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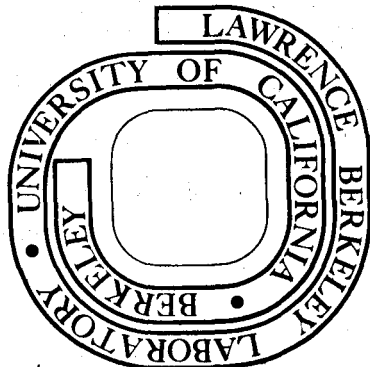
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INCREASING CROP PRODUCTION THROUGH

MORE CONTROLLED PHOTOSYNTHESIS

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INCREASING CROP PRODUCTION THROUGH MORE CONTROLLED PHOTOSYNTHESIS

Can Knowledge of 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, actual malnutrition. In less developed countries ("LDC's")
the people may have to depend on largesse 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, leading to diminshed
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 revolu-
tion" whereby food production was greatly increased in developing countries
through the selection of improved plant varieties through breeding for
desirable characteristics, and by the application of fertilizer, pesticides,
and herbicides, and better methods of tilling, irrigation, harvesting, etc.
Limitations are becoming apparent, however, particularly as the cost of fixed
nitrogen fertilizers rise 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 disease and pests. Nearly complete establishment of high-producing 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, herbicides, and even excessive amounts of nitrogen fertilizers. New worries stem from the gloomy predictions of a worsening weather pattern for agriculture on a global scale--predictions that seem more frightening 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 shall 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 place to turn for these alternative supplies is to green plants. Already in Brazil ethyl alcohol from the fermentation of wastes in sugar processing is being added to gasoline for automobiles. Probably there will 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 uses 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 forsee 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 can 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 thus is of vital importance not only to food production but also to materials and energy production. Not surprisingly, plant biochemists and physiologists are being asked (and are asking themselves) how they can use their rapidly growing knowledge 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, organic chemists synthesizing pesticides for industry, etc. The detailed information about the plant's mechanisms of photosynthesis and biosynthesis (which together constitute photosynthesis) have been acquired at an accelerating rate over the past 30 years, but have 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 towards 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 faming, high productivity per acre is even more important since energy as a "crop" does not have a high economic value even at today's energy costs compared to most conventional crops. 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 the use of aquatic plants, either in fresh water (water hyacinths are popular) or ocean farming [for example, kelp attached to wire racks (9)]. Special considerations are required for aquatic plants: CO_2 supply, arrangements for light absorption, mineral supply, etc. The remainder of this discussion will be limited to land plants.

Maximum Photosynthetic Efficiency

Total dry mass of organic material produced by a land plant, and to a variable and lesser extent the yield of the harvested organ (seed, root, fruit, etc.) 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 (seeds, etc.), an increase in photosynthesis does not necessarily translate lineraly into increased crops in such cases. When the crop is the whole plant, however, and the plant is harvested while still growing rapidly (before senescence sets in) there should be such a relationship. If the crop is alfalfa, for example, and it is harvested repeatedly, yield will depend on rate of photosynthesis.

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 (10,11,12).

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 membranes inside contain the light-absorbing pigments, chlorophylls a and b, and carotenes, as well as various electron carriers, membrane-bound enzymes, etc. All are required for the conversion of light energy to chemical energy. The membranes are formed into very thin hollow discs (thylakoids).

As a result of photochemistry in the membranes, water is oxidized inside the thylakoids, releasing protons and molecular oxygen, O_2. The electrons are carried through the membranes and bring about the oxidation 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 molecules. Each electron following this course must be transferred through a number of steps. In each of two of these steps, a photon of light is used with a quantum efficiency of 1.0. The light requirement for the transfer of four electrons is thus eight photons.

$$2\ H_2O + 4\ Fd^{+3} \xrightarrow{\text{eight photons}} 4\ H^+ + O_2 + 4\ Fd^{+2}$$
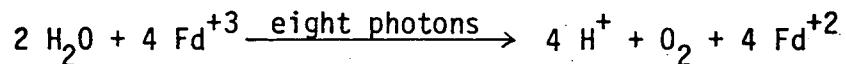
This equation does not give the entire result of what happens in the thylakoids. Concurrent with the electron transfer, there is a conversion of adenosine diphosphate (ADP) and inorganic phosphate (P_i) to the biological acid anhydride, adenosine triphosphate (ATP). It appears that about three ATP molecules are formed for each four electrons transferred, so the approximate complete equation becomes:

$$2\ H_2O + 4\ Fd^{+3} + 3\ ADP^{-3} + 3\ P_i^{-2} \xrightarrow{8\ h\nu} H^+ + 3\ ATP^{-4} + 4\ Fd^{+2} + O_2$$
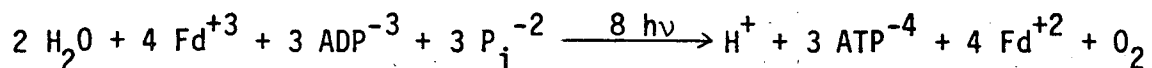
The important point is that with the utilization of eight einsteins (moles of photons), the thylakoid photochemical apparatus produces four moles of reduced ferredoxin and about three moles of ATP. These are the amounts of reduced ferredoxin and ATP needed to bring about the reduction of one mole of carbon dioxide to sugar in the dark reactions that follow. This occurs in the stroma region of the chloroplasts, outside the thylakoids. The usual convention is that photosynthesis is complete when carbon dioxide has been converted to the glucose moiety as starch, a major storage product in chloroplasts. By considering only a sixth of a mole of such a glucose moiety, one can write a simplified equation for the entire process of photosynthesis:

$$CO_2 + H_2O \xrightarrow{\text{8+ photons}} \underset{\text{1/6 glucose moiety}}{(CH_2O)} + O_2$$
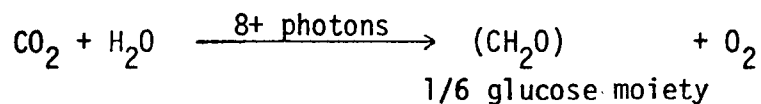
The free energy stored by this reaction is about 114 Kcal per mole of CO_2 reduced to starch. (There is a bit more energy stored per carbon in starch than in free glucose.)

Green plants use only light with wave lengths from 400 nm to 700 nm. This photosynthetically active radiation (P.A.R.) constitutes only about 0.43 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 monochromatic light at 575 nm. An einstein of light has an energy content 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 λ = wavelength = c/ν, in nm. An 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 x 49.74) = 0.286.

For total solar energy conversion, it is necessary to multiply by the ratio of P.A.R. to total energy, 0.43, giving an efficiency of 0.286 x 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.

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 reaching the overall upper limit to be expected from a plant under growing conditions. These are far less precise, being subject to great variation among plant species, stage of growth, plant spacing and a host of other factors. One of the 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, fruit, etc. 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 only as a "ball-park" figure.

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

Maximum Dry Matter Production of Field Crops

The solar energy incident at the earth's surface, averaged over 24 hr per day and 365 days per year is 3,390 $Kcal/m^2$ day for the United States as a whole (average) and is 4,610 $Kcal/m^2$ day in the United States Southwest (Table I). The amount of energy that could be stored by a land plant growing under year round optimal conditions of temperature, water, fertilizer, and leaf canopy would be 0.066 x 4,610 = 304.3 $Kcal/m^2$ day. 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 (M.W. 18) per glucose moiety (M.W. 180), the actual weight added per CO_2 reduced is (180-18)/6 = 27, so 2.67 x 27 = 72 g of cellulose or starch is formed per m^2 day. This corresponds to 263 metric tons/hectare year (Table II). Other values of daily solar energy in $Kcal/m^2$ day may be converted to expected maximum dry weight stored in metric tons/hectare year by multiplying the energy by 0.057.

Doubtless this theoretical upper limit is unobtainable under any present of projected future growing conditions. What are the actual maximum rates reported? Reports from a variety of sources (Table II) (15) give values for both the maximum growing season and the annual production. The highest values during maximum growing season, for corn and sorgum, are about half the theoretical maximum. On an annual basis sugar cane, 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 severly restrict growth for even those plants such as sugar cane that grow year round. The maxima lend credibility to the proposition that under year round optimal conditions of temperature and growth, yields corresponding to 4 to 5% energy conversion efficiencies would be achievable.

The Photosynthetic Carbon Reduction Pathways

The terms "C-4" plants and "C-3" plants encountered in Table II refer to important characteristics of photosynthetic carbon metabol that require some discussion. All known green plants and algae cap of oxidation of water to O_2 employ the reductive pentose phosphate cycle RPP Cycle) (16,17). This RPP cycle begins with the carboxylation of a five-carbon sugar diphosphate (RuDP, Figure 1). The six-carbon proposed intermediate is not seen, but is hydrolytically split with internal oxidation-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, 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, ribulose 1, 5-diphosphate (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 thence 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 non-photosynthetic part of the cell for biosynthesis. Some of this exported

carbon and reducing power may be converted to 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 which 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 sugar cane, corn, crab-
grass, sorgum, etc. have, in addition to the RPP cycle, another CO_2 fixation
cycle (18-20). In this cycle, CO_2 is first fixed by carboxylation of phos-
phoenolpyruvate, (PEPA) to give a four carbon acid, oxalacetate (OAA), which
is then reduced with NADPH to give malate (or in some cases the amino acid
aspartate).

The malic or aspartic acids are believed to be translocated into the
chloroplasts in 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 chloroplasts containing the RPP cycle. Finally, the pyruvate is
converted by reactions which use up two ATP molecules to reform the PEPA.
Since the first compounds into which CO_2 is incorporated in this cycle are
four-carbon acids, plants with this cycle are called C-4 plants. The site
of the conversion of pyruvate back to PEPA appears to be in specialized
mesophyll cells whose chloroplasts do not contain a complete RPP cycle (RuDP
carboxylase is missing). The exact locations of the sites of various

reactions of the C-4 cycle and the possible intracellular transport of metabolites remain the subject of some controversy.

The net result of the C-4 cycle appears to be the fixation of CO_2 at sites removed from the RPP cycle chloroplasts, the translocation of the product into these chloroplasts, and the release of CO_2 close to RuDP carboxylase. The cost is two ATP's 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 II. 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 (21)

The reason for the difference lies in the virtual abolition of photorespiration in C-4 plants. In C-3 plants, in air under bright sunlight, and especially on a warm day where growing conditions should be very favorable, a certain part of the sugar phosphates formed in the chloroplasts by photosynthetic fixation are reoxidized, and are in part converted back 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, any increase in photosynthetic CO_2 uptake is negated by increased photorespiration. Net photosynthesis, the difference between the two processes, cannot increase beyond a certain point. The limiting effect on C-3 plants can be removed by reduction of the level of O_2 in the atmosphere to 2% or by elevating the CO_2 pressure, but in the field plants must live with the natural atmosphere which contains 0.033% CO_2 and 20% 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. The production of glycolate is favored in C-3 plants by high light, atmospheric or higher O_2, low CO_2 pressures, and elevated temperatures. Its formation is inhibited by elevated CO_2, although there is reported to be some glycolate formation insensitive to CO_2 pressure inside the chloroplasts where the C-3 cycle is operating, 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 the PEPA 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 CO_2 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, the result being that O_2 binds competitively at the CO_2 binding site (24,25,26). 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).

C-3 plants are not completely defenseless against this attack, as it appears that part of the complex regulatory mechanism of the 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, the enzyme 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 levels of CO_2. Very high levels 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 doesn't 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 by 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, sedoheptulose 7-phosphate, and xylulose 5-phosphate) 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. The chemical, 2,3-epoxypropionic acid (glycidic acid) has been found by Zelitch (32) to inhibit glycolate formation by 50%, with a concurrent 50% 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).

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 cycle (OPP Cycle) and glycolysis,

certain enzyme activities 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 FDP and 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 day 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 DHAP or both (39,40,41). 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 FDPase activity compared to the carboxylase activity. For a given rate of carboxylation, increase in FDPase 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 regualtions of starch synthesis and triose phosphate export. Starch synthesis is accelerated by increased PGA concentration and diminished by increased P_i (phosphate, P_i) /concentration in the chloroplast. 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 (42,43,44). This

results in higher P_i and lower triose phosphate levels in the chloroplasts, leading to diminished starch synthesis (45). The level of P_i in the cytoplasm thus controls the amount of starch formed compared to triose phosphate exported. In the dark the P_i level 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 photosynthesis 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. PP_i 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/PP_i (46,47). Plant hormonal control of 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 Vs. Sugar Translocation

Once the photosynthate is in the cytoplasm, an important branch point of biosynthesis is the alternative conversion of the triose phosphate to sucrose to be exported to other parts of the plant or conversion to pyruvate, leading to synthesis of fats, proteins, etc. inside the green cell. In Chlorella, increased intracellular ammonium ion concentration strongly increases the conversion of PEPA (formed from triose phosphate by the sequence Gal3P → 3-PGA → 2-PGA → PEPA) to pyruvate at the expense of sucrose synthesis (48). In the dark, sucrose breakdown coupled with increased conversion of PEPA to pyruvate occurs. Similar but unpublished results

have been seen with leaves of higher plants. The increased pyruvate synthesis is accompanied by increased flow of carbon into amino acids and fat... 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, 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 possible 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 N_2 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, peanuts, etc., 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 improvements in N_2 fixation in legumes exposed to air enriched with CO_2 (49).

As mentioned earlier, photorespiration can be abolished in C-3 plants if they are grown in an atmosphere enriched with CO_2. There is in fact a two-fold effect on photosynthetic rate in such plants with increased CO_2, since the carboxylation rate increases while photorespiration ceases. The detailed study by Gaastra (51) showed that for sugar beet, turnip, cucumber, spinach, and tomato increases in photosynthetic rate of two-fold or more could be obtained by increasing the CO_2 pressures from about air levels (0.032%)

to 0.13%. A more recent study (52) (Table III) shows similar increases.

When legumes are allowed to photosynthesize with increased levels of CO_2 there is an increase in photosynthesis and a dramatic increase in N_2 fixation. A three-fold increase in CO_2 level resulted in the amount of fixed nitrogen increasing from 75 to 425 Kg per hectare! The amount of fixed nitrogen obtained from the soil decreased from 220 to 85 Kg per hectare (49).

Conclusion and a Proposal

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.

I would like to discuss one "far-out" idea which brings together many of the considerations mentioned so far. The proposal is to cover large areas of the U.S. Southwest with large greenhouses. The canopies would have to made from tough, sun-resisting inflatable plastic. The structures might be 1 Km^2 in area and 300 meters high (at maximum extension) with a capacity to go up and down daily. I will not attempt to define further the obviously difficult engineering details. A requirement would be to maintain growing temperatures year round. Under this canopy would be grown a high-protein forage legume such as alfalfa. It would be harvested periodically during the year, leaving after each harvest enough of the plant to produce quickly a good leaf canopy. Growth would be year round. The atmosphere would

be enriched in CO_2 and neither water vapor or CO_2 would be allowed to escape, although some CO_2 would diffuse through the plastic canopy.

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 CO_2 enrichment (photorespiration eliminated), maximum photosynthetic efficiency should be possible. At a 5% conversion efficiency the yield would be 200 metric tons/hectare year. The whole plant would be harvested and used.

2. Most of perhaps all of the nitrogen requirements would be met by N_2 fixation, due to stimulation at these high photosynthetic rates.

3. Alfalfa grown under optimal conditions has as high as 24% protein content based on dry weight. It is feasible and economic to remove a 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 (53). The residue is a high value animal feed. Most of the feeding of expensive cereal grains to cattle could be replaced by this alfalfa, and the cereal grains could be sold for human nutrition in the U.S.A. and abroad where there is a rapidly growing market. The protein extract of the alfalfa has a high value as animal (poultry, for example) feed. An interesting alternative is to convert part of it to a protein product for human consumption (54). Nutritionally it is as good as milk protein (55) and far superior to soy protein.

4. Land with relatively low value at present because of lack of water could be used because of water recycling. 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 gasses from fossil fuel

power plants, thus decreasing the amount of such CO_2 discharged to the atomsphere. Alternatively, CO_2 from CO_2 gas wells might be used (52).

6. Once the needs for cattle feed are satisfied, additional capacity could supply fuel for power plants (Figure 2) (56). 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 an area of 10,000 Km^2, or 1 million hectares.

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. The plastic would have to be tough, sun-resistant, not too permeable to CO_2, 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. Considering the advantages of the system, it seems worth further study.

Irrespective of this scheme, there is a need for plant chemists and physiologists to find ways of increasing photosynthetic efficiency by reducing photorespiration, whether by CO_2 enrichment, chemicals, or breeding. We need better understanding of regulation leading to increased conversion of photosynthate into useful products, whether conventional (seeds, roots, or fruit), whole dry matter, or useful chemicals such as hydrocarbons. Translation of increased photosynthesis into increased N_2 fixation in legumes and possibly other plants needs to be further utilized. The intensified research activities now underway in these and other areas promises greater impact of basic plant biochemical research on crop productivity in the future.

TABLE I

SOLAR ENERGY AT EARTH'S SURFACE IN U.S.

	b.t.u./ft^2 day	cal/cm^2 day	Kcal/m^2 day	watts/m^2
Average (annual basis)	1,450	393	3,930	190
U.S. Southwest (annual basis)	1,700	461	4,610	223
U.S. Southwest (summer)	2,500	678	6,775	329

TABLE II

MAXIMUM PHOTOSYNTHETIC PRODUCTIVITY AND MEASURED MAXIMUM YIELDS

IN SELECTED PLANTS

	gmm^2/day	tons/ acre yr.	metric tons/ hectare yr.	eff. %
Theoretical max. (Table II)				
U.S. Average annual	61	100	224	
U.S. Southwest ave. ann.	72	117	263	
U.S. Southwest, summer	106	172	387	
Maximum Measured				
C-4 plants				
Sugar cane	38	(62)	(138)	2.4
Napier grass	39	(64)	(139)	2.4
Sudan grass (Sorgum)	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				
Sugar cane	31	50	112	2.8
Sudan grass (Sorgum)	10	16	36	0.9
Corn (Zea mays)	4	6	13	0.4
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

TABLE III

RATE OF PHOTOSYNTHESIS AT AIR LEVELS AND ELEVATED LEVELS OF CO_2*

(milligrams CO_2/dm^2 hour)

Plant	Air	Elevated CO_2
Corn, sorghum, sugar cane	60-75	100
Rice	40-75	135
Sunflower	50-65	130
Soybean, sugar beet	30-40	56
Cotton	40-50	100

*From Witwer ( ).

Figure 1.

The Reductive Pentose Phosphate Cycle

The heavy lines are for 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 GA13P.

Abbreviations: RuDP, ribulose 1,5-diphosphate; PGA, 3-phosphoglycerate;
DPGA, 1,3 diphosphoglycerate; GA13P, 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;
TPP, thiamine pyrophosphate.

Figure 2. 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 version
shown here, serve as fuel for power plant. Combustion CO_2 and H_2O from
this and fossil fuels would be returned to greenhouses.
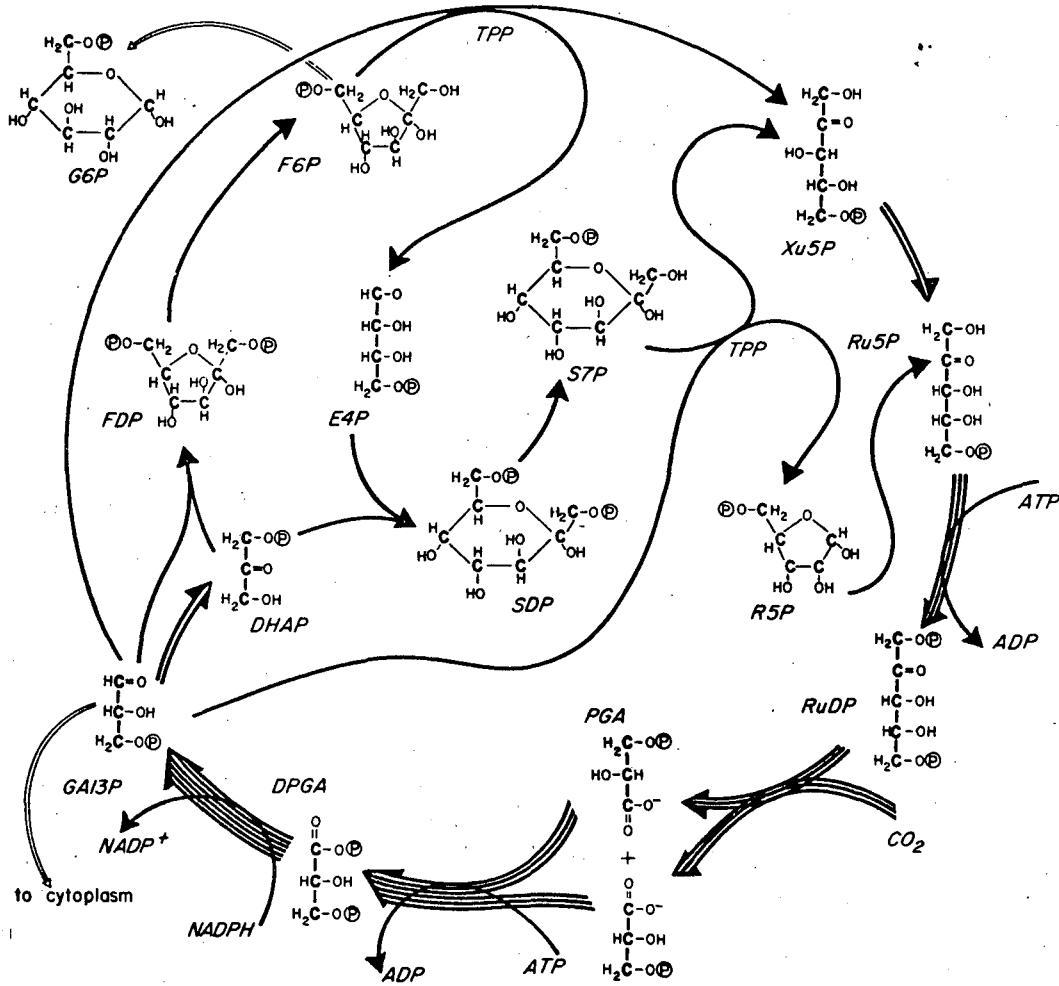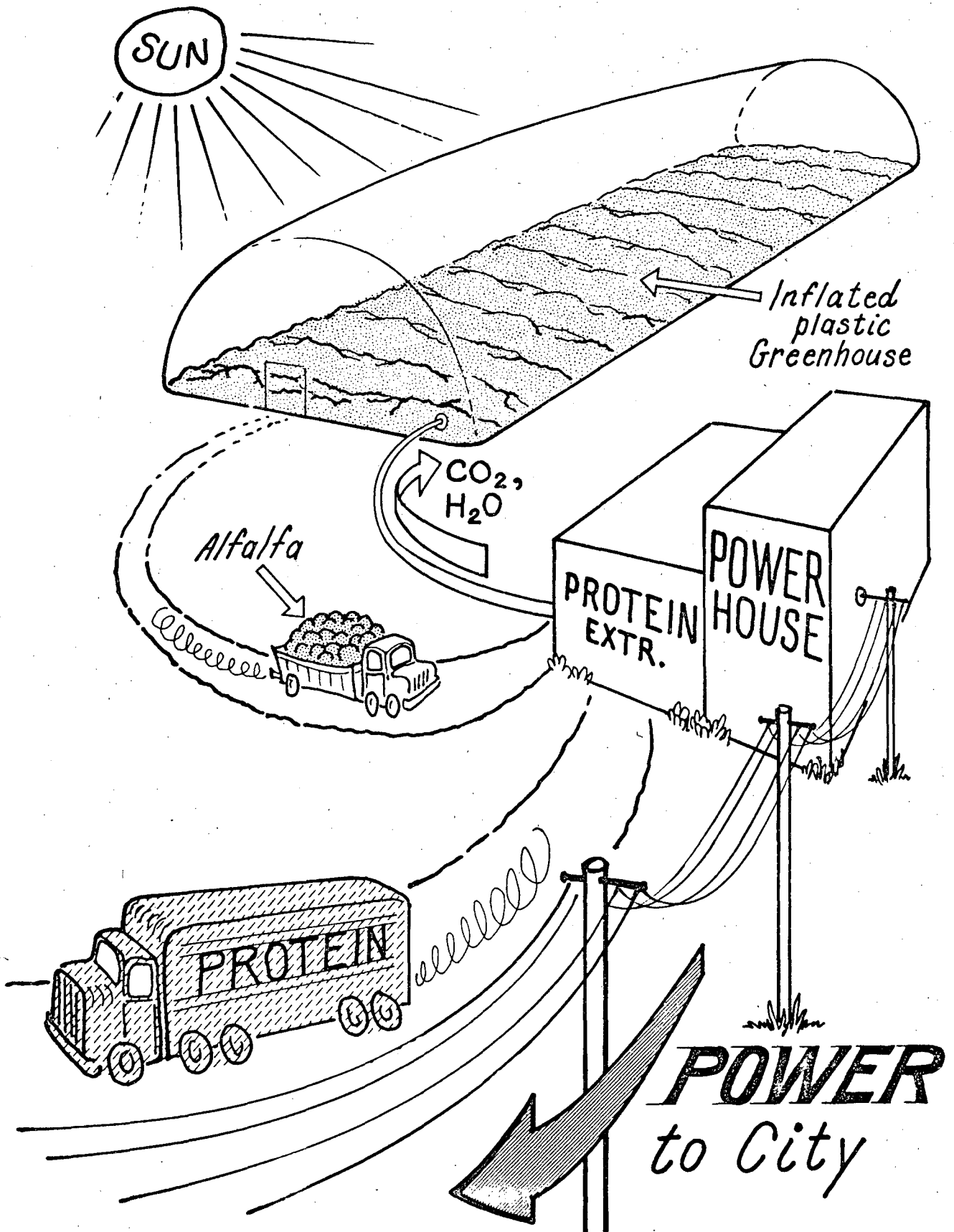
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Figure 1.

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Figure 2.

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