reaction whereby sugar phosphates are converted to glycolate. It appears that two such oxidative reactions occur in the chloroplasts. It is not yet settled which is the more important in causing photorespiration in the field. The enzyme RuDP carboxylase cannot totally discriminate between CO_2 and O_2, with the result that O_2 binds competitively at the CO_2 binding site (*24–26*). When this happens, O_2 reacts with RuDP, producing one molecule of PGA and one molecule of phosphoglycolate. A specific phosphoglycolate phosphatase is available to form free glycolate (*27*).

The C-3 plants are not completely defenseless against this attack, as it appears that part of the complex regulatory mechanism of RuDP carboxylase is designed to control the damage. When the enzyme is exposed to one of its substrates, RuDP, in the absence of CO_2, it undergoes a conformational change to a form which has a greatly increased binding constant (decreased binding) for both CO_2 and O_2 (*28*, *29*). This form persists for some minutes even in the presence of subsequently added physiological concentrations of CO_2. Very high concentrations of CO_2 quickly reactivate the enzyme. This suggests that chloroplasts of C-3 plants, exposed to abnormally low CO_2 levels in the light, would adjust by having RuDP carboxylase in a form incapable of reacting RuDP with either CO_2 or O_2, thus minimizing the amount of endogenous sugar phosphates burned by photorespiration. Of course, such a mechanism does not help net photosynthesis since CO_2 uptake is also blocked. Plant physiologists have been looking for chemical agents or other conditions which would inhibit the oxygenase activity of the RuDP carboxylase without decreasing CO_2 fixation, but so far there has been little success.

There are indications that another pathway to glycolate may be oxidation of sugar monophosphates of the RPP cycle (*22*, *30*, *31*). In the RPP cycle, two-carbon fragments are transferred as a glycolaldehyde adduct of thiamine pyrophosphate (TPP) from ketose phosphates [fructose 6-phosphate (F6P), sedoheptulose 7-phosphate (S7P), and xylulose 5-phosphate (Xu5P)] to aldose phosphates. These sugar phosphates can be oxidized to give glycolate by illuminated reconstituted chloroplasts in the presence of TPP (*30*).

It seems probable that the relative importance of these two possible pathways of glycolate synthesis from sugar phosphates varies with physiological conditions, and it may be premature, given the available evidence, to draw a firm conclusion as to which pathway is predominant under the more common field conditions. Furthermore, other pathways of glycolate formation have been suggested (*21*), although the details of these paths, if they exist, are unknown. 2,3-Epoxypropionic acid (glycidic acid) has been found by Zelitch (*32*) to inhibit glycolate formation by 50 percent, with a concurrent 50 percent inhibition of photorespiration and a corresponding increase in net photosynthesis in tobacco leaves. As might be expected, the compound had little effect on the net photosynthesis in maize (a C-4 plant) even though it did inhibit the small amount of glycolate synthesis. Glycidic acid did not inhibit the oxygenase activity of isolated RuDP carboxylase.

Even though imparting full C-4 characteristics to C-3 plants may not prove to be practical, it is possible that breeding of C-3 plants can produce varieties with lower photorespiration correlating with higher rates of net photosynthesis (*33*, *34*).

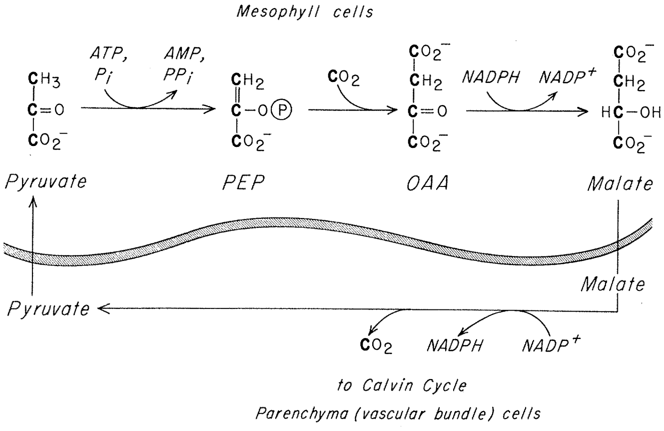

Fig. 2. The C-4 cycle of photosynthesis. This is one version of the preliminary CO_2 fixing cycle which occurs in certain tropical grasses as well as in a scattering of other plant species. This cycle by itself does not result in any net fixation of CO_2 into organic compounds, but rather serves as a vehicle to move CO_2 from cell cytoplasm and perhaps outer leaf cells into the chloroplasts of the vascular bundle cells in these plants. This CO_2 transport is thought to be responsible for the minimization of photorespiration in these cells (see text). In some plants, another version (not shown) of the C-4 cycle is found in which OAA is converted to aspartate rather than malate for transport. Abbreviations: *PEP*, phosphorenolpyruvate; *OAA*, oxaloacetate.

Regulation of the RPP Cycle

The general features of the regulation of the RPP cycle are now fairly well understood (*34*,*35*). Regulation of the cycle has several important functions. First, since chloroplasts have an oxidative metabolism in the dark involving both the oxidative pentose phosphate (OPP) cycle and glycolysis, certain enzymes such as fructose 1,6-diphosphatase have to be switched on in the light and off in the dark (*36*) in order to avoid futile cycles. Such "light-activated" steps include the conversions of fructose 1,6-diphosphate (FDP) and sedulose 1,7-diphosphate (SDP) to their respective monophosphates, F6P and S7P; the conversion of Ru5P with ATP to RuDP; and the carboxylation reaction. Complementing the light activation of RPP cycle enzymes is the inactivation in the light and activation in the dark of a key OPP cycle enzyme, glucose-6-phosphate dehydrogenase (*37*), which converts G6P to 6-phosphogluconate.

The second kind of regulation of the RPP cycle occurs while the light is on and is needed to keep in balance the levels of the various intermediate compounds as they are used for biosynthesis. The principal storage product in the chloroplasts is starch made from G6P (Fig. 1). The principal export from the chloroplasts (besides glycolate) is triose phosphate—either Gal3P or dihydroxyacetone phosphate or both (*38*–*40*). As the relative amounts of triose phosphate and hexose phosphates withdrawn from the cycle change in response to the needs of the cell, concentrations may be kept in balance by "fine-tuning" of the fructose diphosphatase activity compared to the carboxylase activity. For a given rate of carboxylation, increasing the fructose diphosphatase activity will lower the steady-state level of triose phosphates and FDP and raise the level of F6P and G6P.

It seems doubtful that increased plant productivity can be achieved by manipulation of either the light-dark or fine-tuning regulation of the chloroplasts. More promising are the interrelated regulations of starch synthesis and triose phosphate export. Starch synthesis is accelerated by an increased PGA concentration and diminished by an increased P_i concentration in the chloroplast (*41*). Triose phosphate export is accelerated by increasing P_i in the cytoplasm. The P_i enters the chloroplasts in exchange for triose phosphate coming out, the exchange being mediated by a specific translocator (*42*–*44*). This results in higher P_i and lower triose phosphate concentrations in the chloroplasts, leading to diminished starch synthesis (*45*). The concentration of P_i in the cytoplasm thus controls the amount of starch formed compared to the amount of triose phosphate exported. In the dark the P_i concentration inside the chloroplasts rises to a point where starch synthesis stops completely and starch breakdown mediated by starch phosphorylase is activated.

The control of P_i in the cytoplasm is thus important in regulating phytosynthesis which depends on export of triose phosphate. One factor affecting the P_i level may be the rate of conversion of inorganic pyrophosphate (PP_i) to P_i. Inorganic pyrophosphate is produced by protein synthesis and by sucrose synthesis, as well as certain other biosynthetic reactions. The enzyme inorganic pyrophosphatase in green plant cells is strongly activated by Mg^{2+}. The cytoplasmic level of Mg^{2+} thus may be one factor in adjusting the steady-state ratio of P_i to PP_i (*46*, *47*). Plant hormonal control of the cytoplasmic P_i concentration, pyrophosphatase, Mg^{2+}, or other factors affecting P_i may ultimately regulate the flow of photosynthate into biosynthesis, either in the green cells or following translocation to other parts of the plant.

Green Cell Growth Versus Sugar Translocation

Once the photosynthate is in the cytoplasm, there is an important branch point of biosynthesis: the triose phosphate may be converted to sucrose, which is exported to other parts of the plant, or it may be converted to pyruvate, leading to synthesis of fats, proteins, and so on inside the green cell. In *Chlorella*, an increased intracellular ammonium ion concentration strongly increases the conversion of PEP (formed from triose phosphate by the sequence Gal3P → PGA → PEP) to pyruvate at the expense of sucrose synthesis (*48*). In the dark, sucrose breakdown coupled with increased conversion of PEP to pyruvate occurs. Similar but unpublished results from our laboratory have been seen with leaves of higher plants. The increased pyruvate synthesis is accompanied by increased flow of carbon into amino acids and fats. It would appear that the regulatory mechanisms in the green cells responsible for switching the cell's metabolism from growth and division to export of sucrose might work through the intracellular NH_4^+ concentration.

In turn, the NH_4^+ concentration may be governed by the rate of reduction of NO_3^- in the cytoplasm and of the resulting NO_2^- in the chloroplasts. The control in the cytoplasm should be by means of some effect on either the rate of entry of NO_3^- into the cell or the rate of reduction of NO_3^-. Elucidation and manipulation of this control of NO_3^- entry or reduction could be the key to switching green cells from protein and fat synthesis to sucrose export or vice versa.

Nitrogen Fixation

Another large and exciting field in crop productivity is the study of fixation of nitrogen in bacteria in close association with plants (*49*). This includes the well-known fixation by bacteria in root nodules of legumes such as beans, peas, alfalfa, and peanuts, and also some less well integrated systems reported for other plants (*50*). Space will not permit even a cursory discussion of this rapidly expanding subject, but one aspect must be mentioned in an article devoted primarily to carbon dioxide fixation. This is the dramatic improvement in nitrogen fixation in legumes exposed to air enriched with carbon dioxide (*49*).

As mentioned earlier, photorespiration can be abolished in C-3 plants if they are grown in an atmosphere enriched with carbon dioxide. There is, in fact, a twofold effect on the photosynthetic rate in such plants with increased carbon dioxide, since the carboxylation rate increases while photorespiration ceases. A detailed study by Gaastra (*51*) showed that for sugar beet, turnip, cucumber, spinach, and tomato, increases in the photosynthetic rate by a factor of 2 or more could be obtained by increasing the carbon dioxide levels from about 0.032 percent (ambient) to 0.13 percent. A more recent study (*52*) (Table 3) shows similar increases.

When legumes are allowed to photosynthesize with increased levels of carbon dioxide there is an increase in photosynthesis and a dramatic increase in nitrogen fixation. A threefold increase in carbon dioxide resulted in an increase in the amount of fixed nitrogen from 75 to 425 kilograms per hectare. The amount of fixed nitrogen obtained from the soil decreased from 220 to 85 kg/ha (*49*).

Conclusions

I have discussed some of the information about photosynthesis and related biosynthesis that might be used to develop strategies for increasing crop yields. Of necessity, many important areas have been neglected or mentioned only very briefly. It seems possible that techniques of plant breeding can be used to exploit or improve some of the biochemical characteristics now understood for green plants. There may be specifically designed chemicals—for example, glycidate—that can alter production. Finally, we can use the new knowledge to improve physiological conditions.

Table 3. Rate of photosynthesis at ambient and elevated CO_2 levels. The data are from Wittwer (*52*). Values are expressed as milligrams of CO_2 per square decimeter per hour.

Plant	Rate ($mg\ dm^{-2}\ hour^{-1}$) Ambient CO_2	Rate ($mg\ dm^{-2}\ hour^{-1}$) Elevated CO_2
Corn, sorghum, sugarcane	60–75	100
Rice	40–75	135
Sunflower	50–65	130
Soybean, sugar beet	30–40	56
Cotton	40–50	100

Each of these techniques can be used to try to improve rate-limiting steps. For example, plant breeding to improve the carboxylation efficiency has been tried with several plants. Genotypic variation in soybeans may cause observed differences in rates of reactions of the RPP cycle (*53*). The quantity and properties of RuDP carboxylase have been found to vary among tomato genotypes (*54*). Variations in net carboxylation exchange among tomato genotypes were attributed to either the concentration and kinetic properties of RuDP carboxylase or the amount and kinetic properties of the photochemical reaction centers (*55*), and there was a positive association between carboxylation efficiency and amount of carboxylation enzyme among four genotypes examined. Photochemical capacity and carboxylation capacity seem sometimes to vary together among genotypes. It seems likely that the net carboxylation exchange of C-3 plants can be improved by breeding—in some cases because of differences in the RuDP carboxylase activity in vivo. Such differences could be due to differences in such factors as the amount and kinetic properties of the enzyme (such as the Michaelis binding constant for CO_2), ratio of carboxylase to oxygenase activity, degree of optimization of regulating conditions in the chloroplasts (for example, Mg^{2+}, pH, or $NADPH/NADP^+$), and rate of entry of CO_2 into the chloroplasts.

A particularly good use of plant breeding techniques (including tissue culture with genetic modification) may be in increasing the distribution of photosynthate to desirable chemical products. Greater knowledge of the regulation of biosynthetic pathways in plants may be helpful in carrying out such genetic modifications, although much can be done empirically.

The effect of glycidic acid in reducing photorespiration was described earlier. Another agent studied, naphthenic acid, has been reported to increase the RuDP carboxylase and PEP carboxylase activities in the leaves of bean and corn plants, with a reduction in compensation point in the bean plants (*56*). The compensation point is the level of carbon dioxide in a closed system at which photosynthesis equals photorespiration, and is one measure of photorespiration. Regulation of the partitioning of photosynthate to various parts of the plant is probably one of the functions of various plant hormones such as gibberellic acid, which, when applied to alfalfa, increased stem growth at the expense of root growth (*57*). It is clear that there are many opportunities to alter quantitatively the various steps in photosynthesis and biosynthesis. Whether such alterations are useful depends, of course, on the crop and on a variety of environmental conditions.

Chemicals may be found which can improve yields of desired products by inhibition or stimulation of specific biochemical pathways. Considering costs of application and environmental considerations, this approach may be less desirable than plant breeding.

Many physiological conditions leading to optimal productivity have generally been provided already in areas with modern agriculture. Provision of adequate soils, fertilizer, temperature, water, light, and so on is standard agronomical practice. Nevertheless, a detailed knowledge of factors affecting productivity and regulation of biosynthesis makes it possible to refine the selection of optimal conditions for a particular species. Perhaps the one obvious environmental variable not so far exploited except for limited use in greenhouses is the level of carbon dioxide.

A Proposal

I would like to suggest one extreme idea for using carbon dioxide enrichment. The proposal is to cover large areas of the U.S. Southwest with huge greenhouses. The canopies would have to be made from tough, sun-resisting inflatable plastic. The structures might be 1 square kilometer in area and 300 m high (at maximum extension), perhaps with a capacity to go up and down daily. A requirement would be to maintain growing temperatures year-round. Under this canopy a high-protein forage legume such as alfalfa would be grown year-round. It would be harvested periodically during the year, leaving enough of the plant after each harvest to produce a good leaf canopy quickly. The atmosphere would be enriched in carbon dioxide and neither water vapor nor carbon dioxide would be allowed to escape, although some carbon dioxide would diffuse through the plastic canopy.

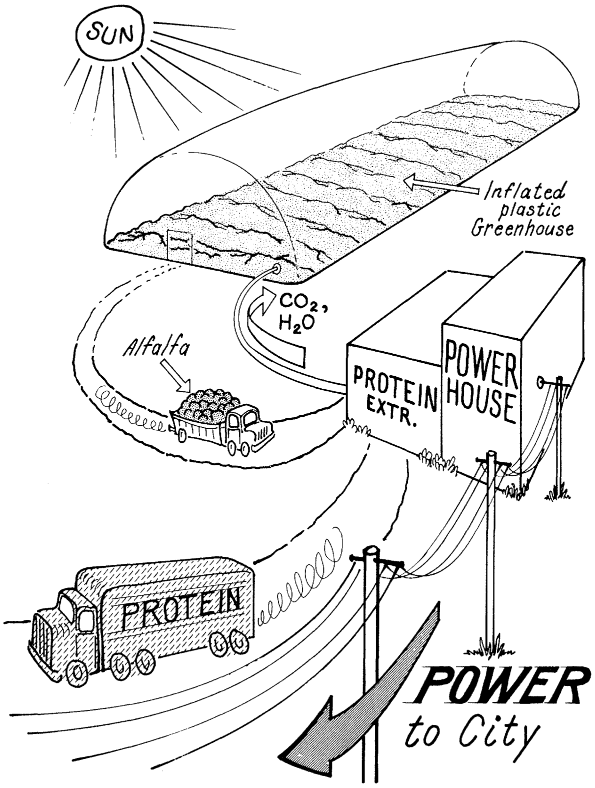

Fig. 3. Scheme for energy and protein production by covered agriculture. Alfalfa, grown under transparent cover year-round with CO_2 enrichment, would be harvested and processed to remove some protein as a valuable product. The residue would be used as animal fodder or, in the version shown here, as fuel for power plants. Combustion CO_2 and H_2O from this and fossil fuels would be returned to the greenhouses.

Leaving aside for a moment the problems of this system (economic, engineering, and physiological) I will list the advantages.

1) With year-round growth and carbon dioxide enrichment (photorespiration eliminated), maximum photosynthetic efficiency should be possible. At a 5 percent conversion efficiency the yield would be 200 metric tons per hectare per year. The whole plant shoot would be harvested and used.

2) Most or perhaps all of the nitrogen requirements would be met by nitrogen fixation, because of stimulation at these high photosynthetic rates.

3) Alfalfa grown under optimal conditions has a protein content as high as 24 percent based on dry weight. It is feasible and economic to remove part of this protein as a high-value product, using the methods developed at the Western Regional Research Laboratory of the U.S. Department of Agriculture at Albany, California (*58*). The residue is a high-value animal feed. Most of the expensive cereal grains fed to cattle could be replaced by this alfalfa, and the cereal grains could be sold for human nutrition in the United States and abroad, where there is a rapidly growing market. The protein extract of the alfalfa has a high value as animal (for example, poultry) feed. An interesting alternative is to convert part of it to a protein product for human consumption (*59*). Nutritionally, it is as good as milk protein (*60*) and far superior to soy protein.

4) Land with a relatively low present value due to lack of water could be used because the water would be recycled. With water vapor containment, only a few percent of the present irrigation requirements for desert land would have to be met.

5) Carbon dioxide could be obtained from flue gases from fossil fuel power plants, thus decreasing the amount of such carbon dioxide discharged to the atmosphere. There has been considerable concern over the possible effects of projected increases of carbon dioxide in the atmosphere when fossil fuels are all burned on the future temperature and climate of the earth. Alternatively, carbon dioxide from CO_2 gas wells might be used (*52*).

6) Once needs for cattle feed are satisfied, additional capacity could supply fuel for power plants (Fig. 3) (*61*). The material left after removal of some of the protein could be burned in the power plants along with the fossil fuels. Ash might be recycled as mineral fertilizer. Calculations suggest that all the electric power needs of California in 1985 might be met by the material obtained from an area of 10,000 km^2, or 1 million hectares (*62*).

7) The modular nature of the system would help in the prevention, containment, and elimination of plant diseases.

Of course, there are many problems, some very serious. The greenhouse effect would have to be controlled, perhaps by allowing daily expansion of the canopy. Contraction of the canopy at night would tend to maintain a greater temperature gradient across the plastic, allowing faster heat transfer out through the plastic. Expansion by day would reduce the daytime temperature excursion. The plastic would have to be tough, sun-resistant, not too permeable to carbon dioxide, perhaps capable of synthesis from materials grown under the canopy, and inexpensive—a tall order. There are other problems, but they may all be solvable. These very serious engineering and economic problems are not to be lightly dismissed, but a detailed discussion of possible solutions will require considerable prior engineering study and is beyond the scope of this article. Such a scheme, if workable, may not become feasible for many years. Considering the potential advantages of the system, it seems worth further study.

Apart from this scheme, there is a need for plant chemists and physiologists to find ways of increasing photosynthetic efficiency by reducing photorespiration, whether through carbon dioxide enrichment, chemicals, or breeding. We need a better understanding of regulation leading to increased conversion of photosynthate into useful products—conventional ones (seeds, roots, or fruit), whole dry matter, or useful chemicals such as hydrocarbons. Translation of increased photosynthesis into increased nitrogen fixation in legumes and possibly other plants needs to be further utilized. The intensified research activities now under way in these and other areas promise a greater impact of basic plant biochemical research on crop productivity in the future.

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Earthquake Injuries Related to Housing in a Guatemalan Village

Aseismic construction techniques may diminish the toll of deaths and serious injuries.

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In the last decade, three major and many lesser earthquakes along the Pacific Coast of Central and South America have claimed approximately 100,000 lives and left an even greater number injured. Since the majority of these deaths and injuries are caused by the collapse of man-made structures, many changes in construction have been advocated to diminish the health consequences of earthquakes. Even in the simplest environment, the application of the principles of aseismic construction in fact might reduce the loss of property and life substantially.

The earthquake of 4 February 1976 devastated a large area of Guatemala leaving 22,778 dead and 76,504 injured (*1*) (Fig. 1). In the aftermath of this disaster, an opportunity arose for us to study the patterns of death and serious injury in the village of Santa Maria Cauque and to relate them to the different types of construction employed in the town. In particular, we wanted to determine which types of building materials and which designs of houses currently in use were most effective in preventing major trauma. We also thought that this might help to substantiate the health consequences of aseismic building practices.

For 15 years, Santa Maria Cauque has been the focus of many longitudinal epidemiological studies of the Institute of Nutrition for Central America and Panama (INCAP) (*2*). The village, located in the highlands 30 miles west of Guatemala City, had a population of 1577 Indians of Maya-Cakchiquel extraction for whom Spanish is a second language. The villagers farm and raise chickens and for the most part live in one-room shelters made of adobe brick or cornstalk, roofed with thatch, tile, or corrugated tin. The health center with its physician and team of nurses and aides is accepted by the Indian community and was available for the collection of the data in this article.

The earthquake, which registered as 7.5 on the Richter scale, occurred at 3:05 in the morning, when all the villagers were asleep. It lasted 39 seconds, and this prevented anyone from leaving his home or seeking safer refuge under furni-

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