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REVIEW PAPER

SOLAR ENERGY USE THROUGH BIOLOGY —PAST, PRESENT AND FUTURE†

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Abstract—Each year plant photosynthesis fixes about 2×10^{11} tonnes of carbon with an energy content of 3×10^{21} J—this is about 10× the world's annual energy use and 200× our food-energy consumption. All the atmospheric CO_2 is cycled through plants every 300 yr, all the O_2 every 2000 yr and all the H_2O every 2 million yr. The magnitude and role of photosynthesis is largely unrecognized principally because we utilize such a small fraction of the fixed carbon and because we do not realize the important recycling phenomena. Fortunately for us plants are very adaptable and exist in great diversity—they could thus continue indefinitely to supply us with renewable quantities of food, fibre, fuel and chemicals. Photosynthesis in the past provided all our fossil carbon resources. It now seems time that we recognize seriously and evaluate what photosynthesis can do for us in the future via traditional and non-conventional mechanisms, e.g. H_2 production, carbon fixation.

INTRODUCTION[1-7]

There are not many people nowadays who need reminding that our fossil carbon reserves—whether for fuel or chemicals—are the products of past photosynthesis. Photosynthesis is *the* key process in life and as developed by plants can be simply represented as:

$$H_2O + CO_2 \xrightarrow[\text{solar energy}]{\text{plants}} \text{organic materials} + O_2.$$

In addition to C, H and O, the plants also incorporate nitrogen and sulphur into the organic material via light-dependent reactions—this latter point is often not appreciated. Thus the basic processes of photosynthesis have determined life as we know it (dependent on organic materials and oxygen) and will continue to play *the* major role in the integration of bioenergetic systems in the future.

In the past photosynthesis has given us coal, oil and gas, fuelwood, food, fibre and chemicals. The relative use of these fixed carbon sources has varied over the years and will undoubtedly do so in the future. It seems necessary now to look at how photosynthesis fits into the biosphere and how we could possibly use biological solar energy conversion in the future as a source of raw materials—and not necessarily in the traditional ways.

Each year plant photosynthesis fixes about 2×10^{11} tonnes of carbon with an energy content of 3×10^{21} J; this is about 10× the world's annual energy use and 200× our food-energy consumption, even though the photosynthetic process is operating at only a 0.1 per cent efficiency (total incoming radiation on earth's surface over whole year). The efficiency on land may be about 0.2–0.3 per cent overall, whereas average agriculture may be about 0.5 per cent efficient (see later). It should be realized early on that these efficiencies represent *stored energy* and not just the initial conversion efficiencies so often quoted in other energy systems. All the atmospheric CO_2 is cycled through plants every 300 yr, all the O_2 every 2000 yr and all the H_2O every 2 million yr. The magnitude and role of photosynthesis is largely unrecognized principally because we utilize such a small fraction of the fixed carbon and because we don't realize the important recycling phenomena—any interference in this latter role from pollution could have serious consequences. Fortunately for us plants are very adaptable and exist in great diversity—they could thus continue indefinitely to supply us with renewable quantities of food, fibre, fuel and chemicals. If the impending liquid fuel problem which is predicted to be upon us due to shortages and/or large price increases within the next 10–15 yr comes about, we may turn to plant products sooner than we expect to help solve the problem. Let us be prepared to have a viable choice of options!

EVOLUTION AND PAST PHOTOSYNTHESIS[8-14]

It probably all started about 3.3 billion yr ago when an anaerobic fermenting bacteria, like *Clostridium*, developed with the ability to use the abundant organic compounds present on the primitive earth as a source of carbon and energy. The earth's atmosphere contained H_2 and N_2 but no O_2—thus with good reason these bacteria also acquired the ability to metabolize H_2 and fix N_2. Figure 1 shows a simplified evolutionary tree based on the amino-acid sequences and structures of proteins like ferrodoxins and cytochromes—the electron transport protein ferredoxin occurring in all organisms so far investigated. There are obviously problems in constructing such a tree but a combination of geological, microfossil, biochemical and systematic evidence points toward such a scheme being a reasonable approximation. Dis-

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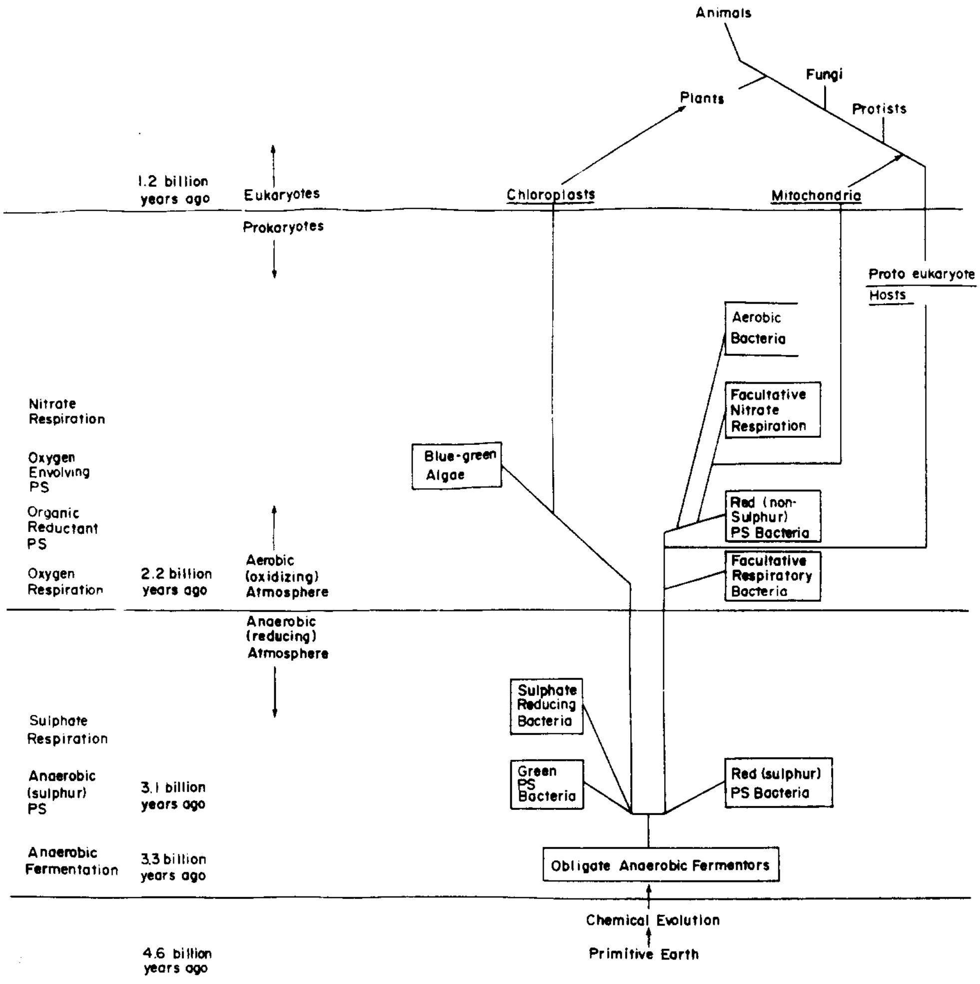


Fig. 1. Simplified evolutionary tree adapted from protein sequence data of Schwarz and Dayhoff[11] and Dickerson[14] and discussion by Towe[11]. Methane producing bacteria may have arisen soon after the photosynthetic bacteria.

agreements exist most notably on the stages at which blue-green algae and respiratory bacteria developed and on the symbiotic origin of chloroplasts and mitochondria in eukaryotic (higher) organisms.

The development of the chlorophyll-membrane system in photosynthetic bacteria (green and red) at about 3.1 billion yr ago allowed these bacteria to use H_2S as a source of electrons and CO_2 as a source of carbon, so liberating them from dependence on organic compounds and starting the evolution of photosynthesis. There is, and probably was, a close relationship between the green photosynthetic bacteria and the sulphate-reducing bacteria which can use the sulphate (produced by photosynthetic oxidation of H_2S) as a terminal electron acceptor in its own metabolism, in turn producing reduced sulphur compounds for re-use by the photosynthetic bacteria—hence a sulphur cycle driven by solar energy. The microfossils and stromatolites from the Onverwacht Series of Southern Africa, dated between 2.8 and 3.3 billion yr old, suggest diverse microbial forms representative of anaerobic fermentors and photosynthesizers including a green filamentous, gliding bacterium like *Chloroflexus* which may be an intermediate stage between photosynthetic bacteria and blue-green algae.

At about 2.2 billion yr ago geological evidence from banded-iron formations shows that oxygen started to become abundant in the earth's atmosphere. Prior to this some oxygen was produced by UV induced photolysis of water so providing selective pressures for developing enzymes to protect against the toxic effects of O_2 and also to develop processes of respiration to use the O_2 as a terminal electron acceptor—so deriving much greater quantities of energy from the oxidation of the organic substrates. Facultative bacteria evolved which were able to use O_2 or other electron acceptors under anaerobic conditions. Undoubtedly the development of O_2-evolving photosynthesis by the blue-green algae e.g. *Anabaena* changed the course of evolution dramatically. These algae acquired the ability to split water as a source of electrons for CO_2 fixation thus availing themselves of an unlimited substrate (H_2O). They did this probably by adding on a second photosystem to the photosystem I of green photosynthetic bacteria. Figures 2 and 3 show the electron transport schemes of photosynthesis in bacteria

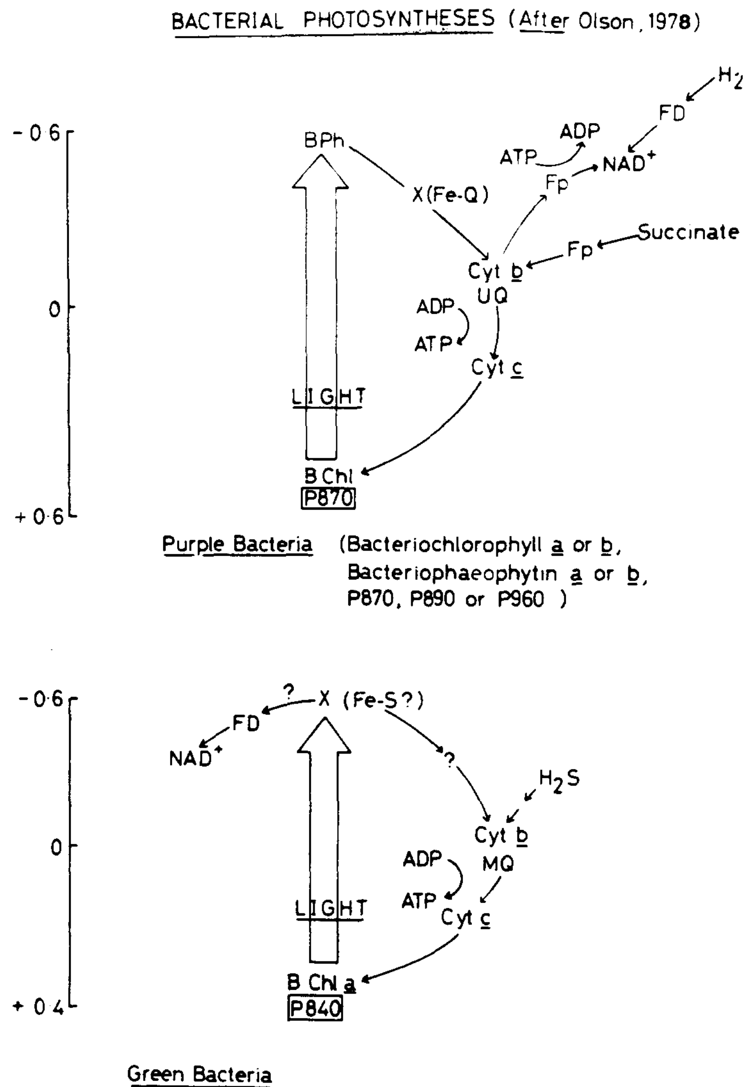


Fig. 2. Electron transport schemes in purple and green photosynthetic bacteria (after J. M. Olson in "Evolutionary Biology", T. Dobzhansky *et al.*, eds., Vol. II, pp. 1–37, Plenum Press, New York, 1978).

and plants (algae)—Fig. 3(b) shows how the electron transport components may be oriented across the chloroplast membrane. Recently algae have been found, e.g. *Oscillatoria*, which are able to use either H_2O or H_2S as a source of electrons so switching back and forth between operating as blue-green algae or photosynthetic bacteria. Two very important consequences of H_2O splitting photosynthesis are: (i) oxygen is evolved as a by-product; and (ii) we learnt that biological systems cannot split water into H_2 and O_2 by visible light except by the input of two quanta of light (photosystems II and I) for every electron transferred from H_2O (this principle may also be true for the photochemical splitting of water using simpler systems than the complex biological membranes).

The red photosynthetic bacteria (sulphur type, e.g. *Chromatium*) evolved into the non-sulphur type, e.g. *Rhodopseudomonas*, which have the ability to live photosynthetically under N_2 or by respiration in the dark in the presence of oxygen—the same electron transport chain is used in both photosynthesis and respiration. Whether or not they arose before the facultative respiratory bacteria, e.g. *Bacillus*, is difficult to decide but there is little doubt that the ability to use oxygen was a great advantage to these red photosynthetic bacteria. It is likely that the red non-sulphur bacteria were precursors of nitrate respirers, e.g. *Paracoccus denitrificans*, and mitochondria since the metabolism and other characteristics of all three are similar in many respects.

At about 1.2 billion yr ago the eukaryotes (higher organisms) probably evolved as a result of several independent symbiotic associations between prokaryote hosts and chloroplasts and mitochondria. These early symbioses in turn led to protists (e.g. amoebae), fungi, plants (including higher algae) and animals. The chloroplasts of eukaryotes share a recent ancestry with blue-green algae and the mitochondria with red photosynthetic bacteria (non-sulphur) and certain respiring bacteria like *P. denitrificans*. Once eukaryotic organisms had been formed the way lay ahead for a great proliferation

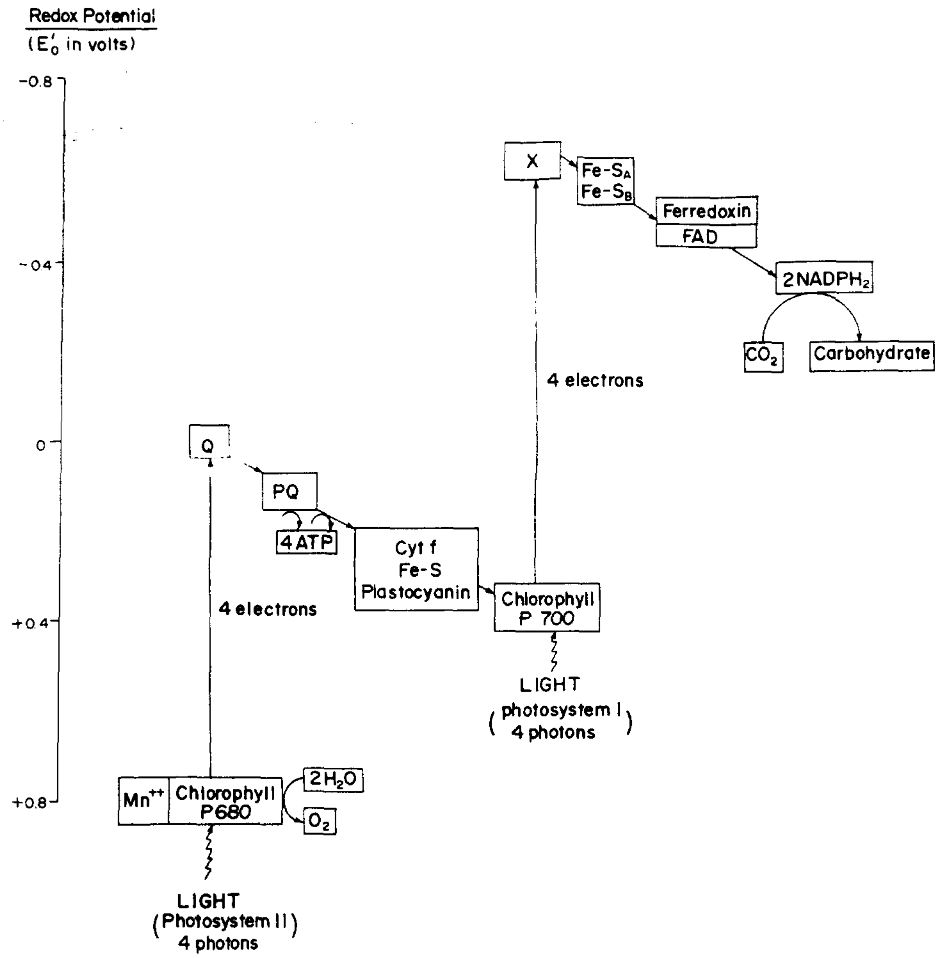


Fig. 3(a). Electron transport scheme in plant photosynthesis showing the two photosystems required to split H_2O and produce $NADPH_2$ to fix CO_2[7].

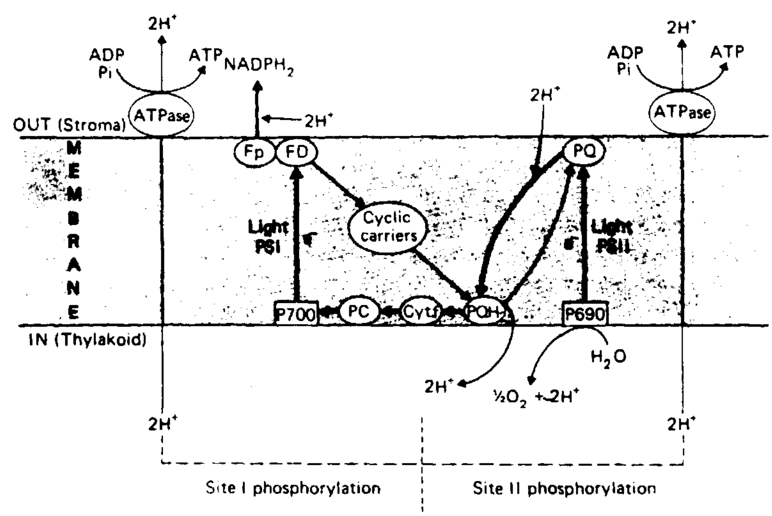
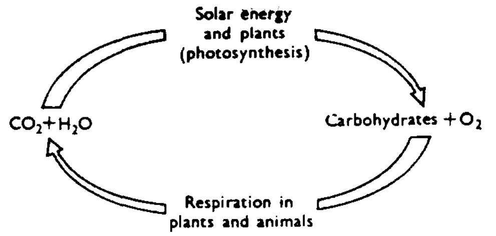


Fig. 3(b). Possible orientation of photosynthetic electron transport across a chloroplast membrane, also showing sites of ATP formation and translocation of protons[1].

and diversity of organisms leading to life as we know it at present. It is ultimately dependent on plant-type photosynthesis to provide the reducing power to fix C, N, H and S into organic compounds and to evolve O_2 in respiration—thus closing the cycle (Fig. 4).

The fossil fuels (coal, oil and gas) are the result of past



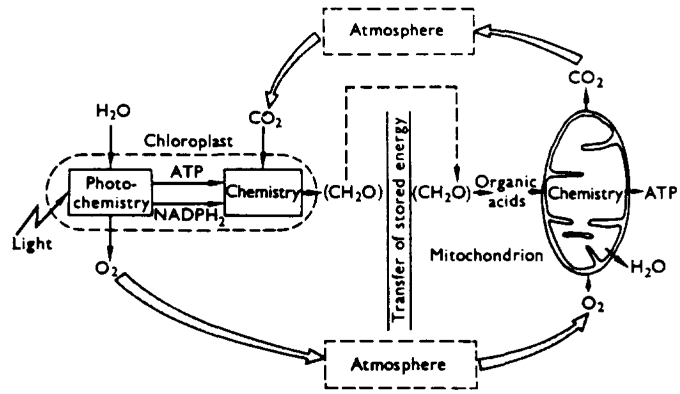


Fig. 4. The energy and carbon cycle in Nature[1].

photosynthesis which occurred mainly during the Carboniferous era, about 300–350 million yr ago. Dense forests decayed under the anaerobic conditions of swamps so ultimately storing the fixed carbon as coal. The exact microbiological mechanisms for the formation of oil and gas do not seem to be known for certain but the reactions probably occurred in a marine environment. Whatever the mechanisms of formation, degradation and storage it can be seen from Table 1 that large quantities of fossil fuels were stored. However, it should be noted that the proven fossil fuel reserves of 9×10^{11} tonnes only equals the amount of carbon presently stored in the world's biomass and that the total estimated fossil resources are only 10 times this amount. Thus the stored fossil carbon may only represent a small proportion of the photosynthetically fixed carbon which was formed during the Carboniferous era over the tens of millions of years.

PRESENT PHOTOSYNTHESIS[7, 15–55]

Table 1 also shows that the present net photosynthesis "produces" energy at about 3×10^{21} J per annum which is about 10 times the world's annual use of energy of about 0.3×10^{21} J; also the energy content of the 8×10^{11} tonnes carbon (about 20×10^{21} J) presently stored in the world's biomass (90 per cent in trees, only 2 per cent in the oceans) is nearly 100 times the world's annual energy use. The amount of carbon in the world's biomass is approximately equal to the carbon present as CO_2 in the atmosphere and present as CO_2 in the ocean surface layers (these three quantities lie between 6 and 8×10^{11} tonnes). These figures naturally lead to the question of carbon cycling in the biosphere and the related problems of CO_2 accumulation in the atmosphere (a 25 per cent increase since 1850) due to burning of fossil fuels over the last century. Fortunately much has been published on these matters over the last year or so but the complete quantitative aspects of the carbon balances still remain unresolved.

Figure 5 depicts the global carbon balances showing the main carbon deposits and annual exchanges of carbon into and out of the atmosphere.

CO_2 *in the atmosphere*

The present-day carbon content of the atmosphere (7×10^{11} t) represents a CO_2 concentration of 334 ppm. There is a winter to summer oscillation of 5–15 ppm due to photosynthesis. Stuiver estimated that in 1850 the CO_2 content of the air was approximately 268 ppm—thus there has been about a 25 per cent increase over the last 125 yr (i.e. 0.5 ppm increase per annum). In the century after 1850 about 1.8×10^9 tonnes of carbon per annum were added to the atmosphere—2/3 of this increase is attributed to net CO_2 release from the biosphere mostly between 1860 and 1930, e.g. wood burning and deforestation (which has decreased the land biomass by 7 per cent) and 1/3 of the increase due to burning of fossil fuels. Present day fossil fuel use is at the rate of about 5×10^9 t carbon per annum which would increase the CO_2 content of the air by an amount of 2.4 ppm per annum if all of it accumulated in the atmosphere. Herein lies the dilemma since the measured annual increase is only about 1 ppm, corresponding to an increase in CO_2 of the air of 2.3×10^9 t/yr, i.e. only about a half of the

Table 1. Fossil fuel reserves and resources, biomass production and CO_2 balances (data calculated from Grenon[17], Woodwell[24], Stuiver[25], Boardman[15] and Pimentel[44])

(1) *Proven reserves*	Tonnes coal equivalent		
Coal	5×10^{11}		
Oil	2×10^{11}		
Gas	1×10^{11}		
	8×10^{11}t	$= 25 \times 10^{21}$J	
(2) *Estimated resources*	Tonnes coal equivalent		
Coal	85×10^{11}		
Oil	5×10^{11}		
Gas	3×10^{11}		
Unconventional gas and oil	20×10^{11}		
	113×10^{11}t	$= 300 \times 10^{21}$J	
(3) *Fossil fuels used so far* (1976)	2×10^{11}t carbon	$= 6 \times 10^{21}$ J	
(4) *World's annual energy use*		3×10^{20}J	(5×10^9t carbon from fossil fuels)
(5) *Annual photosynthesis*			
(a) net primary production	8×10^{10}t carbon $= 2 \times 10^{11}$t organic matter	$= 3 \times 10^{21}$J	
(b) cultivated land only	0.4×10^{10}t carbon		
(6) *Stored in biomass*			
(a) total (90 per cent in trees)	8×10^{11}t carbon	$= 20 \times 10^{21}$J	
(b) cultimated land only (standing mass)	0.06×10^{11}t carbon		
(7) *Atmospheric CO_2*	7×10^{11}t carbon		
(8) *CO_2 in ocean surface layers*	6×10^{11}t carbon		
(9) *Soil organic matter*	$10 \rightarrow 30 \times 10^{11}$t carbon		
(10) *Ocean organic matter*	17×10^{11}t carbon		

These data, although imprecise, show that (a) the world's annual use of energy is only 0.1 of the annual photosynthetic energy storage, (b) stored biomass is equivalent to the proven fossil fuel reserves, (c) the amount of carbon stored in biomass is approximately the same as the atmospheric carbon (CO_2) and the carbon as CO_2 in the surface layers of the ocean. Destruction of forests and soil humus is thought to release about 4–8×10^9t carbon to the atmosphere each year—equivalent to that released by burning fossil fuels.

carbon appears in the atmosphere. Thus there is a balance of 2.7×10^9 t of fossil fuel carbon/yr which must be accounted for. It is calculated on present assumptions that the oceans might with difficulty absorb a maximum of 3×10^9 t carbon/yr. (However, see Wong's estimate of 4.1×10^9 t carbon absorption by the ocean). This carbon balance from fossil fuels would be quantitatively correct if there was no net present day CO_2 release by the biosphere through, for example, the destruction of forests and the oxidation of soil organic matter. However a number of workers now present evidence that the biosphere has not been, and is not now, a sink or deposit for atmospheric CO_2 and in fact is a source of CO_2. Woodwell calculates a net release from biomass at 4 to 8×10^9 t carbon/yr, (i.e. about the same as the release from fossil fuel combustion) while Bolin's figures show about 2×10^9 t/yr. [Stuiver seems to disagree since, from his carbon isotope distribution measurements, he states that "At present, fossil fuel combustion is the dominant factor because net biospheric fluxes appear to have been negligible over recent decades."] If we use Woodwells' average figure of 6×10^9 t from biomass and add 2×10^9 t from the oxidation of soil organic matter (humus) we have an amount of about 8×10^9 t of carbon/yr which must be accounted for, since it does not appear in the atmosphere. Either the capacity of the oceans to absorb this amount of carbon has been underestimated or there are other terrestrial sinks which have not been recognized. Forest biomass has been suggested as such a sink but the recent evidence suggests that forests are being cleared at an increasing rate—especially the tropical rain forests which "represent the largest single pool of carbon in the biota and also have the highest net primary production". If the rate of clearing of tropical forests was about 1 per cent per annum, as the evidence suggests, this alone would release 4.5×10^9 t carbon per yr. Replacement of these primary forests by agriculture or secondary forests results in much lower average primary productivity and less storage of carbon as biomass. Thus on these assumptions plants do not appear to be a sink for excess carbon but are actually a source of CO_2 in the air.

Increases in atmospheric CO_2 have been postulated to have serious consequences on the earth's climate. Doubling the preindustrial CO_2 level in the air to about 540–590 ppm would increase the global atmosphere temperature by about 3°C, with increases of 6 or 7°C towards the poles and only 1°C at the equator. There would also

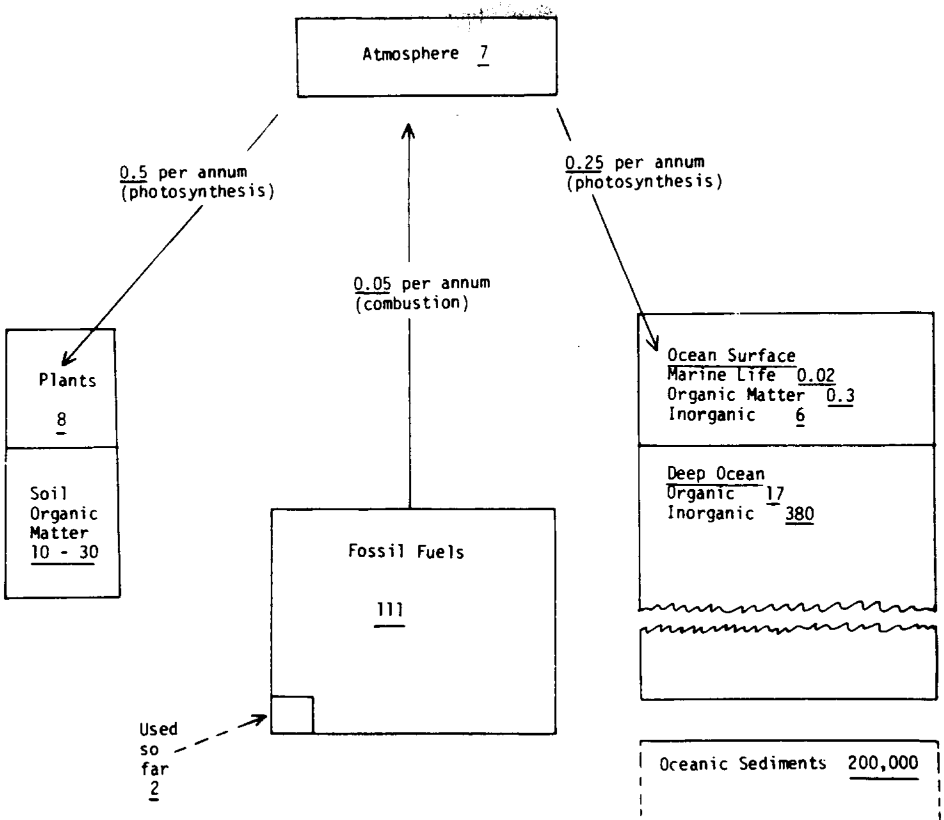


Fig. 5. The global carbon balance sheet showing the main carbon deposits and annual exchange rates. A simplified diagram adapted from Woodwell[24] and Stuiver[25] and Table 1. Units = 10^{11} tonnes. The total carbon reservoir is about 430×10^{11} tonnes of which the atmosphere represents 1.6 per cent, the biosphere (plants, marine life and organic matter in soil and ocean surface) 4.3 per cent, and the ocean 94.2 per cent.

be an overall 7 per cent increase in precipitation but the lower latitudes would become drier and the higher latitudes wetter. If these climate models are correct the CO_2 increases would result in profound changes in the patterns of vegetation, desertification and agriculture. Increases in CO_2 concentrations, temperature and rainfall all benefit plant productivity to various degrees but whether it would be a regional effect only, or not, would determine global photosynthetic productivity and carbon balances.

Siegenthaler and Oeschger have estimated the amount of fossil fuel which we may burn if we do not want to increase the atmospheric CO_2 to a level greater than 50 per cent above the preindustrial level—which would lead to "only" a 1–2°C global temperature increase with not too disastrous climatological consequences. In such a scenario we could continue burning fossil fuels until the turn of the century at the present rate but then "new technologies would have to take over a substantial part of global energy production". If their assumptions are correct "we may burn over the next centuries not much more than 10 per cent of the known fossil fuel reserves". After such production of CO_2 from fossil fuels "At equilibrium the atmosphere would still contain at least one eighth of the total man-made CO_2". Thus we could not easily restore the original CO_2 level of the atmosphere just by stopping the burning of fossil fuels. The sooner we can put solar-based energy systems into operation the better for the atmosphere!

Efficiency of photosynthesis

The average efficiency at which photosynthesis operates is not very high. The world's annual net production of organic matter (2×10^{11} t) with an energy content of 3×10^{21} J is only equivalent to a photosynthetic efficiency of 0.1 per cent since the total incoming radiation at the earth's land (and sea) surface is 3×10^{24} J per annum. This figure is an average of about 0.3 per cent for land areas (30 per cent of the world's total surface area) and the very low efficiencies of the large ocean areas. Nevertheless it should be appreciated that there are many limiting factors such as water and temperature which dictate the overall low efficiencies of photosynthesis (besides the physiological ones listed in Table 2). It should also be recognised that these efficiencies represent *stored energy* and are not just instantaneous conversion efficiencies as are often quoted for other energy systems—without considering the storage factor. Tables 3–5 show average-to-good yields for agriculture and yields from specific crops. It is seen that "good" agriculture seldom operates at an efficiency of greater than about 0.5 per cent in temperate zones and 1 per cent in warmer zones—expressed on a whole-year basis for total incoming radiation and not just for the growing season with photosynthetically active radiation. Figure 6 shows how the photosynthetic efficiency affects the yield of organic matter—naturally if overall efficiencies can be increased by good plant-growth practices and/or manipulation of plants for optimum yields, so will the

Table 2. Photosynthetic efficiency and energy losses[7]

	Available light energy
At sea level	100 per cent
50 per cent loss as a result of 400–700 nm light being the photosynthetically usable wavelengths	50 per cent
20 per cent loss due to reflection, absorption and transmission by leaves	40 per cent
77 per cent loss representing quantum efficiency requirements for CO_2 fixation in 680 nm light (assuming 10 quanta/CO_2)† and that the energy content of 575 nm red light is the radiation peak of visible light	9.2 per cent
40 per cent loss due to respiration	5.5 per cent
	Overall PS efficiency

†If the minimum quantum requirement is 8 quanta/CO_2, then this loss factor becomes 72 per cent (instead of 77 per cent) giving a final photosynthetic efficiency of 6.7 per cent (instead of 5.5 per cent).

Table 3. Average-to-good annual yields of dry matter production[7]

	Tonnes/hectare/yr	$g/m^2/day$	Photosynthetic efficiency (percent of total radiation)
Tropical			
Napier grass	88	24	1.6
Sugar cane	66	18	1.2
Reed swamp	59	16	1.1
Annual crops	30	—	—
Perennial crops	75–80	—	—
Rain forest	35–50	—	—
Temperate (Europe)			
Perennial crops	29	8	1.0
Annual crops	22	6	0.8
Grassland	22	6	0.8
Evergreen forest	22	6	0.8
Deciduous forest	15	4	0.6
Savanna	11	3	—
Desert	1	0.3	0.02

efficiencies of conversion of radiation into stored energy be increased.

Food production

The author belongs to the school of thought which believes that it is very easy to produce food—the problem comes from post-harvest losses and the inability to distribute the food to the people who may require it. There are many reasons for these two inadequacies in different regions of the world—they have been well documented so I will not discuss them. The land areas devoted to arable (cultivated cropland) agriculture are really rather small—in the U.K. and the U.S.A. only about 0.2 of their total land areas, and in the U.S.A. about 60 per cent of this cropland is used for growing animal feed. In both these countries there are surpluses of animal and plant products which can be difficult to store and economically subsidize. A point to make is that many countries of the world have surplus land areas which are not necessarily devoted to conventional agriculture and could be used for producing more organic material for subsequent use as food, fuel, fibre or chemicals—of course, circumstances vary tremendously around the world but each country could well take a more detailed and possibly dispassionate, but pragmatic, look at its own land use potentials.

On a global basis Buringh has estimated the maximum food production capacity of the world and pointed out the advantages of "modern" agriculture as opposed to "labour-oriented" agriculture. He calculates that the total potential agricultural land of the world is 3419 million hectares (equal to 0.25 of the total land area) compared to the 1406 million hectares presently cultivated—at present two-thirds of this land is used for cereal crop production. He makes the staggering claim that thirty times the grain production could be achieved in the world compared to present production. He believes that it makes far more sense to increase the productivity of existing cultivated land by using modern techniques instead of opening up new land with low productivity. Only 0.2 of the presently cultivated land is used for improved or "modern" agriculture while the remaining 0.8 has low productivity levels. Reclaiming new land is seen as poor agricultural practice and uneconomic. Productive agriculture on "one-third of the presently cultivated and grazing land can produce enough food for the present population and consequently even more land is available for forest and wildlife". Of course, there are many problems in introducing "modern" agriculture all over the world, e.g. water, fertilizers, energy, soil erosion, technical expertise, social practices, and so on. However, the advantages seem very great, especially since it would free, or leave untouched, large areas which could be reforested for other uses, such as fuelwood provision, maintaining ecological and climatological balances, energy farming operations, etc.

Table 4. Some high short-term dry weight yields of crops and their short-term photosynthetic efficiencies[7]

Crop	Country	$g/m^2/day$	Photosynthetic efficiency (% of total radiation)
Temperate			
Tall fescue	U.K.	43	3.5
Rye-grass	U.K.	28	2.5
Cocksfoot	U.K.	40	3.3
Sugar beet	U.K.	31	4.3
Kale	U.K.	21	2.2
Barley	U.K.	23	1.8
Maize	U.K.	24	3.4
Wheat	Netherlands	18	1.7
Peas	Netherlands	20	1.9
Red clover	New Zealand	23	1.9
Maize	New Zealand	29	2.7
Maize	U.S., Kentucky	40	3.4
Sub-tropical			
Alfalfa	U.S., California	23	1.4
Potato	U.S., California	37	2.3
Pine	Australia	41	2.7
Cotton	U.S., Georgia	27	2.1
Rice	S. Australia	23	1.4
Sugar cane	U.S., Texas	31	2.8
Sudan grass	U.S., California	51	3.0
Maize	U.S., California	52	2.9
Algae	U.S., California	24	1.5
Tropical			
Cassava	Malaysia	18	2.0
Rice	Tanzania	17	1.7
Rice	Phillippines	27	2.9
Palm oil	Malaysia (whole year)	11	1.4
Napier grass	El Salvador	39	4.2
Bullrush millet	Australia, NT	54	4.3
Sugar cane	Hawaii	37	3.8
Maize	Thailand	31	2.7

Other yields: Loomis and Gerakis[28] discuss figures for (a) sunflower, growth rates of 79 to 104 $g/m^2/day$ have been reported, with a three week mean rate of 63.8 $g/m^2/day$ giving a photosynthetic efficiency of 7.5 per cent, (b) carrot, growth rates of 146 $g/m^2/day$ and a dry matter yield of 54.5 tonnes/ha after 160 days were reported.

Note: Yields in $g/m^2/day$ can be converted to tonnes/ha/yr by multiplying by 3.65.

Table 5. Efficiencies of solar energy conversion for a whole year[29]

	Sugarcane (one crop/yr)	Cowpea (four crops/yr)
Incident solar energy	100	100
Incident photosynthetically active radiation (PAR)	48	48
PAR trapped by crop	37	15
Potential value of energy fixed by photosynthesis	5.7	3.2
Actual value of energy fixed by gross photosynthesis	2.9	0.9
Energy fixed in the biomass (gross PS minus respiration)	2.1	0.6
Energy fixed in aerial parts of the plant	1.6	0.5

Energy ratios

In any agricultural system it is important to consider how much energy is derived from the system compared to how much is put in to operate it (energy output/input ratio)—sunlight via photosynthesis provides a "free" energy input compared to the costly energy inputs such as fertilizers, tractor fuel, etc. Table 6 shows some ratios which highlight the problem of energy intensive agriculture, such as greenhouse production, and the low energy conversion efficiencies of animal systems. Both greenhouses and animals convert less than a tenth of the input energy into usable energy. Both greenhouse and animal products are important components of our modern agriculture. However, a small decrease in the rearing of animals for food would release large amounts of organic material for food, fuel, etc. if this was considered desirable. Calculations in the United States on energy output:input ratios in the production of maize grain have shown that this ratio has fallen from 3.7 in 1945 to 2.8 in 1970; that is a doubling of yield has been achieved (most important) by a trebling of energy input, mostly as a result of increased fertilization. In the U.K. where maize production is mostly for forage and the whole plant is considered, the output:input energy ratios are between 5 and 9. If the great use of nitrogen fertilisers (which often contribute 50 per cent of the energy input) could be decreased without lowering yields, e.g. by N_2 fixation or

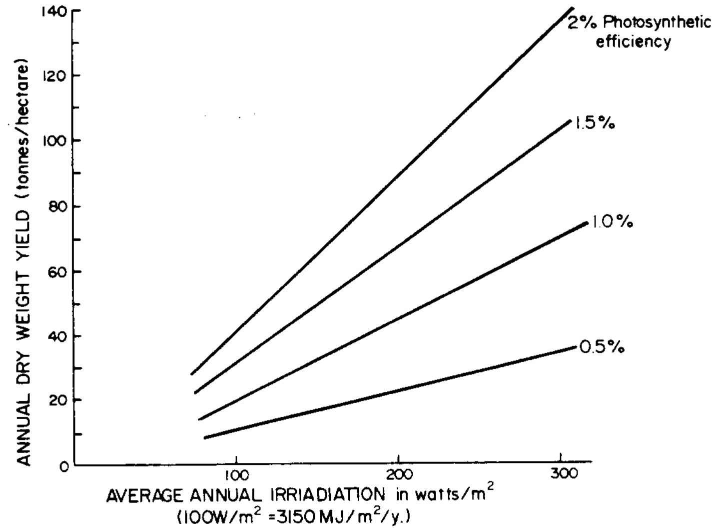


Fig. 6. Expected annual plant yields as a function of annular solar irradiation at various photosynthetic efficiences[7].

Table 6. Energy output/input ratios for the U.K.[43]

Whole farms (average)	
Specialist dairy	0.38
Mainly dairy	0.55
Cattle and sheep	0.59
Sheep	0.25
Pig and poultry	0.32
Cereal	1.9
Barley (and oats)	2.4
Maize (grain)	2.3
Wheat (grain)	3.4
Potatoes	1.6
Sugarbeet	
Sugar	3.6
Gross output	4.2
Grass	
Low efficiency—grazing	9.1
Low efficiency—grazing and hay	5.6
High efficiency—hay	2.4
High efficiency—silage	2.4
Peas—fresh	0.9
—canned	0.1
Carrots	1.1
Brussels sprouts	0.2
Greenhouse lettuce	0.002
Poultry—meat	0.1
—eggs	0.1
Fish	0.05
Milk	0.4

manure, considerable savings in energy could result. Even though there has been some criticism of the excessive use of nitrogen fertilizers in the past, it should be pointed out that for every joule of N fertilizer energy added to the plant about 6 J of plant energy is produced—photosynthesis is the catalyst which "increases" this energy and the plant cannot operate efficiently unless it has optimum amounts of nitrogen (and other minerals like P, K, and trace elements).

Greenhouses

I want to briefly touch on greenhouses since I think these have a good future in the specialised agriculture field. In the past greenhouses have been generally poorly designed and have used large amounts of energy for heating and cooling. Presently new designs are being used which use selective filtering of light, heat storage, radiative cooling, utilization of waste heat, newer irrigation systems, mechanized multi-storey buildings for precise control of the environment, and so on. Generally, one wishes to produce a high-value and quality product on a year-round basis. Besides speciality foods, chemicals and pharmaceuticals can be produced from plants grown in such greenhouses. Land use is decreased to a minimum which gives high productivitity on a hectare basis; careful analysis has to be made of the energy inputs and the economic and labour benefits.

FUTURE PHOTOSYNTHESIS[7, 15, 32–40, 56–109]

Plants occur in great diversity of form and environment. They also synthesize a vast range of chemicals which can be used as sources of food, fuel, fibre and chemicals (Fig. 7). Plants are also highly adaptive and can be manipulated genetically and chemically—they will undoubtedly be so manipulated to an increasing extent in the future.

Biomass

Solar energy is a very attractive source of energy for the future but it does have disadvantages—what energy source does not! Solar energy is diffuse and is intermittent on a daily and seasonal basis thus collection and storage costs can be high. However plants are designed to capture diffuse radiation and store it for future use. Thus there is much serious thought—and money—being given to ideas of using biomass (specially grown and/or residues) as a source of energy—especially for liquid fuels, but also for power generation. The author is personally aware of biomass programmes in the U.K., Ireland, France, Germany, Denmark, Sweden, U.S.A., Mexico, Brazil, Australia, New Zealand, India, Philippines.

The following advantages have been identified: (a)

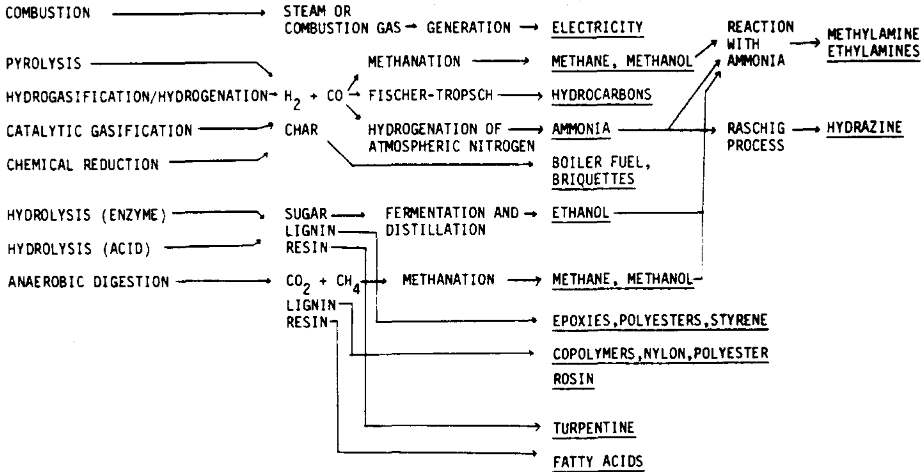


Fig. 7. Potential biomass energy conversion processes and by-products after Ref. [64].

capable of storing energy for use at will; (b) renewable; (c) dependent on technology already available, with minimal capital input; (d) can be developed with our present manpower and material resources; (e) reasonably priced; (f) ecologically inoffensive and free of hazards, other than fire risk. The easily identified problems are (a) land use competition; (b) land areas required; (c) supply uncertainty in the initial phases; (d) fertilizer and water requirements. The long term advantages are however very considerable which is why so much work is going into these systems. The programmes vary in their emphasis, depending on many local factors, but do show that most of the research and development should be done locally without relying too heavily on other countries. Such research and development is an ideal opportunity to develop and encourage local scientists, engineers and administrators in one field of energy supply. Even if biomass systems do not become significant suppliers of energy in a specific country in the future, the spin off in terms of benefits to agriculture, forestry, land use patterns, bioconversion technology, etc. are, I think, significant.

U.S.A.

The U.S.A. has a very large research and development programme on biomass which had a 1977/78 budget of $22m. Details of the type of research and development being funded are available in numerous, bulky publications, but a number of articles in "Science" have appeared over the last year which give invaluable details and references. The most recent by Burwell entitled "Solar biomass energy: an overview of U.S. potential" gives a good general picture and presents some of his own ideas of the "best" systems for the future. Many points are made in the article. The 1975 U.S. use of energy was 71×10^{18} J—the total standing forest inventory has an energy content three times this annual use of energy. The total annual biomass growth of commercial forests is 9.3×10^{18} J of which 6.6×10^{18} J is potentially collectible. Cropland agriculture produces energy totalling about 12×10^{18} J annually of which about 40 per cent is represented by residues left on the land. Grain crops alone produce about 7.1×10^{18} J annually of which 5.9×10^{18} J is the net collectible energy yield—3.8×10^{18} J of this is in the form of residues. A detailed analysis of "potentially usuable biomass residues" shows that of the residues currently collected 2.1×10^{18} J could be obtained from urban solid wastes, 1.0×10^{18} J from animal feedlots, canneries, wood manufacture, etc. Uncollected residues such as cereal straw, cornstalks and logging residues could contribute 5×10^{18} J per annum. Burwell considers that major opportunities for energy provision lie in the use of forest residues and improved management of productive forest land. He also makes the interesting point that 60 per cent of U.S. cropland is dedicated to the production of livestock—and this excludes the contribution that 282 million hectares (38 per cent of mainland U.S.A. area) of pasture and rangeland make to livestock support. There are thus large areas of land which could be used in the future for the production of biomass, if society so wished!

The concept of intensive silviculture biomass farms or energy farms has been the subject of detailed analysis in the U.S.A. Fast-growing deciduous trees which coppice (resprout from stumps) have been examined as have numerous other trees, including those which fix N_2 to NH_3. One recent major study came to some of the following conclusions.

"Major energy products which could be economically derived from wood biomass at sometime in the future include electricity, ammonia, methanol, ethanol, and possibly medium-Btu fuel gas"; "the major opportunity for biomass in electric generation is in small plant retrofit or co-firing with coal"; "Production of ammonia from wood biomass is estimated to be marginally competitive today"; "methanol production from wood could become competitive within the next decade". One interesting fact to emerge from this detailed study on 10 areas (6 non-agricultural, 2 agricultural, 1 swampland and 1 forest) is that only 10 per cent of the land in a given area need to be used for energy farming so alleviating the necessity of acquiring 20,000–40,000 acre blocks of lands to fuel a power station—the limiting factor seems to be the distance required to transport the timber from the farm to the conversion facility.

The use of agricultural residues as a source of energy in the U.S.A. has been the subject of another major evaluation. Following a nationwide county-by-county estimate of the quantities of residue produced and their availability, a detailed analysis was made of ten areas each with a radius of 50 miles or more. Both studies indicated that a national total of 430 million dry tons was available each year—this figure is made up from 280 million tons of crop residues 120 million tons of residues from logging (at the mill and on the forest floor) and 30 million tons from animal manure. Excluded from these figures were residues from food processing, grazing animals, and hay and forage crops. Theoretically these 430 million tons of residue could supply 31 per cent of the electricity, 20 per cent of the natural gas, or 8 per cent of the oil requirements of the U.S.A. This is very unlikely to ever happen since at present 20 per cent of the residues are used, and 58 per cent are returned to the soil—leaving only 22 per cent classified as excess. However, these percentages will change as other uses (energy, chemicals, etc) and prices emerge. This detailed report came, *inter alia* to the following important conclusions (a) 8 of the 10 study areas have significant quantities of relatively low-cost residues, (b) process steam and electric power production and anaerobic digestion are the most economically feasible, proven conversion technologies (c) residue conversions by these technologies is frequently cost-competitive with energy production at new facilities fueled with oil, propane, coal or natural gas. At present electricity production from residues is cost-competitive at 5 study areas, process steam at 7 areas and synthetic natural gas (compared to propane costs) at 2 areas. Overall the two most important factors which determine the feasibility of conversion of residues to energy are price and availability—factors affecting these are both discussed at length.

In another study in the U.S.A. Lipinsky outlines why he considers that fuels from biomass should be integrated with food and material production systems, i.e. adaptive systems should be encouraged which will "modify themselves to meet evolving needs and constraints". Such adaptive systems contrast with energy farms and the use of agriculture residues—but of course, the three systems can blend into each other depending on circumstances. Thus biomass intermediates (besides food) are processed into fuels or materials depending on relative price levels. Two examples cited are corn and sugarcane production. It is "theoretically possible to reorganize the present U.S. corn biomass system to permit the production of $10–18 \times 10^9$ l of ethanol (or its equivalent in other fermentation products) while obtaining the same quantity of end-use food products in the form of beef, poultry and pork". The ethanol could be blended at 10 per cent with 0.25 of U.S. gasoline. Sugarcane produces numerous byproducts such as molasses, alcohol and bagasse which can be used for power generation, fermentable substrates, substitute wood, etc. Newer processing techniques could make it easier to adapt sugarcane processing to prevailing market needs for sugar and byproducts. Lipinsky concludes that "fuels from biomass may possibly supply 10 per cent or more of a curtailed U.S. energy consumption", "competitive costs for fuels from biomass would depend primarily on the integration of fuel production with food and materials production", and that "knowing when and where to switch from emphasis on food and materials to emphasis on fuels is just as important as knowing how to produce the fuels".

Looking at biomass from the petrochemical point of view is the subject of an article by Wishart of the Union Carbide Corporation. He sees "the costs for oil and gas converging with and eventually exceeding the costs for some substitutes by the year 2000". The alternatives considered range from synthesis gas (CO and H_2) from coal to biomass and solid wastes—these may provide 10–15 per cent of the chemical feedstocks by the year 2000. The attractiveness of biological material is that it is the only chemical feedstock which is known to be renewable. At present the fermentation industry monthly produces ethanol and citric acid besides glycerol, furfural, sorbitol, mannitol, etc.—however, the use of starch and sugar as sources of chemicals is increasing since these are in surplus. In some cases biologically produced alcohol is competitive with synthetic alcohol from ethylene. It is calculated that 0.20 of the U.S. corn crop could be fermented to chemical products equivalent in bulk to the total petrochemical product from ethylene and higher olefins. Wishart identifies four crops/substrates as most likely to yield sufficient chemicals "without significantly affecting the other uses of the product or its price structure". (a) Fermentable sugars; (b) cellulose-rich products and wastes; (c) corn; and (d) other crops grown on energy farms.

The production of alcohol from molasses, corn, wheat and sugar beet has been studied and undertaken in Japan and the U.S.A. Costs vary from $0.99 to $2.20 per U.S. gallon compared to the 1975 production cost of $0.95 per U.S. gallon from ethylene (costing $0.15 per pound)—the cost of synthetically produced alcohol is slightly less than that produced from crops but "the gap is narrowing rapidly". Nebraska has a very interesting GASOHOL programme (10 per cent ethanol in gasoline). The economics and energy ratios using corn of low quality to produce ethanol look favourable. In New Zealand it has been calculated that ethanol production from sugar beet could economically replace 10 per cent of the petrol requirements using 54,000 hectares of dryland farming (0.6 per cent of the total area under cultivation). The production of ethanol for fuel (or a chemical source) from pine trees has been shown to be profitable for processing facilities above a certain size. It can be shown that theoretically 25,000–35,000 hectares of radiata pine would satisfy all of New Zealands present liquid fuel requirements.

Canada

Canadian studies on the large scale production of methanol from biomass show that by 2025 between 4 and 42 per cent (depending on total energy use) of the transport fuels could be provided by such methanol.

"Methanol represents a rather unique fuel combining the portability of liquid petroleum products and the clean even-burning characteristics of natural gas". It is shown that commercial production of methanol fuel would be feasible under certain conditions, e.g. methanol value of \$0.70/gal. and electricity power costs of 10 mills or \$0.55/gal. and power at 14 mills; if the methanol price was only \$0.40/gal. at the refinery it would not be attractive.

The Federal Government announced in July 1978 that it plans to spend \$180 million of its \$380 million new 5 yr solar energy programme on biomass research and development and incentives to industry.

Australia

Traditionally we think of energy plantations as forests, but increasingly we should consider alternatives, such as shrubs, weeds, agricultural crops, grasses and algae (fresh-water and marine); for example, in Australia five species have been selected, namely *Eucalyptus*, *Cassava*, *Hibiscus*, Napier Grass (*Pennisetum*) and Sugar Cane as being potentially the most desirable high-yielding crops which can be harvested over the whole year. Recent calculations show that alcohol produced from cassava (starch-rich) is an economically viable system but that if processing to destroy cell walls is required, the costs become too high. The cost of alcohol from *Cassava* is calculated to be \$Aus. 250/tonne from a 100,000 tonne/yr batch-process plant which compares favourably with the current market price of alcohol (\$Aus. 275/tonne) as an industrial solvent. Alcohol production from eucalyptus by acid or enzyme hydrolysis is calculated to be \$Aus. 400–600/tonne because of the expensive chemical pretreatment or fine milling required. Methane and pyrolytic oil production from cereal straw and eucalypts is calculated to be 2–4 times the equivalent fuel costs in 1975 in Australia. If the prices of fossil fuels increase the economics of photobiological processes will become more favourable since fossil fuels and electricity account for only 10–25 per cent of the cost of photobiological fuels.

Philippines

In the Philippines a feasibility study has shown that a 9100 hectare fuel wood plantation "would supply the needs of a 75 MW steam power station if it were not more than 50 km distant". The investment requirements and cost of power produced look favourable and competitive with oil-fired power stations of similar capacity. Twenty five such sites have been pinpointed some of which could support power plant capacities as high as 225 MW. The best species of fast growing tree seems to be the "giant ipil-ipil" (*Leucaena acidophila*) which fixes nitrogen to ammonia—a very desirable trait.

Europe

In Europe a number of countries are conducting feasibility studies of the potential which biomass may have for supplying a source of energy and/or fuels in the future. Trial plantings of alder, willows, poplars, etc. are being undertaken in addition to assessing energy yields from agricultural residues, urban wastes, techniques of conversion, wasteland and forest potentials, algal systems, etc. Little has been published as yet but a recent study (Project Alter) in France by "Le Groupe de Bellevue" proposes that in the long term France could produce liquid and solid fuels, comprising 11 and 14 per cent of its total energy requirement respectively, from biomass sources. Land use constraints will be a problem but considering Europe as a whole, its past vegetation history, with its diverse climates and land use patterns, and its already burgeoning food (including liquid) surpluses, there may be far greater potential for biomass production than is commonly imagined.

Brazil

By far the most ambitious biomass programme which has been planned is that in Brazil for the production of alcohol from sugarcane, sorghum, cassava and other crops. This National Alcohol Programme (PNA or Proalcool) was established in November 1975. The alcohol will be used to blend with petrol—up to a 20 per cent mixture (by volume) requires no adjustment to the engine (over the last 10 years the State of San Paulo has varied the alcohol content of its petrol from 0.4 to 13.5 per cent—and 18 per cent in 1978—depending on the availability of alcohol and price of molasses). Up to August 1977, 141 new alcohol distilleries were authorized by Proalcool which would require an investment of about \$900 million and would supply 3.2×10^9 l. of alcohol by 1980—this is about a fifth of the projected gasoline requirement. By 1985 total production of alcohol could reach 5×10^9 l. An economic analysis of the production of alcohol from sugar cane and cassava calculated selling prices as fuel, ex distillery, of $\$333/m^3$ ($= \$0.33/l. = \$16.7/10^6$ Btu) to $\$363/m^3$. These estimated prices are 81–83 per cent of the present retail price of gasoline on a volume basis, but are \$43 to $\$73/m^3$ more costly than the present fixed market price of alcohol of $\$290/m^3$; gasoline sells for $\$413/m^3$ ($= \$13.8/10^6$ Btu). Thus the consumer is encouraged to use alcohol instead of gasoline, but the producer must receive an economic price in the future besides the Government-guaranteed purchase of all biologically produced alcohol. Estimates of the energetics of alcohol production from sugarcane and cassava are favourable since the energy output/input ratios have been calculated at between 6 and 9. These estimates may be somewhat high but only large scale agriculture and processing can finally determine the net energy ratio. What is clear is that Brazil is embarking on an ambitious programme of fuel import substitution using the natural advantages of land and climate which it has—and it may be a very useful demonstration to other countries.

Fuelwood problem

I want to touch briefly on the fuelwood problem in developing countries. It is not often appreciated that wood presently supplies about 10–15 per cent of the world's total energy consumption—and this percentage can be much higher for individual countries. The problem of deforestation and desertification has highlighted the lack of fuelwood in many countries. A recent Dutch study of the Sahel region points out two possible solutions: (a) decreasing fuelwood demand by using stoves which reduce consumption by 70 per cent and (b) increasing the supply of fuelwood by establishing "forest plantations" and by converting the wood into charcoal since it is more efficient to use instead of wood, especially if fuel has to be transported over long distances. Costs of reforestation and fuelwood production have been calculated for the tree species and the conclusion is that "under the conditions assumed it is an economically feasible activity". Naturally there are institutional problems which impinge on agriculture and other practices of the society but if such countries are to achieve even a modicum of internal fuel production they should seriously consider such biomass systems.

Algal systems

Thoughts of using algae and bacteria in biological solar energy systems are not new but have received more serious attention over the last few years. One advantage of such microbial systems is that they can be technologically sophisticated or simple depending on local conditions. The choice of the most suitable species will also depend on local occurrences and preferences, e.g. taking into account salinity and temperature; the species selected can then be fitted into the environmental requirements quite easily.

Many liquid and semi-solid wastes from our houses, industries and farms are ideal for the growth of photosynthetic algae and bacteria (Fig. 8). Under good conditions rapid growth with about 3–5 per cent solar conversion efficiency can be obtained. The harvested algae may be fed directly to animals, fermented to produce methane, or burnt to produce electricity. Simultaneously, waste can be disposed of and water purified; it is estimated that such algal systems are 0.5–0.75 times as expensive as conventional waste disposal systems in California. The main economic problem is harvesting costs but the development of new techniques and using different, easily-harvested species of algae is proving important. Two-stage algal ponds for complete liquid waste treatment are being tested. Algae which can be harvested by straining are grown in the first pond while nitrogen-fixing blue-green algae (also easily harvested) grow in the second pond deriving their nutrients from the first treatment ponds. Utilization of CO_2, e.g. wastes from industry, also increases productivity. The harvested biomass can be fermented to methane (equivalent to

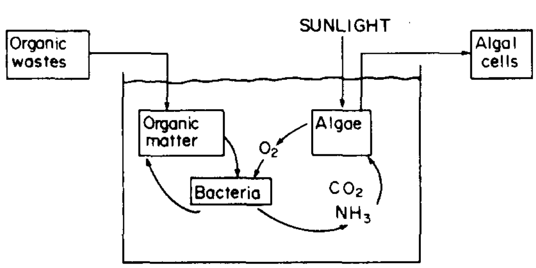


Fig. 8. Production of algal biomass in an algal-bacterial pond (after Ref. [97]).

5000 Btu/lb algae) while the residues would contain virtually all the N and P of the algal biomass, so providing a good agricultural fertilizer—one acre of algal ponds could supply the fertilizer required by 10–50 acres of agriculture. By optimization of yields and including energy inputs and conversion losses a net production of 200 million Btu per acre per yr of methane seems feasible—at a 30° latitude this would represent a 1.5 per cent annual photosynthetic conversion efficiency. The cost of the methane so produced is calculated to be \$2.75–4.10/million Btu depending on land costs and the size of the pond. These costs are high but do not take into account the benefit value of waste treatment (which is becoming increasingly expensive) and any byproducts, e.g. fertilizers and organic chemicals. It is estimated that complete municipal waste treatment plus microalgal biomass and bioconversion systems could provide about 5 per cent of local (U.S.A.) methane usage—if animal wastes were available this figure may reach 10 per cent.

In California average yields of algae in excess of 100 kg dry weight/ha/day are obtained, with peak production in summer reaching three times this figure. Yields of 50–60 tonnes dry weight/ha/yr would produce 74,000 kW hr of electricity. Oswald has constructed algal ponds of 10^6 litres which give a 2–3 per cent photosynthetic efficiency on a steady-state basis. Large feeding systems for cattle and chickens have now been provided with algal ponds where the animal waste is fed directly into the ponds; about 40 per cent of the nitrogen is recovered in the algae, which is subsequently re-fed to the animals. Oswald calculates that 4 million ha of algal pond systems producing an average of 12 g dry weight/m^2/day could produce all the U.S. protein requirements (compared to the presently used 121 million ha of agricultural land). The green algae presently grown have 50–60 per cent protein but blue-green algae are being tried which contain 60–70 per cent of extractable protein. Algal ponds for oxidation of sewage are operating in at least 10 countries of the world and the interest in these systems as possible net energy and fertilizer producers and as water purifiers is increasing rapidly. They will obviously never provide major portions of any country's primary energy requirements but these algal systems have many advantages not the least of which is their energy conserving characteristics.

Wastes

The use of organic waste materials as a source of energy—solid, liquid or gaseous—is progressing rapidly both technologically and commercially. The conversion processes can be chemical, physical or biological. Newer biological routes look promising especially since we are learning so much more about the enzymatic degradation of the lignocellulosic components of cell walls. The hope is to bypass the expensive (in money and energy terms) chemical and/or mechanical pretreatment of plant material required before it can be degraded to useful forms for industrial and/or energy use.

Leaf protein

Leaves are potentially a large source of protein.

Traditionally they are composted, discarded as waste, or fed to animals for conversion to meat, which is an energy inefficient process. Techniques have been developed for the extraction of leaf protein which yield at the same time other useful products, namely fibre and soluble components such as carbohydrates, nitrogen and inorganic nutrient compounds. The composition of leaf protein is about 60–70 per cent protein, 20–30 per cent lipid, 5–10 per cent starch. Yields of 2 tonnes of dry leaf protein per hectare have been obtained without irrigation and three tonnes can be expected. In the south-west U.S. it has been proposed that if the yields of alfalfa (grown in an enclosed environment) reached that of sugarcane at 100 tonnes dry weight/hectare/yr, about 25 tonnes of protein could be extracted per hectare from alfalfa. Once extracted the protein is probably more valuable as a food than an energy source—by-products from the extraction process could be used for energy or raw materials.

The choice of suitable crops for the extraction of leaf protein, fibre and other products should be carefully examined. Besides those crops usually considered (fodder crops, potatoes, sugar beet and peas) consideration should also be given to perennial crops such as grasses and clovers, trees and bushes and crops re-generating themselves making it economical to obtain a number of cuts in a given time. Additionally, both annual and perennial weeds, especially those species that start to grow early in the year despite low root temperatures and that provide maximum year round cover, may provide very good sources of leaf protein. Integrated approaches for using all possible leaf material, produced either as a by-product in conventional agriculture, or from plants grown specifically from such extraction, would seem to be of benefit in many countries of the world. Pilot scale and demonstration projects are in operation in some countries of Europe and Africa and in India and New Zealand.

FAR FUTURE AND SYNTHETIC PHOTOSYNTHESIS [5–7, 15, 32, 33, 36, 57, 110–147]

One of the problems with photosynthesis is that it requires a whole plant (or alga) in order for it to function—and the problem with whole plant photosynthesis is that its efficiency is usually low (less than 1 per cent) since many limiting factors of the environment and the plant itself interact to determine the final overall efficiency. The most easily identified limiting factors are light intensities, high and low temperature, CO_2 concentration, water availability, supply of nutrients especially nitrogen, availability of sinks for the products of photosynthesis, respiration (light and dark), the patterns of development and their timing over the growing season, responses to stress, and so on. Knowing how these factors operate individually is obviously important but what seems much more important is to try to understand how they interact in determining whole plant yields. This is an immense task but is worthwhile tackling since plants do produce a *stored product*—at a seemingly low efficiency (but possibly not all that bad when other energy systems are compared with their storage efficiencies included).

Thus a task for photosynthesis of the far future is to try to select and/or manipulate plants which will give higher yields (biomass, fuel, fibre, chemicals, food) with acceptable energy output/input ratios. We need much more effort placed on studies of whole plant physiology and biochemistry and their interactions with external (environmental) factors. Already this type of research is being increasingly funded by both industrial and government organisations who see a good future for plant-based systems. Unfortunately in the past research in the plant sciences has been a poor relation in the scientific world—it has been taken for granted far too long. Now many questions, seemingly simple, are being asked to help solve problems of plant productivity in different environments—however, we have few answers and it takes time to get them because of the lack of basic knowledge. But all is not doom and gloom; I for one think the potential is there and we must try to provide the answers so that we can try to use plants more efficiently in the future.

C_3, C_4 and photorespiration

The discovery of the C_4 pathway of photosynthesis, in which certain types of plants, e.g. maize, fix carbon dioxide into a C_4 compound as their initial product (instead of the conventional C_3 sugar which is normally formed by temperate plants, e.g. wheat) has given us a deeper understanding of the intricacies of photosynthesis. This discovery also led to the hypothesis that increased productivity might be achieved by manipulating plants to emulate some of the C_4 characteristics such as the efficient utilisation of low concentrations of CO_2, the ability to grow under water stress and high salt concentrations, and the ability to use intense light efficiently. It has also been suggested that the process of photorespiration may decrease yields up to 50 per cent. This loss arises from recycling of the photosynthetically fixed carbon in the plant so as to re-evolve CO_2 which is thus lost from the plant. Utilising our knowledge of C_4 characteristics of plants and of photorespiration *may* allow the breeding and selection of efficient photosynthetic plants. Chollet and Oxygen put it strongly. "The control of this process (photorespiration) and the associated oxygen inhibition of photosynthesis has emerged as representing one of the most promising avenues for dramatically increasing the world supply of food and fibre". Even though this is a scientifically very controversial field, the advantage of slowing photorespiration by biochemical or genetic manipulation is undoubtably great *if* it can be realised.

A re-evaluation and possible utilization of CAM-type photosynthesis (Crassulacean Acid Metabolism) may be worthwhile. These CAM plants fix CO_2 to acids at night when their stomata are open and then during the day (stomata closed and no water loss) the prefixed carbon is reduced to the level of carbohydrate. Thus a photosynthetic system has developed which can take place with minimal water loss. Such an attribute would be very useful in crop plants and it *may* be possible to select or incorporate such characteristics into desired plants.

Genetics

Genetic engineering using plant cell tissue cultures is a recently developed technique which has great promise for improving plants. Species and genus crossings and creation of new hybrids by mutations induced in the cultures are possible. There seems little doubt that these cell culture techniques may ultimately become routine tools in the difficult task of plant improvement, greatly increasing the scope of plant breeders who are the mainstay of plant selection and improvement; providing plant breeders with more physiological and biochemical tools for their trade is essential.

In selecting plants during breeding or tissue culture it may be very useful to have a "multiple test analysis" system, e.g. tests of levels of key enzymes, constituents and salts, etc., which could give a rapid view of the potential of a plant(s). This idea is analogous to current batteries of medical tests routinely given to patients. Such multiple tests for plants still need to be developed but there are indications of key enzymes or physiological processes, which *may* give predictions of yield, fertilizer status, and so on, e.g. nitrate reductase, ribulose bisphosphate carboxylase, etc. Much work needs to be done if this "multiple test analysis" system were to become practical.

Selection

Selecting plants which have salt tolerances, high and low temperature tolerances, longevity or delayed senescence, lower fertilizer requirements, low water requirements, adaptability to various soil characteristics, and so on, should be a challenging problem. For example, it has recently been reported that barley can be cultivated using sea water. There is a revival of interest in studying plant productivity in saline and hot environments. This is long overdue since so much of the world's land area suffers from these problems. It is surprising how many plants and algae can thrive under these supposedly extreme environments. Each country should develop its own selection procedures in order to choose crops (for food and fuel?) which will suit local conditions best, i.e. soil, climate, social and economic factors, etc.

Regulation and selection of products

Usually crops are grown for one final product, such as grain or root, containing constant proportions of carbohydrate, protein and fats. The possibility exists that we could alter biochemical reactions at defined times during the growing season in order to obtain more or less of a given constituent. It is also possible that we could regulate detrimental processes in the plant, such as photorespiration and water losses, giving greater net plant yields. There is some work on algae but whole plant systems should be investigated.

A considerable amount is known about the carbon cycle (Fig. 9). The possibility of regulation of the final products of carbon dioxide fixation in plants also deserves consideration. Work in some industrial laboratories

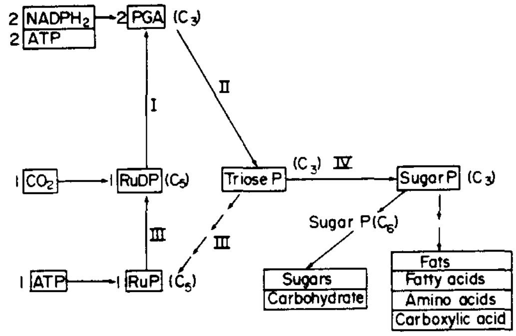


Fig. 9. The cycle of photosynthetic CO_2 fixation resulting in various final products [1].

shows that certain plant and algal products, such as sugar, rubber, starch, proteins and lipids, can be used in the production of many different products, such as detergents, plastics and in these cases the plant is operating as an intermediate CO_2 fixation apparatus, whose continuously renewable product is used in the chemical industry. In these days of surplus starch and sugars it seems important to have alternative uses—both chemical and food. Substitutes for sugar do not seem a long way off so sugarcane and sugarbeet crops can be used for other final products. The production of rubber or lower molecular weight products from *Hevea* and guayule, liquid waxesfrom jojoba, resins from pine trees under the influence of "paraquat", ammonia from algae, glycerol from the green alga *Dunaliella*, oil from the alga *Botryococcus* are a few examples. Glycerol production by *Dunaliella* is an interesting example which is now being tried on a pilot plant scale—it is estimated that 9000 tonnes/yr/km^2 plus an equivalent weight of food could be produced at a cost of \$200 per tonne each for glycerol and food meal. The efficiency of photosynthesis is high—possibly up to 10 per cent. The blue-green alga *Spirulina* is being harvested at the rate of 5 tonnes dry weight/day from Lake Texcoco near Mexico City—it is 75 per cent protein and also has an interesting complement of pigments which could replace artificial dyes in foods etc. if it became necessary following the introduction of stricter additive laws. Two *Euphorbia* species are undergoing trial plantings in California for the extraction of hydrocarbons with low molecular weight for processing to oil substitutes. It has been calculated the equivalent of 10 barrels of oil could be produced per acre per yr at a total cost of \$20 a barrel, an attractive proposition if a sustainable yield can be achieved.

Nitrogen metabolism

A recently published idea is the photosynthetic reduction of nitrate to ammonia using membrane particles from blue-green algae (Fig. 10). This process naturally seems to occur by light reactions closely linked (via reduced ferredoxin) to the primary reaction of photosynthesis i.e. not involving the CO_2 fixation process. It is an interesting way to produce ammonia!

It is thought that one of the major limitations of the N_2-fixing capability in both symbiotic and associative symbiotic systems is an inadequate supply of carbo-

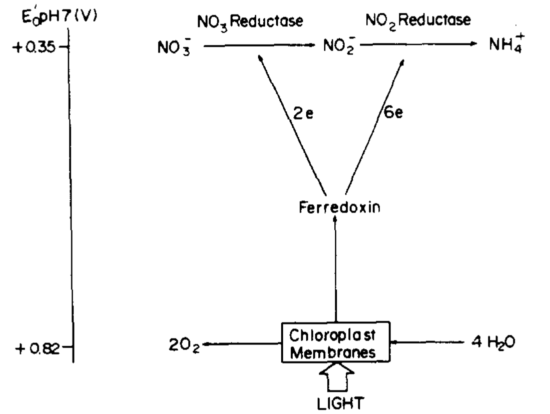


Fig. 10. The photosynthetic reduction of nitrate to ammonia by chloroplast or algal membranes[126].

hydrate to the N_2 fixing bacteria: more efficient photosynthesis and translocation of substrates to the roots could overcome some of these problems. When soya beans are grown under greenhouse conditions, a 3-fold increase in CO_2 concentration in the atmosphere resulted in a 6-fold increase in the amount of N_2 fixed/ha: yields increased from 76 to 424 kg of fixed N_2/ha. CO_2 enriched soya beans fixed 85 per cent of their N_2 requirement, whereas the unenriched plants fixed only 25 per cent obtaining the rest from the soil in the form of nitrate fertilizers. It is possible that this increased net production of photosynthesis under high CO_2 atmospheres, and hence N_2 fixation, is made possible by a decrease in the O_2 inhibition of photosynthesis or photorespiration due to the increased CO_2 concentration in the atmosphere. Another significant limiting factor may be due to the fact that the nitrogenase enzyme can also catalyze H_2 evolution which results in the loss of energy. The root nodule bacteria have a hydrogenase which can recapture some of this H_2 by "fixing" the H_2 back into reduced compounds thus decreasing energy loss to the atmosphere.

The interesting discovery of associative symbiotic N_2 fixation in grasses such as maize (and possibly wheat and rice) has also led to the realisation that improved carbohydrate production may be the prerequisite for useful extension of biological N_2 fixation to other crops. Even though the net yield of nitrogen from such non-legume nitrogen fixation may be only 15 kg or less N per hectare per yr, it seems important to understand how such an associative symbiosis functions. Many problems remain in identifying physiological limiting factors but the prospects are so important that much effort is being put into this research—but the basic problems must not be underestimated.

Genetic manipulation of N_2-fixing bacteria is a speculative field of research which may hold promise for introducing new strains of bacteria to different crops and also improving existing strains of bacteria. It may be possible to emulate the *Azolla–Anabaena* symbiosis where the blue-green algae living in the *Azolla* plant fixes N_2 for use by the plant. Increases in yield of 2 to 3 fold in rice fields have been reported where *Azolla* has been ploughed in as a green fertilizer. The blue-green, N_2-fixing alga *Nostoc* has been innoculated in rice fields with yield increases equivalent to adding 80 kg/N hectare. As stated previously how the physiology of the plant may place limiting factors on improving N_2 fixing capabilities of plants is uncertain—an important factor when genetic screening is used in whole plants or in tissue cultures.

The loss of ammonia nitrogen fertilizer from the soil by the process of nitrification (bacteria convert NH_4^+ to NO_3^-) will obviously decrease crop yields since nitrogen availability is so important to the plant. A number of chemicals are now available as nitrification inhibitors which are applied along with the ammonia fertilizer—crop yields are increased at lower energy and monetary costs.

Synthetic photosynthetic systems

Since whole plant photosynthesis operates under the burden of so many limiting factors (internal and external) would it be possible to construct artificial systems which mimic certain parts of the photosynthetic process and so produce useful products at higher efficiencies of solar energy conversion? (A 13 per cent maximum efficiency of solar energy conversion is considered a practical limit to produce a *storable* product). I think that this is definitely feasible from a technical point of view but it will take some time to discover whether it could ever be economic. Note must also be taken of other chemical and physical systems (light driven) which are presently being investigated and may come to fruition before biologically-based systems do so. However if this is the case the spin-off could also be great in terms of our understanding of the process of photosynthesis itself.

Plants perform at least two unique reactions upon which all life depends and which have not yet been emulated in artificial (synthetic) systems viz. the splitting of water by visible light to produce oxygen and protons and the fixation of CO_2 into organic compounds. An understanding of how these two systems operate and attempts to mimic the processes with *in vitro* and completely synthetic systems is now the subject of active research by biologists and chemists alike. Figure 11 shows diagrammatically this ability of plant membranes to produce low (reducing) potentials and the reactions which can be catalysed once the low potential has been produced across the membrane.

H_2 production

The production of H_2 gas by light-activated water splitting using components from plants (chlorophyll-membranes and ferredoxin) and bacteria (hydrogenase) was reported in 1973 (Fig. 12). The rates of H_2 evolution were low, the system only ran for 15 min, and there were questions as to whether the protons did indeed come from water. Since then our laboratory and others have increased the rates and longevity of H_2 production by 10 fold in each case, besides convincingly showing that water is the ultimate source of H_2. The ultimate object of our line of research is to understand how the biological system operates and then construct a completely synthetic system mimicking the algal or plant-bacterial sys-

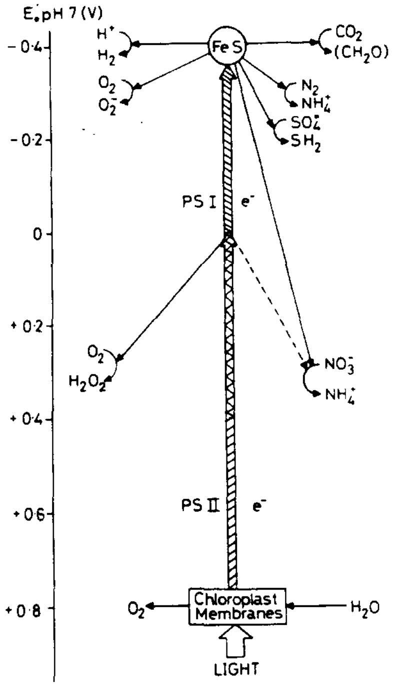


Fig. 11. Schematic representation of the ability of plant membranes to produce low (reducing) potentials and the reactions catalyzed by the reduced Fe–S enzyme catalysts[126].

tems. In this case an Fe–S catalyst would be used instead of a hydrogenase, a chlorophyll layer membrane or vesicle instead of the chloroplast, and a manganese catalyst to evolve the O_2 from H_2O. A two-stage system has been constructed where O_2 is evolved in the light and H_2 in the dark. A single-phase system evolves H_2 and O_2 simultaneously which could then be separated by semipermeable membranes, or the gas mixture burnt directly. There are problems of stability in the living systems which would need to be overcome before any biologically based system could be practical. Progress has been made in identifying stable hydrogenase enzymes from photosynthetic bacteria.

We have also reported the substitution of the ferredoxin (electron carrier from the membranes to the hydrogenase) by two different synthetic Fe–S compounds and two different synthetic Fe–S–Mo compounds—we think this is the first report of these types of substitutions. A synthetic hydrogenase seems too difficult at present but active research is going on in this field of synthetic Fe–S clusters. The water-splitting component in the chlorophyll containing membrane is a Mn-containing enzyme. A number of laboratories are working on synthetic Mn compounds to split water and one laboratory at least is very optimistic of success. At present the main limiting factor we detect is the stability of the membrane. Light and oxygen play havoc on biological membranes. Even though we have found some chloroplast membranes which are much more stable than others, we don't yet know the reason for this—I suspect we must wait until membrane technologists (engineers?) come up with a suitable membrane.

This work on H_2 production from water is going ahead as basic research since this single stage system is unique in having the following three advantages (1) it uses an unlimited supply of substrate—H_2O. (2) It uses an unlimited supply of energy—sunlight. (3) It produces a storable and non-polluting source of energy—H_2 gas. The only other system which emulates this is the two stage photovoltaic solar cell plus electrolysis system. Of course a purely photochemical system to split water with visible light may be discovered and found to be stable—this would then solve all our problems. Lastly one must mention that certain algae produce H_2 continuously under specific conditions and contain the enzyme hydrogenase. This system is being experimented with in a number of laboratories also in conjunction with growing algae on wastes—thus having a three stage system of growth, then H_2 production, and finally harvesting. Photosynthetic bacteria have been shown to grow directly on wastes producing H_2 gas.

H_2O_2 production

Instead of producing H_2 gas from H_2O it is possible to produce H_2O_2 (a fuel) with *in vitro* chloroplast systems—indeed certain green algae can excrete H_2O_2 un-

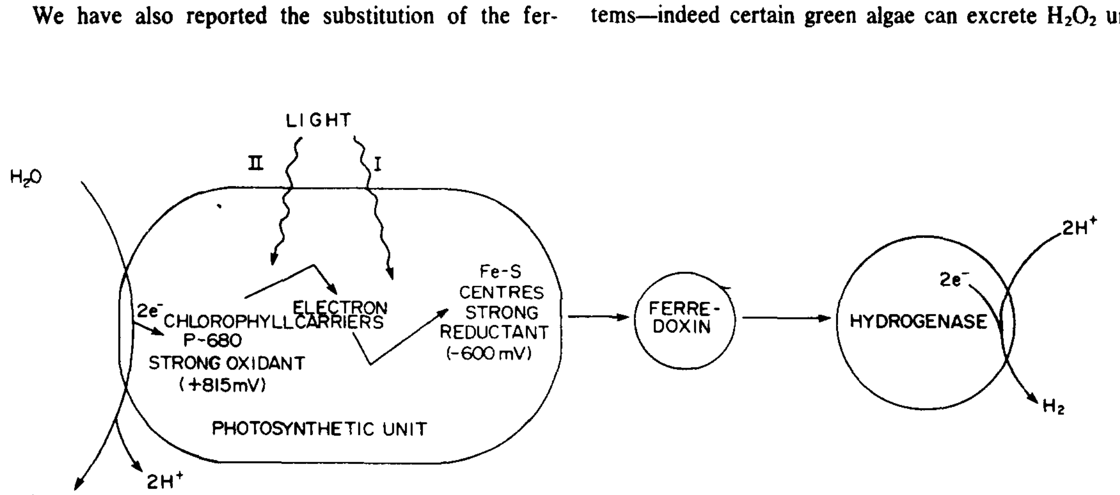


Fig. 12. Coupling of solar energy to H_2 production as a result of H_2O splitting by chloroplast membranes in the presence of the Fe–S enzymes ferredoxin and hydrogenase[139].

der certain conditions. In the proposed *in vitro* system only one of the photosystems of the chloroplast membrane would catalyze the system viz. the water splitting photosystem II which produces a redox potential of about zero volts (at pH 7)—this is sufficient to reduce O_2 to H_2O_2 (redox potential +0.3 V). The overall efficiency would be twice that of H_2 production since only one, and not two, photosystems would be operating. It is premature to speculate on efficiencies of either the H_2- or H_2O_2-producing system until we can produce these compounds on a continuous long-term basis.

Carbon reduction

In vitro systems which emulate the plant's ability to reduce CO_2 to the level of carbohydrate are a very attractive proposition and are being actively investigated by biochemists and synthetic chemists. A report claims the formation from CO_2 of keto-acids (and then amino acids) using an alkyl-mercaptan, an Fe–S protein analogue, and an inorganic reductant. Recent work by two groups has shown the photochemical reduction of CO_2 to formic acid, formaldehyde and methanol.

It may be possible to induce plant systems to reduce carbon to the level of carbohydrate on a continuous basis to produce compounds such as glycolate or formate, instead of carrying out the normal transformation of carbohydrate into other compounds like protein and fats. Algae are known to produce glycolate externally under certain conditions and thus could possibly be used in such a system. A more speculative possibility would be to use the plant's ability to produce light-induced energy-rich reducing potentials at −600 mV in Photosystem I; this could be done via coupled enzyme or catalytic systems to produce carbon compounds. The reducing potential is there and "just" needs to be coupled to carbon fixation.

Chlorophyll systems

The chlorophyll-containing membranes of all photosynthetic organisms are able to separate positive and negative charges on either side of the membrane under the influence of light. This basic photogalvanic (photoelectrochemical) system is a key to photosynthesis which we might be able to use directly for the production of electricity or the storage of energy. Artificial chlorophyll-containing membrane bilayers, vesicles and plasticized particles have been studied and some have shown to produce currents and charge separation. The possibility of utilizing such artificial membranes or vesicles for direct photochemical systems has scope, even though the efficiencies so far achieved are low. In the liposome experiments recently reported photooxidation of ascorbate and the splitting of H_2O in an electrode system was noted—H_2 gas was reported in both cases.

Purple membranes

Very stable "purple membranes" have been isolated from the bacterium *Halobium* which grows naturally under very high salt concentrations and in hot, sunny areas. The isolated membranes can withstand 6N HCl, high temperatures and prolonged exposure to the atmosphere. These purple membranes "function as proton pumps in the bacterium"—this capability has been proposed as a potentially useful means of converting solar energy. Apparently the main function of the light-driven ion (protons and other ions) pump is to maintain the internal concentration of salts and pH at a suitable level. The purple membrane contains the pigmented protein bacteriorhodopsin which consists of seven α-helices which span the membrane—this membrane-bound protein with its pigment acts as the light-capturing chromophore and the selective channel for pumping the ions across the membrane. It seems a very simple and stable system which may be ideal for studying, and possibly emulating in an artificial membrane system. Laboratory systems have been constructed which can: (a) produce photopotentials of 200 mV or more across a membrane: (b) produce pH gradients which may result in the production of H_2 and O_2 in separate compartments; (c) act as desalting devices with Na^+ and K^+ exchanging with H^+; (d) produce ATP if an ATPase enzyme is incorporated into the membrane. The further development of these possibilities are as interesting as they are speculative—they certainly merit substantial research effort.

CONCLUSION

In conclusion I want to reiterate that photosynthesis is a key process in the living world and will continue to be so for the continuation of life as we know it. The development of photobiological energy conversion systems has long term implications from energy, food, fibre chemical points of view. Their applicability might be immediate in some tropical areas and countries with large amounts of sunshine. However, whatever systems are devised in the temperate zones could also be applicable to those countries that have more sunshine and these are predominantly the developing countries of the world. Thus the temperate countries could help themselves by becoming more self-sufficient and help the other countries of the world by not competing for their food and raw materials. Lastly, we might have an alternative way of providing ourselves with food, fuel, fibre and chemicals in the next century and we should consider all our energy options and not put all our money and effort into one or two energy systems as we have in the past.

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