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Title
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Publication Date
1977-11-01

LBL-7214
c.2

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November 1977

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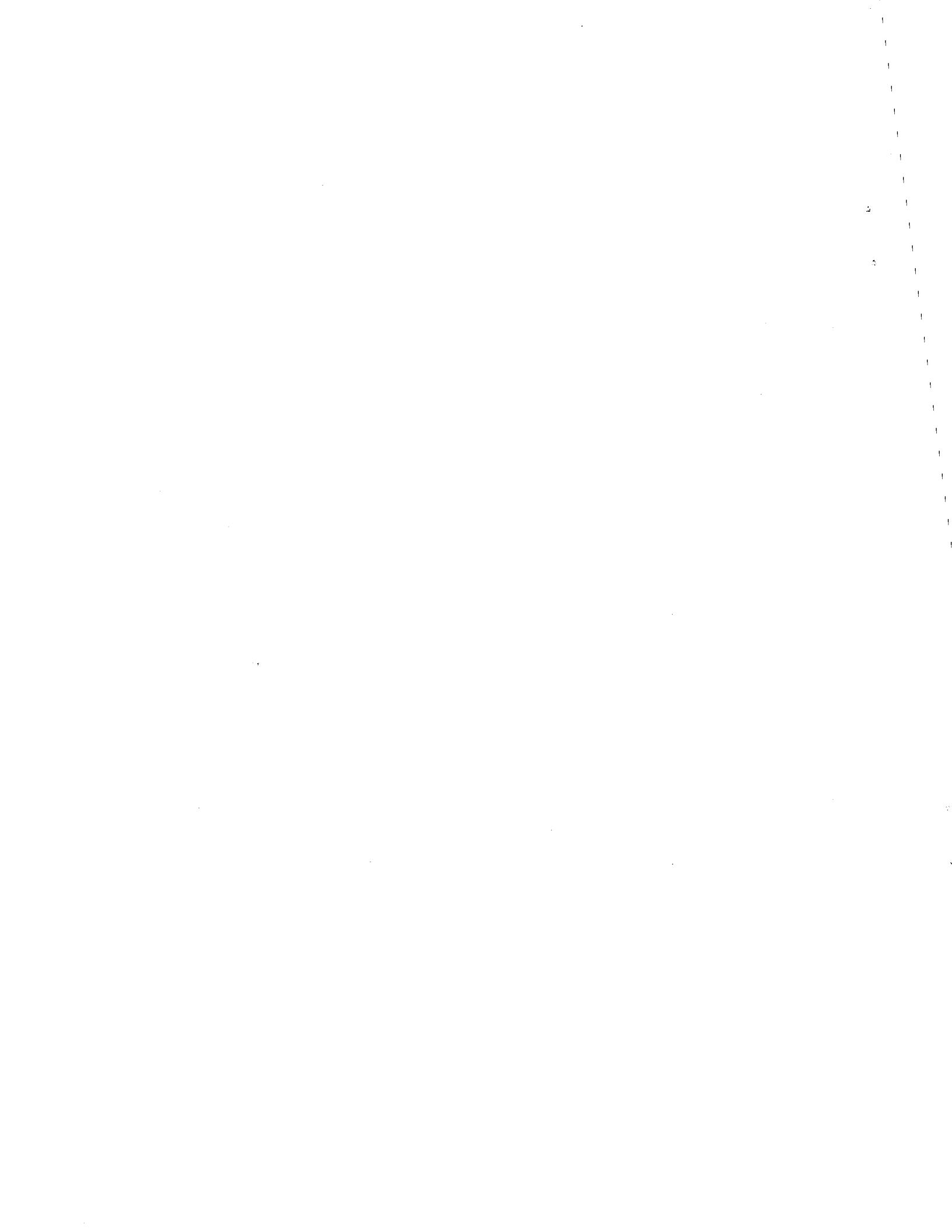Chemical Biodynamics Division

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Introduction

Biomass production by green plants is driven by the renewable energy resource of sunlight. The applications of science and engineering to agriculture can increase both the extent and efficiency of green plant production of substances needed by people. Green plants can supply not only more food for humans and feed for animals, but also fuel, chemicals, and pharmaceuticals. Besides the direct cultivation of plant constituents, we can obtain substrates from plants for conversion to more useful compounds by fungi and bacteria. An example is the yeast fermentation of plant sugars to produce ethanol which can then be used either as a liquid fuel or as a starting point for chemical synthesis.

Within the goals of this regional seminar it is important to consider the potential of green plant photosynthesis in arid and semiarid regions. Some aspects of this potential include the use of aquatic plants and algae and the use of plants tolerant of salt, discussed by other speakers. My remarks will be about the potential of vegetation in arid zones as a source of substrates. Within this topic we shall briefly consider three aspects. The first includes the limitations on efficiency of conversion of solar energy to the stored chemical energy of biomass in green plants, and the subsequent biochemical pathways of carbon dioxide fixation and biosynthesis. Second is the potential of plants endogenous to arid zones. Finally, I will consider the use of covered agriculture or controlled environmental agriculture (CEA) both in its present form and in terms of possible extension to the large scale production of stable crops.

An Urgent Need. Aspects of both arid land plant utilization and of CEA have been subjects of research and development for many years, but there appears to be a relatively recent resurgence of interest which presages rapid growth in the future. This is a part of a general desire to increase production of all kinds of crops wherever possible. That this is so is a direct consequence of the growing awareness of the short-age of adequate food and proper nutrition in many parts of the world, and of the potential contributions that research can make to increasing food supplies. It has been estimated that the developing countries need to increase food production by 3 to 4 percent each year until the end of the century (National Academy of Science Report, 1977b). At the same time there is a wide-spread realization during the past several years that supplies of fossil fuels, especially petroleum and natural gas are finite and are being fairly rapidly depleted. Along with the rapidly growing population of the Earth, and limitation of fossil fuel supplies and food production, there are the increased expectations of people everywhere for supplies of food, energy, and chemicals. All can be supplied to a greater extent than now by increased and more efficient use of agriculture.

A serious limitation to crop productivity in large areas of the world with high solar radiation and long growing seasons (with respect to tempera-ture) is the availability of water. This limitation is felt not only in clearly arid and semi-arid regions but also in areas where the rainfall is highly variable over a period of time. Such variability may occur over a short span of a few years or over a much longer span of centuries. What makes this kind of variation so frightening is the fact that the population of the Earth is now so much greater than during the past periods of history, when there was low rainfall in areas presently used for agriculture.

Dry Lands with High Solar Energy. The arid and semiarid lands of
the world constitute about 36 percent of the land area (Meigs, 1968).
Although some dry lands are found in the arctic regions, the arid and semi-
arid lands with high annual solar energy lie mostly in the regions between
15° and 40° north and south of the equator.

Areas with the most abundant solar energy, averaging more than 200 Kcal/
$cm^2 \cdot yr.$, include the Arabian Penninsula, the south coast of Iran, much of
northern Africa (the Sahara, Egypt, and adjacent areas), parts of the United
States Southwest and northern Mexico, and parts of South Africa and South-
west Africa (Fig. 1)(Calvin, 1977b). Other areas of high solar energy,
averaging over 160 $Kcal/cm^2 \cdot yr$, include nearly all of Australia, the rest
of Africa north and south of 20° latitude as well as the tropical zone of
east Africa, most of southern Asia and southern North America, and
extensive regions of South America.

Productivity of Dry Lands. Without irrigation, the photosynthetic
productivity of dry lands is naturally extrememly low. Desert Scrub,
Dry Desert, and Chaparral lands constitute 19% of the continental area
(Table I) (Leith, 1971), but only 2.3% of the primary photosynthetic
productivity is found there. Most of the continental productivity is in
forests, grasslands, woodlands, wet-lands and lakes, and in cultivated
fields. Very little of the lands in arid regions are cultivated, but
where irrigation is possible, as in the Nile Valley of Egypt, or the
Imperial Valley of the United States, crop productivity is very high,
even though the problem of salt-buildup can become serious in time. In
such areas, further extension of agriculture is usually limited by the
availability of good land, water, or both. Some lands, initially unsuited

to conventional agriculture because they are too sandy, salty, or lack humus, can be improved with appropriate treatment. Water is therefore often the limiting factor. While irrigation projects can be used in some cases to convert desert areas into regions of high productivity, such projects obviously are limited by proximity to and abundance of fresh water in rivers or underground water reachable with wells. In some areas such supplies are nonexistent or prohibitively costly due to distance to rivers, depth of water tables or other factors. These are strong reasons to use whatever fresh water is available for crop production as efficiently as possible.

Efficient Use of Water. Efficient utilization of water can be accomplished in several ways. Plants capable of growing in dry lands can be exploited, application of water to the plants can be made more economically as by trickle irrigation, waste water from municipal and industrial uses can be reclaimed, purified and reused for agriculture, and evaporative losses can be greatly reduced by utilization of CEA, provided the system is sealed to prevent water loss, or sea water evaporation is employed to saturate the air over the plants with water vapor.

Efficiency of Plants as Solar Energy Converters. If we are to develop CEA for widespread application to food and perhaps energy and chemical production as well, it will be vitally important to maximize the efficiency of the systems. One efficiency with which we start is the efficiency of the photosynthetic process itself, which determines just how much of the sun's energy can be captured and stored by the plants. Such efficiency is also very important for desert plants, which must capture and store the

sun's energy while at the same time conserving water. To prevent loss
of water to the low humidity sink of the desert in the daytime, but still
be able to take up carbon dioxide is a major accomplishment of desert
plants. There are four aspects of the plant physiology of green plants
that are especially important in this respect: the primary process of
photosynthesis and its efficiency (Bassham, 1977b), photorespiration,
C-4 metabolism, and Crassulacean Acid Metabolism (CAM).

The Mechanism of Photosynthesis and its Efficiency. Total dry mass
of organic material produced by a land plant, and to 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 (Loomis and Williams, 1963; Loomis and Gerakis, 1975)--the process
of photosynthesis.

Increased photosynthesis is helpful in most cases in increasing the
yield of harvested organs (seeds, etc.), but an increase in photosynthesis
does not necessarily translate linearly into increased crops in such cases.
When the crop is the whole plant, however, and that 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 so that the plants are always growing at high rates,
yield will depend on rate of photosynthesis.

The photosynthetic process takes place entirely in the chloroplasts
of green cells. Chloroplasts have an outer double membrane. Inside the
chloroplasts is a complex organization of membranes and soluble enzymes.
These inner membranes contain the light-absorbing pigments, chlorophylls
a and b, and carotenes, and various electron carriers, membrane-bound

enzymes, etc. All these components 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 the photochemistry in the membranes, water is oxidized inside the thylakoids, releasing protons and molecular oxygen, O_2. The electrons pass 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 the two water molecules takes four electrons from water and these are transferred to four 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 two times four, or eight photons.

$$2 H_2O + 4 Fd^{+3} \xrightarrow{\text{eight photons}} 4 H^+ + O_2 + 4 Fd^{+2}$$
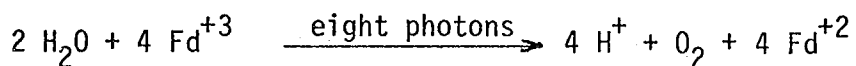
This equation does not give the entire result of what happens in the thylakoids. Concurrent with the electron transfer, there is a conversion of adenosine diphosphate (ADP) and inorganic phosphate (P_i) to the biological acid anhydride, adenosine triphosphate (ATP).

$$H^+ + ADP^{-3} + P_i^{-2} \longrightarrow ATP^{-4} + H_2O$$

It appears that about three ATP molecules are formed for each four electrons transferred, so the approximate complete equation becomes:

$$4 Fd^{+3} + 3 ADP^{-3} + 3 P_i^{-2} \xrightarrow{8h\nu} H^+ + 3 ATP^{-4} + 4 Fd^{+2} + O_2 + H_2O$$
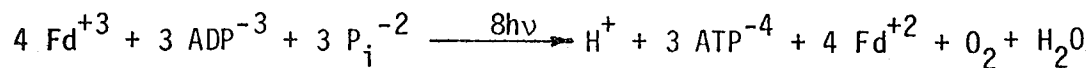
With the utilization of eight einsteins (moles of photons), the thylakoid photochemical apparatus produces four moles of reduced ferredoxin and about three moles of ATP. These amounts of reduced ferredoxin and ATP are needed to bring about the reduction of one mole of carbon dioxide to sugar in the dark reactions that follow. This occurs in the stroma region of the chloroplasts, outside the thylakoids. The early reactions of photosynthesis are complete when carbon dioxide has been converted to the glucose moiety of 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:

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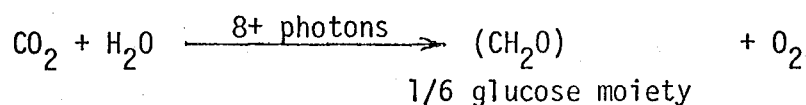
The free energy stored by this reaction is about 114 Kcal per mole of CO_2 reduced to starch. (There is a bit more energy stored per carbon in starch than in free glucose.)

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 at latitudes common to dry lands. All this light is used no more efficiently by the green plant cells than if it were 700 nm light. The integrated solar energy input between 400 and 700 nm at the earth's surface is equivalent in energy 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. At least eight photons of light are required per molecule of CO_2 reduced; eight einsteins of light

are required per mole of CO_2. Probably the actual efficiency is somewhat less, but measurements of quantum requirements under optimal conditions in the laboratory have given quantum requirements in the range of 8 to 10 einsteins required per O_2 molecule evolved (Ng and Bassham, 1968).

The maximum efficiency of 0.286 is for conversion of P.A.R. The efficiency based on total solar radiation incident on the plants with total absorption of P.A.R. is 0.43 x .286 = 0.123. This is the basis for the statement sometimes made that the maximum efficiency for solar energy conversion by photosynthesis is about 12%.

The maximum net efficiency, over a 24 hr period, and under field or aquatic conditions, depends on two other factors: The amount of incident light actually absorbed in the green tissue, and the cost of energy used in respiration and biosynthesis. For land plants it has been estimated that the maximum absorption to be expected from an optimal leaf canopy may be 0.80 (Loomis, et al, 1971). This is due to some light being reflected and some reaching the ground or falling on nonphotosynthetic parts of the plant (such as the bark of trees). With aquatic plants such as unicellular algae that are totally immersed there may be less reflection and with sufficient density of algae, absorption could be essentially complete in green tissues.

A major loss in stored chemical energy results from respiration which occurs in all tissue not actively photosynthesizing. This includes green cells at night or in dim light, and roots, trunks and other organs that are not green or only a little green. The energy derived from respiration is used for various physiological needs of the plant, transport and translocation, conversion of photosynthate to protein, lipids (including hydrocarbons in some plants), cellulose for structures such as stalks and trunks, and so forth. In the green cells during photosynthesis, some energy

from the photosynthetic process itself may be used for such purposes, as
mentioned earlier. Like the light absorption factor, the factor for
respiration/biosynthesis is extremely variable, depending on the physio-
logical conditions and needs of the plant, but it is estimated that in a
typical case respiration and biosynthesis use up one third of the energy
stored by photosynthesis (Loomis et al., 1971). The factor would thus be
0.67.

It may be argued that both the absorption factor and the respiration
factor are not true maximum values, since there may be cases where each
is exceeded. The product of these two factors, 0.80 x 0.67 = 0.53 probably
is close to the maximum, since there is some trade-off between the two
factors. For example, for a land plant to have all brightly illuminated
leaves and hence lower respiration compared to photosynthesis would mean
that its leaf canopy was probably less perfect than required for 0.8
absorption. At the other extreme, when there is dense foliage, little
light may reach the ground, but the respiration in the shaded leaves may
nearly equal photosynthesis. Similarly, an algae pond may be nearly
totally absorbing, but the average light intensity for the cells would
then be so low as to allow a high rate of respiration.

If we combine the photosynthetic efficiency, 0.123, with the product
of the absorption and respiration/ biosynthesis factors, 0.534, we obtain
an overall maximum efficiency for photosynthetic/biosynthetic energy
storage·by green plants of 0.066. This calculated maximum efficiency can
be compared with various reported high yield figures from agriculture.
Before doing this it is useful to convert the efficiency to expected yield
of dry matter.

From the equation and discussion given earlier, the reduction of a
mole of CO_2 to the glucose moiety of starch or cellulose stores about

114 Kcal and results in an organic molecular weight of 27. Each Kcal
of stored energy thus results in the formation of 27/114 = 0.237 grams
of biomass (dry weight), if the biomass were entirely cellulose and
starch. Of course, this is not the actual case, but the assumption
provides a reasonable approximation.

Calculated Maximum Biomass Production and Reported High Yields.

From the foregoing discussion, the upper limit for biomass production
can be calculated by multiplying the efficiency, 0.066 times the daily
total energy times 0.237. For high solar energy areas with 200 Kcal/
$cm^2 \cdot yr$, or $2 \cdot 10^6$ $Kcal/m^2 \cdot yr$, the maximum energy stored would be 0.066
x $2 \cdot 10^6$ = $1.32 \cdot 10^5$ $Kcal/m^2 \cdot yr$. The biomass, if all starch and cellulose,
would be $1.32 \cdot 10^5$ x 0.237 = $3.1284 \cdot 10^4$ grams/yr·m^2, 85.7 grams/day·m^2 or
313 metric tons/hectare yr. This, of course, is the total dry biomass
that could be produced, with continuous optimal growth.

Since optimal conditions of temperature, light absorption, etc. are
never found during all times for crops grown under conventional agriculture,
it is obvious that reported crop yields will not approach closely to this
maximum on an annual yield basis. Also, crops in the temperate zone are
usually grown under lower annual energy imputs. Nevertheless, it is
instructive to compare reported high yields and maximum growth rates with
the calculated values.

What are the actual rates measured? The figures in parentheses (Table
II)[14] are rates during the active growing season, not annual rates. For C-4
plants, these maximum rates range from 138 up to 190 metric tons per hectare
per year. The highest (190) is about half the calculated maximum. Similarly,
the highest reported annual yield, with sugar-cane in Texas, is 112 metric
tons per hectare--again about 1/2 the calculated maximum (263) for the U.S.

Southwest. The energy storage efficiency for these reported yields suggests that 3.3% to perhaps 5% with CEA as the best we can hope for with land plants in the future.

The Photosynthetic Carbon Reduction Pathway (Reductive Pentose Phosphate Pathway). The terms "C-4" plants and "C-3 plants encountered in Table II refer to important characteristics of photosynthetic carbon metabolism that require some discussion. All known green plants and algae capable of oxidation of water to O_2 employ the reductive pentose phosphate cycle (RPP cycle) (Bassham, et al., 1954; Bassham and Calvin, 1957). This RPP cycle begins with the carboxylation of a five-carbon sugar diphosphate (RuDP, Figure 2). 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, 3-phosphoglyceraldehyde (GA13P). 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 mono-phosphate, ribulose 5-phosphate (Ru5P) by a series of condensations, isomeri-zations, 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 Ga13P molecules, there is a net gain of one triose phosphate molecule, equivalent to the three CO_2 molecules taken up. This net Ga13P 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 non-photosynthetic part of the cell for biosynthes·is. 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.high 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.

The C-4 Pathway. 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, crabgrass,sorghum,etc. have, in addition to the RPP Cycle, another CO_2 fixation cycle (Kortschak et al.,1965; Hatch and Slack, 1966; Hatch and Slack, 1970). In this cycle, CO_2 is first fixed by carboxylation of phosphoenolpyruvate, (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) (Figure 3).

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. In another variant, not shown in Figure 3, the malic acid is converted once again to oxalacetic acid in the vascular bundle chloroplasts, and this acid is decarboxylated to give PEPA which is then converted to pyruvate. 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 meso-phyll 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 intercellular 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 C-4 acid products 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. The C-4 plants are believed to have evolved in the very regions we are interested in: the semiarid lands with high solar energy incidence.

Photorespiration (Zelitch, 1975). The reason for the difference lies in the virtual abolition of the effects 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 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 (Zelitch, 1975).

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 (Zelitch, 1975). It is produced in the chloroplasts by oxidation of sugar phosphate to phosphoglycolate and glycolate which is then oxidized outside the chloroplasts to give photo-respiratory 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 inhitibed 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 (Zelitch, 1975). 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 before it can escape from the leaf. C-4 metabolism is of great importance to many plants growing in desert environments. C-4 plants are able to continue net photo-synthetic CO_2 uptake at much lower effective internal CO_2 pressures than C-3 plants, due to the virtual absence of photorespiratory loss of CO_2 from the leaves. This is an advantage when water stress dictates partial or complete closing of stomata, and at other times permits higher rates of

photosynthesis in bright light so that the C-4 plants can grow faster when favorable conditions exist. The importance of Zea mays (corn) to Amerindians of the U.S. Southwest and Mexico stemmed from the ability of this C-4 plant to grow in semiarid environments.

Crassulacean Acid Metabolism. It is of particular interest to consider plants native to semiarid areas and deserts which do not require irrigation. Not surprisingly, many such plants have evolved very long root systems for collecting water from considerable depth and over large areas. They have also developed physiological mechanisms for avoiding water loss. Such mechanisms can conserve water but sometimes at the cost of limited photosynthetic productivity. For example, plants with thick waxy cuticles and with stomata that can be closed during the heat of the day are not able to take in carbon dioxide rapidly; thus photosynthesis is limited. Many desert plants exhibit Crassulacean Acid Metabolism (CAM) in which CO_2 is taken in through stomata open at night. The CO_2 is incorporated by a carboxylation of PEPA to give dicarboxylic acids with four carbon atoms (Figure 4) (for reviews see Osmond, 1975, and Ting, 1975) During the night this PEPA is made from sugars stored in the plant. In the daytime, the stomata are closed, limiting water loss but also CO_2 ingress. The four-carbon acids are decarboxylated, the CO_2 released is reduced to sugars by photosynthesis, and the PEPA is also reduced back to sugars. In the morning and again in the late afternoon there can be intermediate stages when the stomata are open and CO_2 fixation by carboxylation of both ribulose diphosphate (RPP cycle) and PEPA occurs at the same time.

Plants with CAM also exhibit photorespiration in the heat of the day when the stomata are closed. The recycling of CO_2 within the leaf that occurs in such plants is reminiscent of internal CO_2 recycling in C-4 plants (Osmond, 1975).

There are some 18 flowering plant families with CAM metabolism
including the Crassulaceae, the Cactaceae, Alzoaceae, and Succulent
Euphorbiaceae (Ting, 1975). All cacti probably have CAM. Although very
important to desert ecology, there are also many CAM plants found in areas
of high rainfall. In desert CAM plants the cycling of carbon through the
CAM pathway can persist for long periods of time in the absence of any
external water with the stomata closed. In one experiment Opuntia bigelovii
plants were severed at the base and mounted in stands in the desert where
cycling of carbon through CAM on a daily basis persisted for three years
(Ting, 1975). These plants can therefore derive energy from photosynthesis
for very long periods in the desert without opening of stomata in either
night or day. When plants in the desert are watered, the tissue rehydrates,
and the stomata open at night, permitting CO_2 uptake to resume. After
watering by rainfall, the stomatal opening may persist for a longer time in
the morning and more C-3 (reductive pentose phosphate pathway) metabolism
can occur.

Other Physiological Adaptations. The ability to conserve water is
obviously important to desert plants, but there are other requirements as
well. In very hot areas, tolerance of high temperature is required. Desert
plants employ a great variety of physical shapes, reflectances, insulation,
etc. to protect themselves from heat. Since water is a limiting factor,
few species can afford the luxury of extensive cooling by transpiration,
as employed by plants accustomed to plentiful water. One studied species,
which does grow in very hot locations with abundant fresh water demonstrate
the adaptation of enzyme systems to high temperatures. Tidestroma
oblongifola, a C-4 species grows in Death Valley, U.S., at fresh water
springs. Its maximum growth is reached at 45°C, a temperature at which

some temperate zone species greatly decline in growth rate, even if well watered (Bjorkman, 1975). Although accustomed to growth in atmospheres at very low humidity, this plant does very well in chambers maintained at high temperature and high humidity. Plants with such characteristics could prove to be very useful in desert greenhouses when maximum growth rates and minimal cooling are desirable. I will return later to the question of how food and feed might be obtained from such plants.

Desert Agriculture for Food and Chemicals. Many types of utilization of plants growing in the desert might be imagined, from the already widespread (and often excessive) grazing of desert or dryland grasses by livestock to proposals to harvest hydrocarbon-containing plants growing in dry land as a source of liquid fuels and chemical feedstocks, proposed by Calvin (1976). A principal problem with using the desert fringes for grazing livestock is the tendency to over graze, resulting in the conversion of desert fringe to desert (desertification).

One dry land plant which has been suggested as a useful source of food and materials is the common Mesquite (Prosopis species), found growing wild in many parts of the U.S. Southwest (Felkner and Waines, 1977). The pods of this plant have a high food value as protein and carbohydrate and were used by American Indians as an important dietary supplement. Possibly this plant could be used to supply both fuel and food. The plants are legumes and do not require nitrogen fertilization. An annual yield of 43 Kg dry weight of pods was harvested from one large tree in Southern California. The protein has high nutritional value (Felkner and Bandurski, 1977).

Several types of plants well adapted to semiarid environments and capable of producing useful chemicals appear to have considerable potential.

Guayule has been raised in Mexico, and at times in the U.S. for many
years as a source of natural rubber (National Academy of Science, 1977a).
From 1910 to 1946, the U.S. imported more than 150 million pounds of
guayule rubber from Mexico. By 1943, synthetic rubbers were being produced
from fossil fuels, and at the end of World War II these synthetics plus large
supplies of Hevea rubber which became available from Indonesia removed the
necessity for producing Guayule rubber.

In Mexico, however, guayule development has continued, and agencies
of the Mexican government are embarking on rubber production from guayule
plants growing wild over about 4 million hectares. There is considerable
technology available for the production of Guayule, harvesting, extraction
and deresination. From work done in Manzinar, California in 1942-44, it
is clear that good yields of Guayule can be grown in semi-arid regions without
irrigation. Thus, Guayule production may serve as a model for the production
of other dry land plants capable of supplying useful chemicals. Yokayama
(1977) has been able to increase the rubber content of harvested
guayule by a factor of 2 to 3 by treating the 4-week old seedlings with
5000 ppm each of 2-(3,4-dichlorophenoxy)-triethylamine and 2-diethylamino-
ethanol plus a wetting agent, and harvesting three weeks later.

The direct production of hydrocarbons as liquid fuels and chemical
feedstocks by the extraction of latex bearing plants of the Euphorbia family
has been proposed and is being studied by Calvin (1976; 1977a). Test plots
of several species are now being grown in southern California.

Another example of a specialty dry land plant is Jojoba (National
Academy of Science, 1975) This plant is now being grown on Indian reserva-
tions and in other areas in Arizona as a source of a valuable lubricant
with properties which allow it to replace oil obtained from whales.

CEA Installations in Desert Areas. The status of controlled

environment agriculture around the world has been reviewed in 1973 by

Dalrymple (1973), and further discussion of CEA with examples of advanced

CEA systems has been provided in 1977 by the extensive report by de Bivort

(1977). In the latter report it was concluded that CEA could substantially

alleviate the agro-food problems of environmental degradation, regional

shortages of arable land, water, and fertilizers, and unreliability of

production. The costs of present types of CEA systems were found to be

prohibitive for agronomic crops, but acceptable for some high value fresh

vegetables, but new types of CEA systems can be conceived for growing crops

at considerably lower costs and much less total energy consumption than

present CEA. Finally, CEA would appear most attractive if integrated with

solar energy and water management systems for community units of several

thousand people. It was recognized that CEA benefits are of interest to

all concerned with food, energy and water resources and new opportunities

for local self sufficiency (de Bivort, 1977).

In reevaluating the possibilities for low-cost CEA, de Bivort and

his associates proposed a system with a double plastic cover, a cable

suspension, and a solar chimney to pull air over the plants for CO_2 supply

and heat removal. This passive, solar powered system would have dramatically

lowered capital and operating costs, with capital costs estimated to be from

10 to 20 dollars per square meter. There are many other novel ideas in the

proposals, providing an example of the kind of new thinking that will be

required to go from conventional greenhouse raising of very high value plant

crops to the use of CEA for larger scale agriculture.

The system proposed seems designed more for areas with cold winters,

however, than for some of the desert lands we are considering. In the desert

it may be important to <u>lose</u> as much heat at night as possible rather than retaining it by providing a layer of foam insulation.

At the present time, by far the greatest application of covered agriculture is in countries other than semiarid and desert lands. For example, Japan is by far the largest user of covered agriculture, with over 10,000 hectares under cultivation in 1973 (Dalrymple, 1973). Other leading countries, in terms of area under cover include The Netherlands, Italy, Belgium, France, the United Kingdom, USSR, Romania, Greece and South Korea.

Some of the most advanced CEA systems are to be found in arid lands. Although relatively small in area, these facilities are often very productive. The Environmental Research Laboratory (ERL) of the University of Arizona has been a pioneer in the development of CEA for desert environments. Because such environments often contain populations that can otherwise only obtain fresh fruit and vegetables by having them brought in by air at considerable expense, crops grown in CEA can have a high local value, contributing to the cost effectiveness of the installation. The four hectare Environmental Farms, Inc., near Tuscon, Arizona, in the U.S. produces more than one million kilograms of tomatoes annually, with the produce being sold at off season times in the U.S. In Abu Dhabi, nearly a ton of vegetables per day is harvested from five acres of CEA.

Desert greenhouses may be built of air-inflated plastic or combinations of plastic and glass. Sea water can be used for evaporative cooling, and sea water can be distilled to provide for irrigation. Problems of salt disposal in the greenhouses can be controlled because the soils are sandy and can be flushed with fresh water.

Given this promising growth in CEA technology, what is needed for the future? Can the application of CEA, now limited to relatively high value

crops, and to construction requiring rather high investment of capital,
be applied to staple crops such as grains and fodder, and can this
technology ever be constructed by developing nations not favored by the
possession of large deposits of fossil fuel wealth? Finally, can those
inputs of energy from fossil fuels, such as the fuel to drive sea water
pumps, distillation units, and the hydrocarbons required for the synthesis
of plastic be replaced by solar energy? I believe that there is an affirma-
tive answer to these questions.

Besides the above mentioned desert facilities in Arizona and Abu
Dhabi, other covered agriculture in dry lands is to be found in Kuwait,
Iran, Mexico and probably other countries. The system in Abu Dhabi includes
both an air inflated polyethylene structure covering 2.5 hectares, and
structured greenhouses covering one hectare. Cooling is by evaporation
of seawater, with fans forcing air through the cooler and the greenhouses.
Fresh water is obtained by desalting sea water, and considerable care is
taken to use this costly water as efficiently as possible. The water vapor
from the evaporative cooling by seawater is thus extremely important in
preventing excessive water loss to the air from transpiration. Many other
important details of engineering and horticulture have been worked out in
such installations (de Bivort, 1977) and this experience will be a most
valuable resource for the development of larger or more advanced systems.
Further details of CEA, present and proposed, are discussed by de Bivort,
in this workshop.

Can such systems be applied on a large scale to agriculture in arid
or semiarid lands? The author (Bassham, 1977a; 1975; 1976; 1977b) has proposed
covering large areas in dry lands with high greenhouses made from tough,

sun-resistant plastic. The structures might be 1 Km^2 in area and 300 meters 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 would be grown high-protein forage legumes such as alfalfa. They 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 nor CO_2 would be allowed to escape, although some CO_2 would diffuse through the plastic canopy (Figure 5).

While there are serious problems to be overcome with this system (economic, engineering, and physiological), there are a number of important 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 about 200 metric tons (dry weight)/hectare-year. The whole plant except for roots would be harvested and used.

2. 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.

3. Most or perhaps all of the nitrogen requirements in legumes would be met by N_2 fixation, due to stimulation at these high photosynthetic rates. Enrichment with CO_2 can result in a five-fold increase or more in N_2 fixation in the root nodules of legumes (Hardy and Havelka, 1975).

4. 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 (Spencer et al.,1971) The residue is a
feed for ruminants. Most of the feeding of expensive cereal grains to
cattle could be replaced by this alfalfa. 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 (Edwards et al., 1975). Nutritionally it is as
good as milk protein (Stahmann, 1968) and far superior to soy protein.

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

    Since this scheme is envisaged as applicable to areas far removed
from the sea, the use of evaporative cooling with sea water was not
assumed. Instead, it was proposed to include a high enough canopy to
enclose a sufficient volume of air so that the daytime temperature excursion
would not be excessive. This might work in the higher cooler desert areas,
especially where nighttime temperatures are very low, and sufficient loss
of heat through the plastic at night occurs to bring the internal tempera-
ture down by morning. Even so, additional cooling powered by solar energy
collectors outside the enclosure might be required.

    The advantages of a completely closed system over the air flow-through
system would be complete retention of water vapor and more effective
enrichment with added CO_2.

    Of course, there are many problems; some very serious. The green-
house 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 between inside and outside,

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 CO_2, perhaps capable of synthesis from materials grown under the canopy, and inexpensive. In fact, use of fossil fuels to synthesize the plastic could be avoided by making the plastic from some of the solid biomass residue, after protein extraction. Cellulose could be converted to glucose by treatment with exaymes from the fungi (Wilke, ed. 1975) and the resulting glucose could be fermented to give ethanol. Ethanol in turn could be converted to ethylene and thence to polyethylene or other suitable plastic. The insoluble material of plants also contains polymers of xylose. After acid hydrolysis, the sylose can be converted to furfural (Sheppard, 1977), a possible starting material for other plastics.

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 discussion of possible solutions will require considerable engineering study to be meaningful. For example, large structures would require reinforcement of the plastic cover with wire and cable (Figures 6,7), with both internal and external tie-down cables to strengthen the structure against strong winds. For initial installations it might be advantageous to site the structure in a valley in order to minimize wind effects. An important question is whether or not the warming of air under the structure would supply sufficient lift to inflate the canopy. Perhaps if the heating due to "greenhouse effect" is excessive, air would have to be withdrawn from the top of the canopy through very large ducts and passed through solar powered chillers to cool the air and condense water vapor after which both cool air and water could be recycled.

Although use of greenhouses goes far back in man's history, advanced CEA is in its infancy. The promising starts made by several countries around the Persian Gulf and in the U.S. and Mexico should serve as a beginning for more extensive and sophisticated projects. In particular, systems should eventually be powered entirely by solar energy. There are complex problems of mechanical, chemical, and civil engineering involved.

At the same time, CEA can create new conditions for plant growth for which no plants growing in natural environments are fully adapted. The possibilities are very great for plant breeding to produce plants capable of improved properties suitable for CEA. Among these may be mentioned:

1) High temperature tolerance

2) High growth rates at high temperatures and humidity

3) Maximum use of CO_2 enrichment and ability to tolerate substantial levels of sulfur dioxide

4) Resistance to mildew

5) For legumes, high rates of N_2 fixation under CEA conditions.

No doubt many more could be added to this list.

There is a need for a long range, stable (in terms of financial support) program of research and development in CEA, in which engineers, agronomists, economists, plant physiologists, and chemists would interact and work together towards a really new kind of agriculture capable of highly efficient solar energy utilization to produce needed food, feed, and materials.

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TABLE I

PRIMARY PHOTOSYNTHETIC PRODUCTIVITY OF THE EARTH

	Area (total = 510 million Km^2)		Net Productivity (total = 155.2 billion tons dry wt./yr)	
Total Earth	100		100	
Continents	29.2		64.6	
Forests	9.8		41.6	
Tropical Rain		3.3		21.9
Raingreen		1.5		7.3
Summer Green		1.4		4.5
Chaparral		0.3		0.7
Warm Temperate Mixed		1.0		3.2
Boreal (Northern)		2.4		3.9
Woodland	1.4		2.7	
Dwarf and Scrub	5.1		1.5	
Tundra		1.6		0.7
Desert Scrub		3.5		0.8
Grassland	4.7		9.7	
Tropical		2.9		6.8
Temperate		1.8		2.9
Desert (Extreme)	4.7		0	
Dry		1.7		0
Ice		3.0		0
Cultivated Land	2.7		5.9	
Freshwater	0.8		3.2	
Swamp & Marsh		0.4		2.6
Lake & Stream		0.4		0.6
Oceans	70.8		35.4	
Reefs & Estuaries		0.4		2.6
Continental Shelf		5.1		6.0
Open Ocean		65.1		26.7
Upwelling Zones		0.08		0.1

Percentages based on data presented by H. Lieth at the Second National Biological Congress, 1971.

TABLE II

31

MAXIMUM PHOTOSYNTHETIC PRODUCTIVITY AND MEASURED MAXIMUM YIELDS

IN SELECTED PLANTS

	Assumed Radiation Kcal/cm^2·yr	gm/m^2·day	metric tons/ hectare yr.	eff. %
Theoretical max. (Table II)				
High Solar Desert ann.	200	86	313	6.6
U.S. Average annual	144	61	224	6.6
U.S. Southwest ave. ann.	168	72	263	6.6
U.S. Southwest, summer	247	106	387	6.6
Maximum Measured				
C-4 Plants				
Sugar cane	247	38	(138)*	2.4
Napier grass	247	39	(139)	2.4
Sudan grass (Sorghum)	247	51	(186)	3.2
Corn (Zea mays)	247	52	(190)	3.2
C-3 Plants				
Sugar beet	247	31	(113)	1.9
Alfalfa	247	23	(84)	1.4
Chlorella	247	28	(102)	1.7
Annual Yield				
C-4 Plants				
Sugar cane	168	31	112	2.8
Sudan grass (Sorghum)	168	10	36	0.9
Corn (Zea mays)	168	4	13	0.4
C-3 Plants				
Alfalfa	168	8	29	0.7
Eucalyptus	168	15	54	1.3
Sugar beet	168	9	33	0.8
Algae	168	24	87	2.2

*Parentheses indicate maximum rates. Since these are not sustained over a whole year, they are much higher than annual yields.

Figure Captions

Figure 1. Mean Annual Insolation--Worldwide. Smaller area local varia-
tions are omitted in this global map in order to provide a
general view of incidence of solar energy at the earth's surface.
The figures are for total insolation over one year.

Figure 2. 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
GA13P. Abbreviations: RuDP, Ribulose 1,5-diphosphate; PGA, 3-
phosphoglycerate; DPGA, 1,3-diphosphoglycerate; NADPH and $NADP^+$,
reduced and oxidized nicotinamide-adenine dinucleotide phosphate,
respectively; GA13P, 3-phosphoglyceraldehyde; DHAP, dihydroxyacetone
phosphate; FDP, fructose 1,6-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.

Figure 3. 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: PEPA, phosphorenolpyruvate; OAA, oxaloacetate.

Figure 4. Crassulacean Acid Metabolism (CAM). In plants with CAM, stomata are closed during the heat of the day in order to prevent loss of water. This also prevents CO_2 uptake in the daytime. At night, stomata are open, CO_2 is taken up and is incorporated by carboxylation of PEPA, giving rise to C-4 acids. The PEPA is made by glycolysis of stored sugars. In the daytime the C-4 acids are decarboxylated by one of two posssible routes. In some plants the product is pyruvate which must then by converted back to PEPA using ATP. In other plants the C-4 acid is converted directly to PEPA by a reaction using ATP. The CO_2 is then incorporated via the reductive pentose phosphate cycle while the PEPA is converted to PGA which is then reduced to stored carbohydrates. During the early morning and late afternoon hours, some aspects of both the night and day metabolism can occur simultaneously.
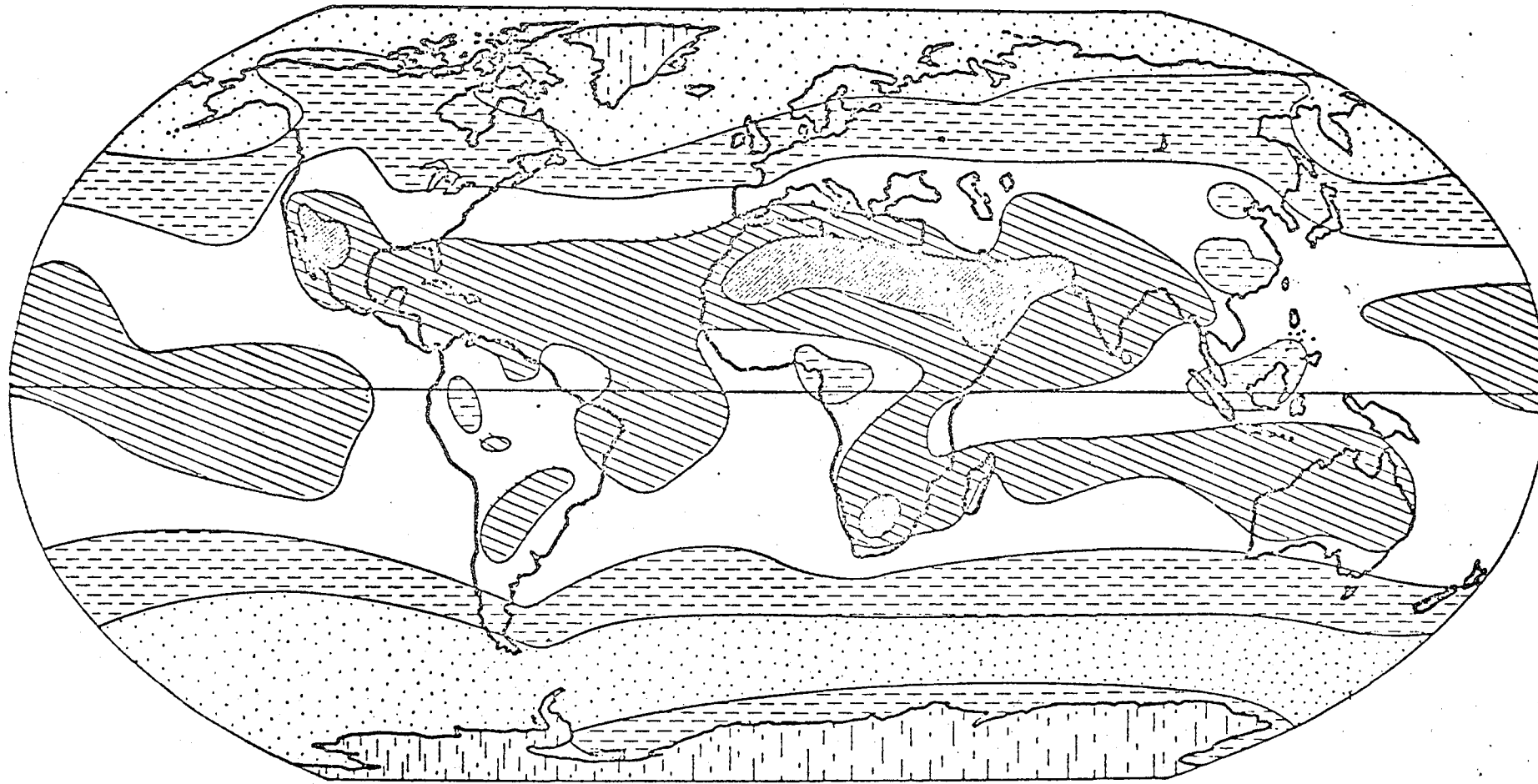
Figure 5. Large Scale Controlled Environment Agriculture (CEA). A schematic version of a possible large scale CEA installation. The canopy for CEA in this version would be an inflated plastic cover reinforced with wire and cable. In the version shown, the installation would be about 1 kilometer wide by 3 kilometers long and about 200 meters

high. Power generating plants burning fossil fuel would be situated nearby and the exhaust gasses containing CO_2 and water would be fed into the greenhouse. The agricultural crops would be harvested several times a year. The installation would thus provide power, food, and feed to a nearby city. If possible, initial installations should be situated in valleys enclosed by hills in order to minimize wind effects. Due to the great height of the canopy sufficient air would be enclosed within the structure to limit the temperature excursion due to greenhouse effect within any single daylight period. Radiation of heat from the plastic canopy to the desert night sky together with some artificial cooling of the air inside the greenhouse would be required to bring the temperature down during the night. Water vapor in the enclosure would condense and "rain down" on the crops, or if heat exchange units were used, could be condensed in the heat exchanger and recycled.
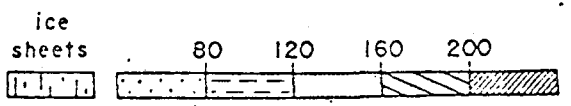
Figure 6. Top View of Reinforced Plastic Canopy. Flexible plastic of sufficient thickness and durability to withstand the pressures of wind and sun would be reinforced with a grid of light-weight steel cables (shown) and possibly a finer grid of fine wire (not shown). Cables attached to the reinforcing cable both inside the structure and outside as shown in this figure and figure 7 would serve to anchor the structure to the earth.

Figure 7. Cross Section of Canopy Structure. The attachment points for tie-down cables would be required both inside and outside the structure. It should be emphasized that both this figure and the previous

figure represent only a preliminary concept and that no engineering studies have been made at this date.
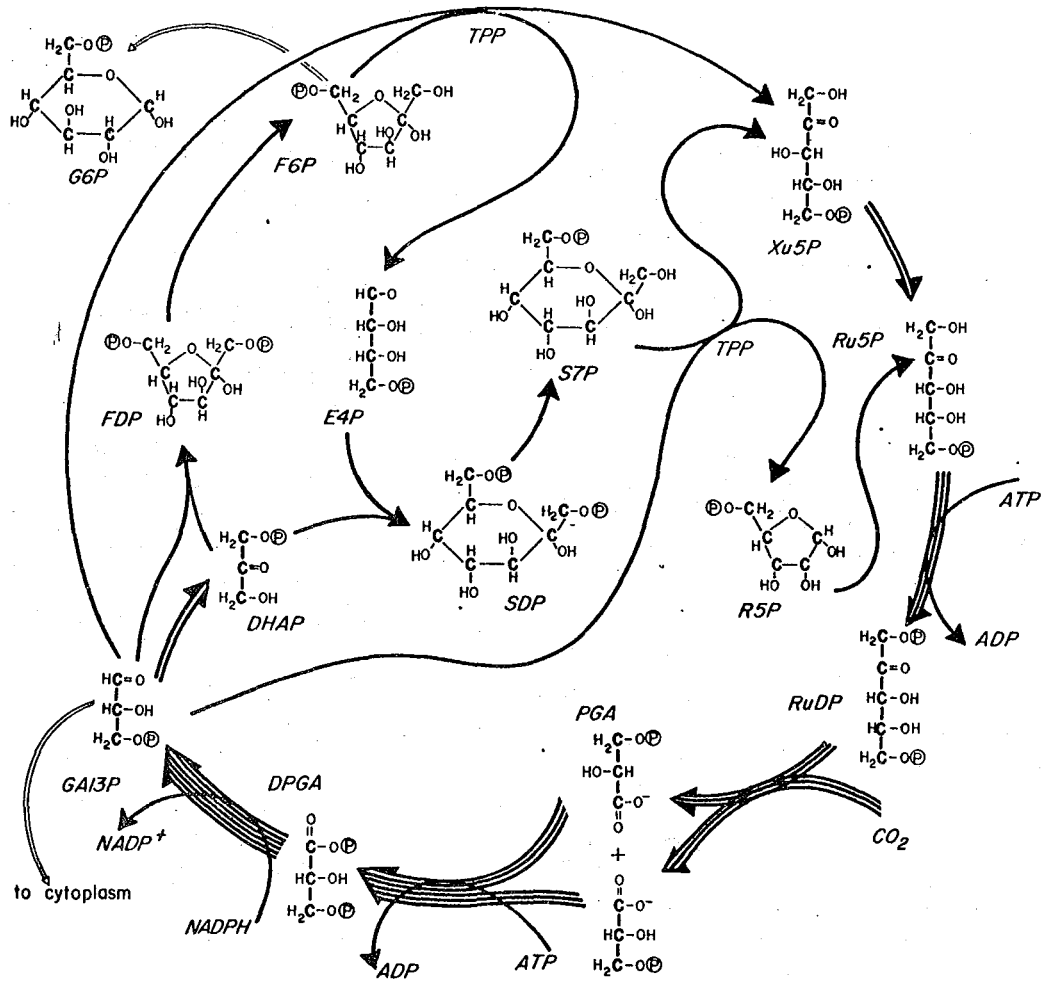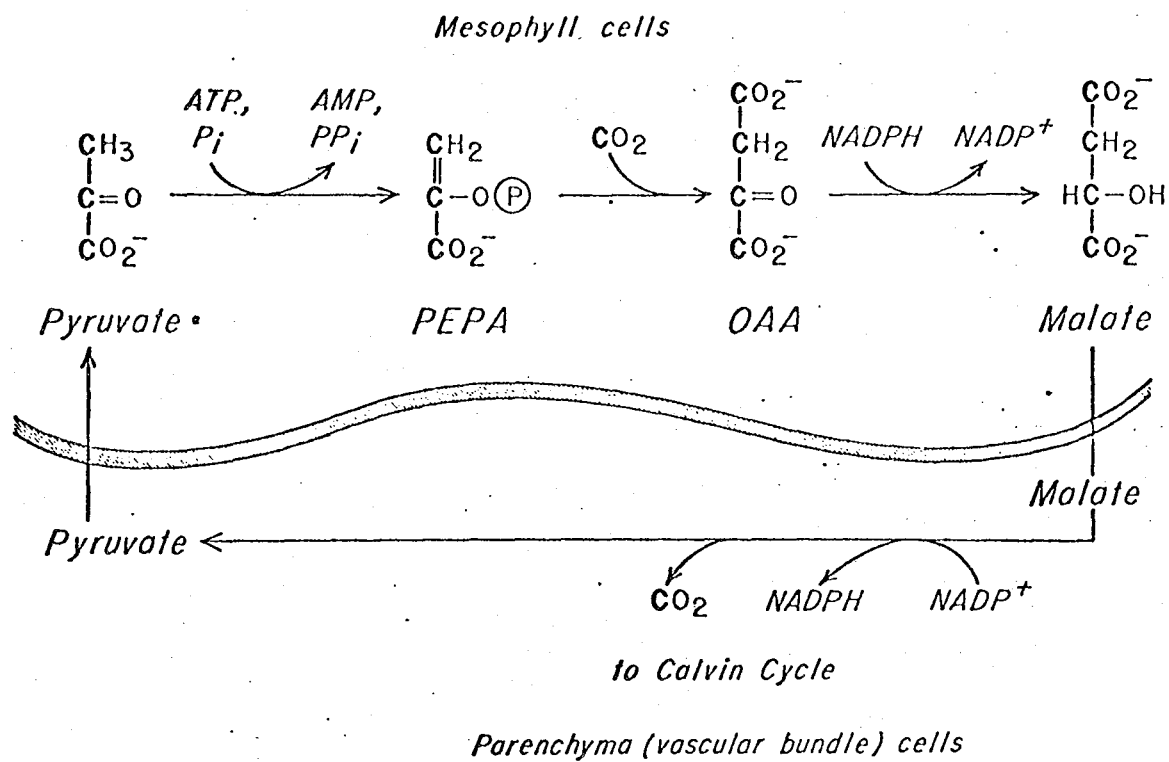
MEAN ANNUAL INSOLATION

kcal/cm^2/yr. (1.33 W/m^2)

ice sheets   80   120   160   200

Bassham, J.A.

Fig. 1

XBL 76ll-9660

Bassham

Figure 2

Mesophyll cells

$$\underset{\text{Pyruvate}}{\begin{array}{c} CH_3 \\ | \\ C=O \\ | \\ CO_2^- \end{array}} \xrightarrow[\substack{P_i}]{ATP,} \quad \xrightarrow{\substack{AMP, \\ PP_i}} \underset{\text{PEPA}}{\begin{array}{c} CH_2 \\ \| \\ C-O\,\textcircled{P} \\ | \\ CO_2^- \end{array}} \xrightarrow{CO_2} \underset{\text{OAA}}{\begin{array}{c} CO_2^- \\ | \\ CH_2 \\ | \\ C=O \\ | \\ CO_2^- \end{array}} \xrightarrow[\substack{NADPH \quad NADP^+}]{} \underset{\text{Malate}}{\begin{array}{c} CO_2^- \\ | \\ CH_2 \\ | \\ HC-OH \\ | \\ CO_2^- \end{array}}$$

Malate

Pyruvate ←

CO_2 NADPH $NADP^+$

to Calvin Cycle

Parenchyma (vascular bundle) cells

XBL 714-5113

Bassham, J. A.

Fig. 3

Glucose-6-P $\longrightarrow$ $\longrightarrow$ $\longrightarrow$ Triose-P $\overline{\underline{NIGHT}}$

GLYCOLYSIS

$$H_2C-O\textcircled{P} \longrightarrow \longrightarrow CH_2 \qquad CO_2 \quad CO_2^-$$

Starch

Sugars

$$HC-OH \longrightarrow C-O\textcircled{P} \longrightarrow C=O \qquad NADPH \longrightarrow$$

ATP

NADPH

$$CO_2^- \longleftarrow \longleftarrow CO_2^- \longleftarrow CO_2^- \longleftarrow$$

3-PGA   PEPA   ATP   or   NADP$^+$

CALVIN
CYCLE

CO_2

Glucose-P

Triose P

Ribulose 1,5
diphosphate

$$\begin{array}{c} CO_2^- \\ | \\ CH_2 \\ | \\ HC-OH \\ | \\ CO_2^- \end{array}$$

Malate
and
other
C$_4$ acids

Fructose-6-P

ATP

ATP,
P$_i$

$$\begin{array}{c} CH_3 \\ | \\ C=O \\ | \\ CO_2^- \end{array}$$

Ribulose-
5-P $\overline{\underline{DAY}}$

PYRUVATE

39
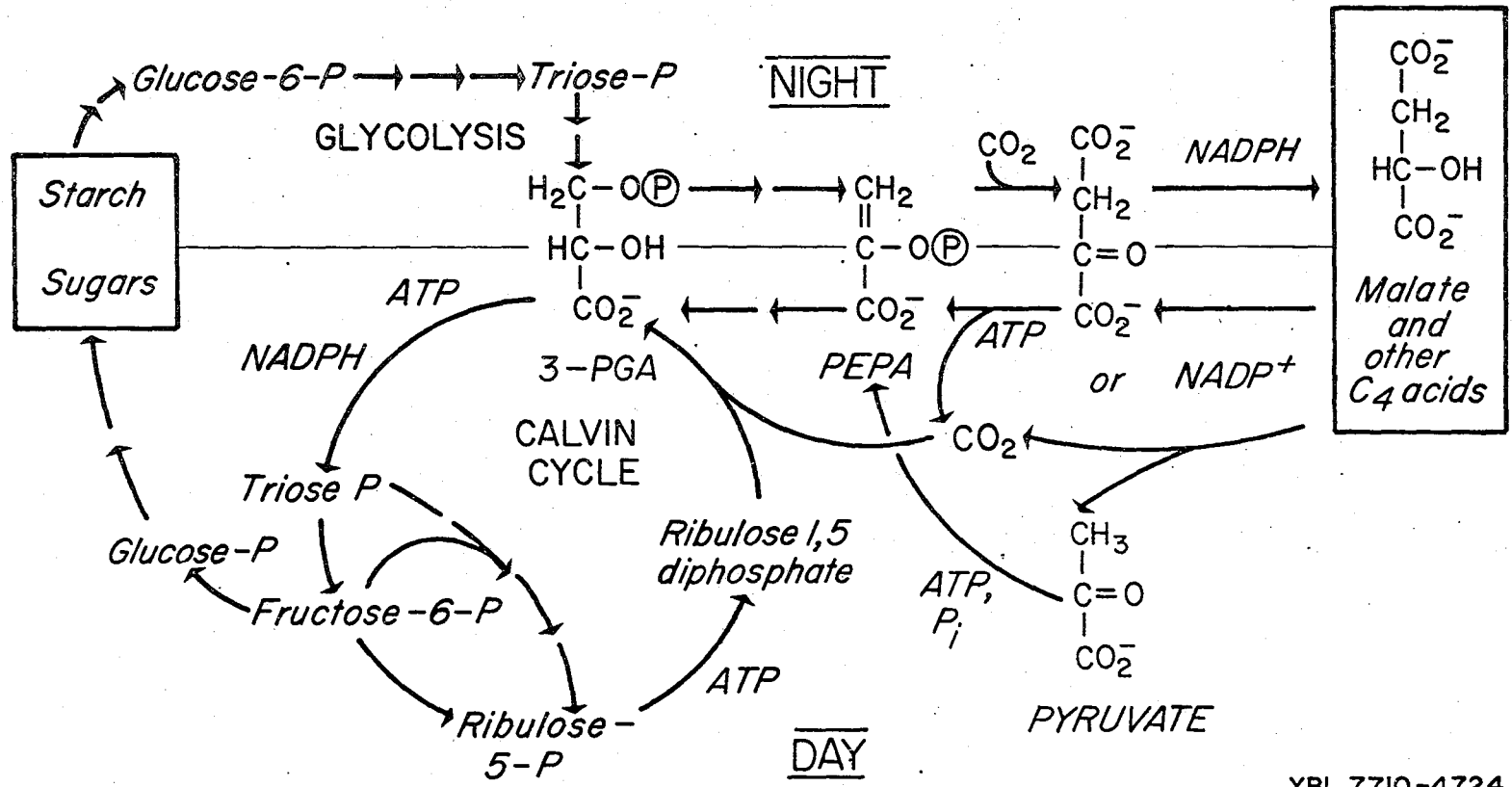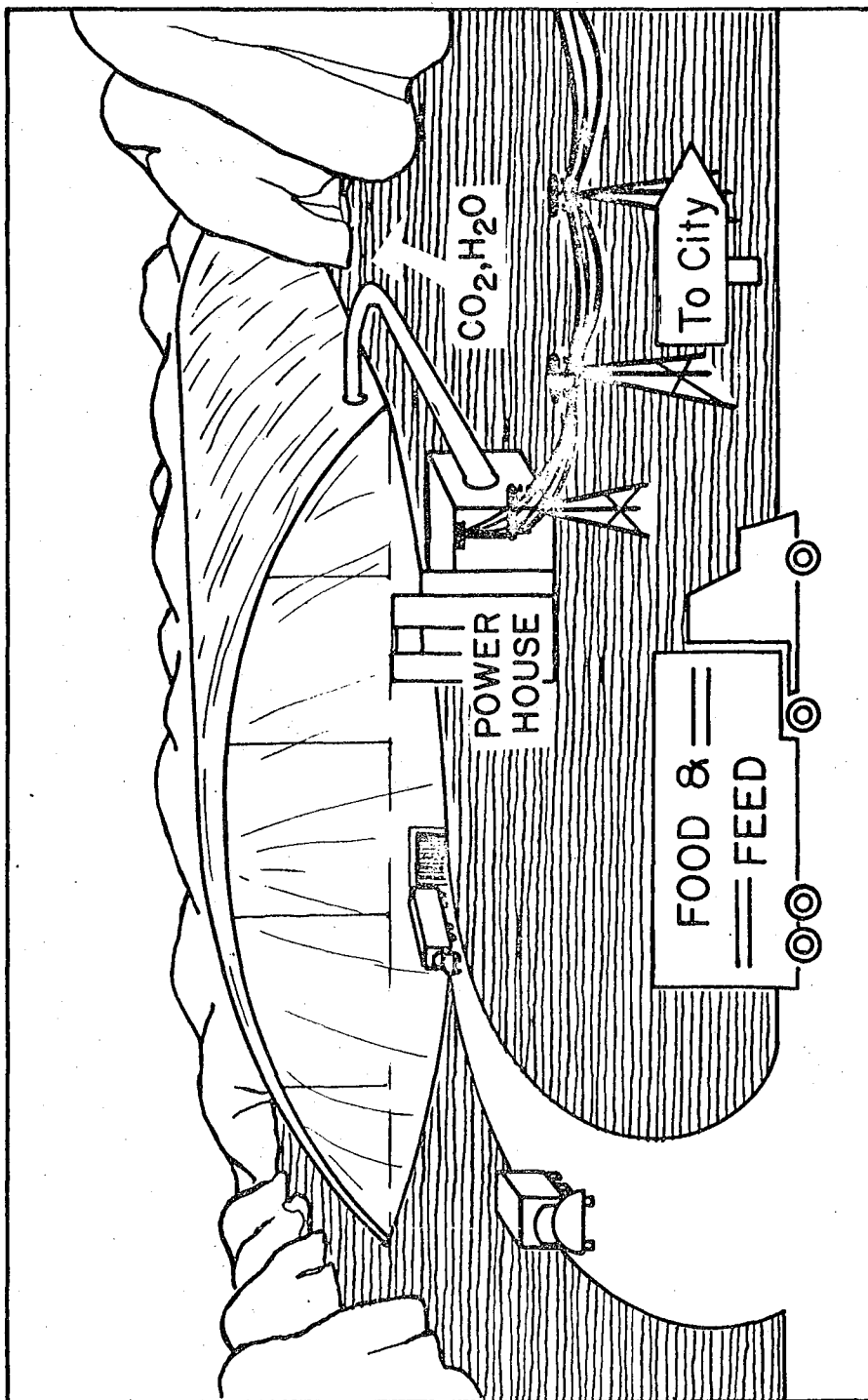
XBL 7711-4738A

Bassham

Figure 5

SECTION OF CANOPY FOR INFLATED GREENHOUSE

TOP VIEW

OUTSIDE CABLE
TIE-DOWN

TIE-DOWN
ATTACHMENT
POINTS

MAJOR CABLE
REINFORCEMENTS

←200m→

PLASTIC WITH WIRE REINFORCEMENTS
(NOT SHOWN)

XBL 7710-4721

41
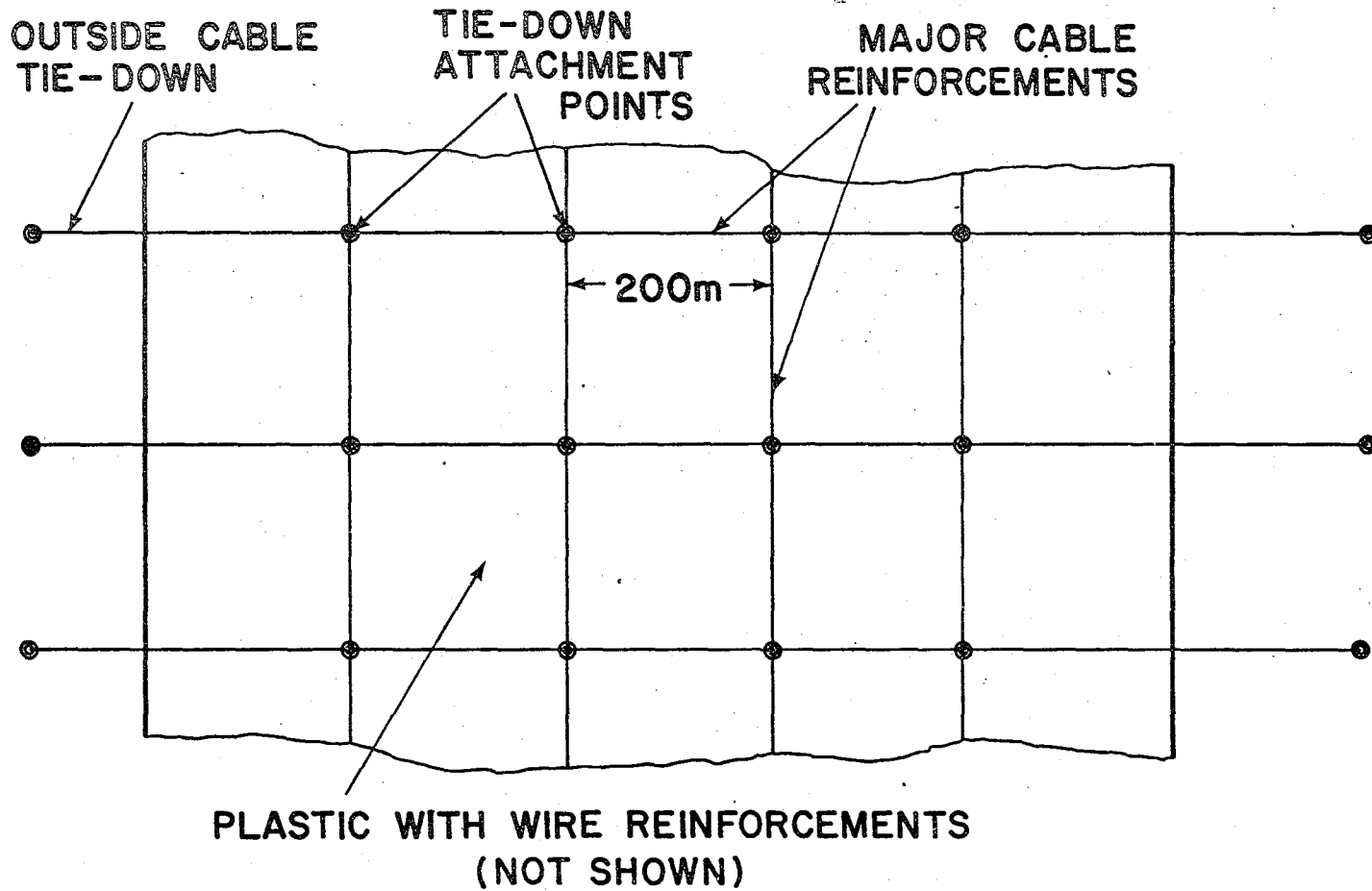
Bassham

Figure 6

INFLATED GREENHOUSE STRUCTURE - CROSS SECTION

PLASTIC CANOPY WITH
CABLE REINFORCEMENT

TIE-DOWN
CABLES

200m

1000m

SEAL

CONCRETE
ANCHORS
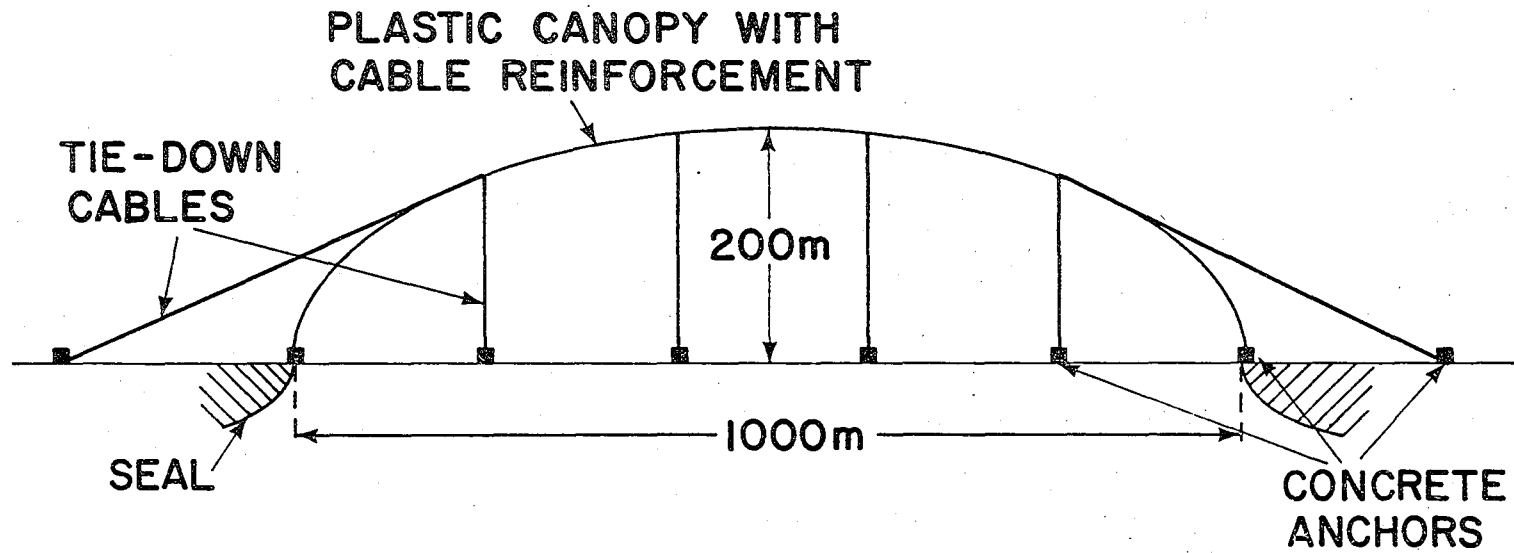
XBL 7710-4722

Bassham

Figure 7