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Photosynthesis and the world food problem

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Abstract

Studies in the field of photosynthesis are particularly predisposed to play an important role in the solving of the main problem of today — food for the world's growing population. The article presents data on the rate of population increase, the size of food production and yields of the most important crop plants. The relationship between the photosynthetic productivity of C_3 and C_4 plants and their yields is discussed. The problem of the rising atmospheric CO_2 concentration and its influence on photosynthesis, photorespiration and accumulation of plant biomass is presented.

Key words: *photosynthesis, plant productivity, food*

INTRODUCTION

One of the most urgent problems of the modern day is providing enough food for the world's growing population. Approximately 2/3 of the earth's current 5 billion inhabitants are undernurished and over 500 million suffer from hunger. During recent years, starvation has taken the lives of approx. 0.5 million people in Ethiopia and 1 million in Bangladesh (Alsudery 1985). It is predicted that in the year 2000, we will number about 6 billion, and that the world's food production will have to double in order to feed this many people. The anthropopressure will increase, and the drive towards a better life will augment the demand to increase the proportion of animal in respect to plant produce. The production of such an amount of food will entail an approximately 3-fold increase in the amount of technical energy used. The problem is complicated and multifacteted. It pertains both to the rules and socio-political systems of nations and to scientific circles and international cooperation. Figure 1 illustrates the rate of world population growth and the participation of individual regions in it. Various fields of science should take part in the solving of the world food problem by indicating the direction in which research and the practical application of its results should take, including not only agricultural practices, but government policies as well (Anderson 1985, Barker 1985, Day 1985, Hess 1985, Johnson 1985, Wittwer 1985). Especially well suited to this end are studies in the field of photosynthesis. Some of the aspects of this problem have been discussed in previous articles (Poskuta 1983, 1984). In this paper, several new aspects will be presented. The essence of photosynthesis comes down to the transformation of the energy of solar radiation into the energy of stable chemical compounds by organisms containing photosynthetic pigments. In higher plants, the photosynthetic reduction of CO_2 can be represented by the summary equation:

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2 - 2860 \text{ kJ}. \qquad (1)$$

Equation 1 indicates that this is a highly endergonic process. The opposite process to photosynthesis is respiration. Plants respirate both in the light (photorespiration) and in darkness (respiration), microorganisms, animals and

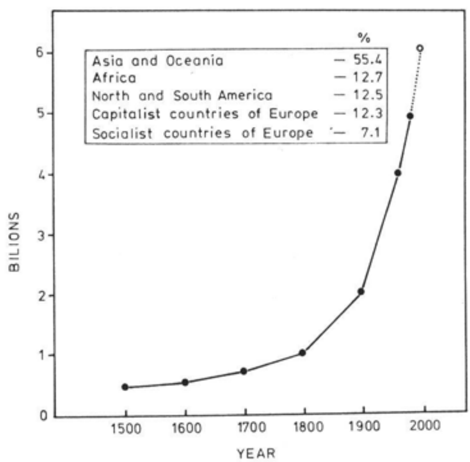

Fig. 1. World's population growth and its present distribution (%)

humans respirate as well. During the evolution of life on earth, a steady state has been established between these processes. The relationship between them is demonstrated on Fig. 2, and the stechiometry of the cycle is given. The earth along with its atmosphere can be treated as a closed circulatory system within which life is supported by the energy emitted

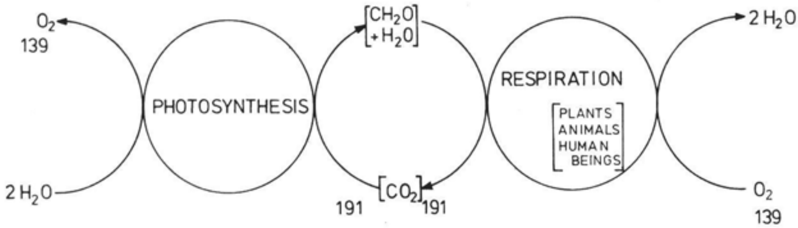

Fig. 2. CO_2 and O_2 exchange in photosynthesis and respiration. Numbers = $\times 10^9$ tons annually

by the sun. Among all of the sources of energy, solar energy is the cleanest form, because it does not pollute the environment.

The equivalence between net photosynthesis and net primary production of biomass can be assumed, and expressed by the following equation:

Net photosynthesis (net primary production) = Actual photosynthesis (total net production) — (respiration + photorespiration). (2)

PHOTOSYNTHESIS AND AGRICULTURAL PRODUCTION

Studies in the field of photosynthesis have, in addition to cognitive values, utilitarian aims set at showing agricultural practitioners ways by which crop plants can utilize more solar energy, increase biomass and yields. Although the relationships between photosynthesis and increase in biomass and yields are complex and still little understood, the data already accumulated on this topic are useful and have been applied in practice to increase yields and their quality. Agricultural practitioners evaluate yields in terms of production aims. If the yield is food or an industrial raw material, only part of the produced biomass is useful. If the biomass is a source of heat energy or transformed into electrical energy in power plants, then the entire biological yield can be of use. From our point of view, that is, the production of food, we obtain a great majority of it from only some ten-odd species of crop plants. The following food-supplying plants are the most important: what, rice, maize, barley, rye, oats, sorgo, potatoes, legumes, sugar beets and sugar cane.

Table 1 presents data on the total production and yields of selected crop plants (Coombs and Hall 1982). Analysis of the numerical data presented in it shows the great differences existing between the yields obtained in the so-called Third World and those in Europe and the United States. Increasing the yields to the levels obtained in the developed countries would completely solve the world's present food problem. Possibilities of increasing food production are still greater. According to Wittwer (1975), average yields in highly developed countries equal (in tons per hectare) 6 for wheat in Holland, barley in Belgium, rice in Japan and maize in

Table 1

Production (in millions of tons) and yields (tons ha^{-1}) of the main crop plants (Coombs and Hall 1982)

	Sugar				Cereal starch								Starch							
	cane		beets		cereals		maize		rice		wheat		root and tuber crops		potatoes		sweet potatoes		cassava	
	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
World	737	56	290	32	1459	1.9	349	3.0	366.0	2.6	386	1.7	570	11.0	272	15.0	138	9.6	110	8.8
Developed countries	70	79	263	32	765	2.5	236	4.7	26.0	5.4	261	1.9	225	15.7	222	15.7	2	14.7	–	–
Developing countries	667	54	26	30	687	1.6	113	1.7	340.0	2.5	125	1.3	345	9.2	70	10.4	136	9.5	110	8.8
Asia	305	52	25	31	603	1.8	54	2.0	335.0	2.6	108	1.3	224	10.3	61	11.2	128	9.9	33	11.2
S. America	187	57	–	–	64	1.7	31	1.8	13.0	1.9	9	1.1	44	11.0	9	9.5	3	10.4	32	11.6
Africa	60	64	16	32	66	0.9	26	1.3	8.0	1.8	8	0.9	73	6.8	4	7.8	5	6.3	44	6.6
Europe	0.3	63	143	38	249	3.5	49	4.2	1.5	3.8	82	3.3	114	18.7	0.1	10.3	–	–	–	–
Oceania	26	75	–	–	16	1.0	0.4	4.5	0.5	5.3	10	0.9	2	10.3	1	23.0	0.6	5.4	2	11.0
Canada	–	–	1	39	42	2.3	48	5.9	–	–	19	1.9	3	22.4	3	22.4	–	–	–	–
U.S.S.R.	–	–	93	25	187	1.5	11	3.2	2.2	4.0	92	1.5	83	11.8	83	11.8	–	–	–	–
U.S.A.	25	82	23	46	273	4.1	161	5.7	5.0	4.9	55	2.0	17	28.0	16	29.2	1	12.4	–	–

1 — total, 2 — yield.

the U.S.A. Record yields of these plants are for wheat and barley — 14, rice — 10 and maize — 24. The record yields correspond to net photosynthesis intensity of a magnitude of 20-25 mg CO_2 dm^{-2} leaf area $hour^{-1}$ for C_3 type plants and 35-40 mg CO_2 dm^{-2} leaf area hour $^{-1}$ for C_4 type plants. The efficiency of utilization of the solar energy falling on the field is then from 2 to 4% (Coombs 1984). It is held that the percent of utilized energy by plants giving the present record yields is maximal and cannot be increased (Austin 1981, Austin et al. 1984). Such high yields are the result of cultivation of modern plant cultivars characterized by increased yield of grain in respect to straw. In such varieties, the grain to straw ratio is about 1. If Austin's opinion is accepted as true, then additional increases in yields can be attained by improved photosynthesis and reduced losses of the carbon, already bound in photosynthesis, as the result of respiration and photorespiration. If plants grow under optimal water and mineral conditions, then the production of biomass depends on the amount of absorbed solar energy. According to Ludlow (1985), biological yield and growth intensity can be presented in the form of an equation:

$$\text{Biological yield} = \text{interception of solar energy} \times \text{efficiency of energy transformation}$$

$$\text{Ton ha}^{-1} \qquad \text{MJ ha}^{-1} \qquad \text{ton MJ}^{-1} \tag{3}$$

$$\text{Growth intensity} = \text{interception of solar energy} \times \text{efficiency of energy transformation}$$

$$\text{g m}^{-2}\text{ day}^{-1} \qquad \text{MJ m}^{-2}\text{ day}^{-1} \qquad \text{g MJ}^{-1}. \tag{4}$$

Under these optimal conditions, the photosynthetic productivity of plants depends on:

1. The intensity of binding of CO_2 calculated in respect to leaf area.
2. The proportion of leaves receiving light saturating photosynthesis in relation to the entire leaf area.
3. The area of leaves most actively absorbing solar energy.
4. The duration of vegetation during which the leaves function with maximum efficiency.

For agricultural practitioners, the sowing density is of particular importance. Increasing the sowing density leads to high early yields due to the increased interception of solar energy by leaves in the spring. However, later on, dense sowing causes mutual shading by leaves, and so decreases the proportion of leaves receiving light saturating photosynthesis. This causes quicker ageing of leaves and reduction of the duration of their photosynthetic activity.

PHOTOSYNTHESIS AND PRODUCTIVITY OF C_3 AND C_4 TYPE PLANTS

According to equation (2), the biomass produced during photosynthesis can be identified with net photosynthesis. It results from the equation that in C_4 plants, in which photorespiration does not occur, or is very low, the production of biomass should be greater. Table 3 presents data on the productivity of selected C_3 and C_4 plant species.

It can be seen from Table 2 that due to the the greater growth intensity during comparable periods of vegetation, C_4 type plants produce more biomass than C_3 plants. The high productivity of C_4 type plants is the result of the interaction of various internal and external factors determining the high intensity of photosynthesis and accumulation of biomass in C_4 plants. The most important differences, from our point of view, characterizing C_3 and C_4 plants, are presented in Table 3.

Table 2

The growth intensity and productivity of selected type C_3 and C_4 crop plants

Species	Vegetation period (days)	Growth intensity, g m^{-2} day^{-1}	Productivity, tons ha^{-1}
C_3			
Manihot esculenta (Java)	365	11.2	41.0
Beta vulgaris (Holland)	160	12.5	22.0
Glycine max. (Japan)	130	6.8	8.9
C_4			
Pennisetum purpureum (El Salvador)	365	23.3	85.3
Saccharum officinarum (Hawaii, USA)	365	18.4	67.3
Zea mays (Colorado, USA)	117	22.7	26.6

The listed traits of C_3 and C_4 plants are the subject of studies aimed at obtaining a set of traits most favorable from the point of view of productivity. The improvement of photosynthesis is therefore the problem which should be worked on by specialists in various fields of science: plant physiologists and biochemists, geneticists as well as mathematicians and physicists creating models of photosynthesis and plant growth aimed at the optimization of plant productivity. Studies at the level of photochemical reactions are concentrating on obtaining plants characterized by the most favorable composition and structure of light-absorbing antennas,

Table 3

Characteristic features of the photosynthetic apparatus and related processes of C_3 and C_4 type plants

Characteristic	C_3	C_4
Leaf structure	disperse mesophyll cells	vascular bundles are surrounded by cells forming so called bundle sheaths
Chloroplasts	mesophyll chloroplasts have grana	chloroplasts of bundle sheath cells do not have grana
Peroxisomes	numerous	few
Carboxylating enzymes	RuBP carboxylase/ /oxygenase	PEP carboxylase
Primary carboxylation products	3-carbon acids: phosphoglyceric, phosphoglycolic acids	4-carbon acids: oxaloacetic, malic, aspartic
Net photosynthesis intensity (mg CO_2 dm^{-2} hr^{-1})	15–35	40–45
Photorespiration to actual photosynthesis (%)	16–20	0.0
Stimulation of net photosynthesis in 1% O_2 as compared to 21% O_2 (%)	20–40	0.0
Stimulation of photosynthesis by 1000 mm^3 dm^{-3} CO_2 (%)	approx. 200	15–20
CO_2 compensation point at 25°C mm^3 dm^{-3}	40–60	0–5
Optimal temperature of photosynthesis (°C)	15–25	35–40
Saturation of photosynthesis by light	about 1/3–1/2 of sunlight intensity	lack of saturation
Transpiration coefficient (g H_2O g^{-1} dry wt.)	700–1000	250–300
Efficiency of transport of assimilates	low	high

composition and structure of electron transport chains and course of photosynthetic phosphorylations. On the level of enzymatic reactions, studies are concentrating around increasing the level and activity of photosynthetic enzymes, especially carboxylating enzymes in order to increase the ratio of carboxylation: oxygenation and thus decrease photorespiration. An important role in productivity may be played by reduction of the intensity of respiration. At the leaf-level, studies are being done on the various aspects of its structure and the role of stomata. They serve to reduce the physical and anatomical-cytological barriers hindering the diffusion of CO_2 to centers of its carboxylation in the leaf.

CO_2 AS A FACTOR IN PHOTOSYNTHESIS AND PRODUCTION OF BIOMASS BY PLANTS

Life on earth is based on carbon compounds. The circulation of this element in nature takes place between the earth's atmosphere, oceanic and sea waters and living organisms. The exchange of carbon takes place on a great scale between these three pools. The data on this process available to date are incomplete and little understood (Gates et al. 1983). It is estimated that the following amounts of carbon exist on our planet: in fossils, that is liquid and solid fuels and shale — 7500×10^9 tons, dissolved in sea and oceanic waters — $36\text{-}39 \times 10^9$ tons and 1760×10^9 tons in the land biosphere. The carbon content of limestones is estimated at 30×10^{15} tons.

The carbon content of the earth's atmosphere and its increase during the industrial era is presented in Table 4. It is estimated that presently,

Table 4

The carbon content of the earth's atmosphere

Year	CO_2 concentration, $mm^3\ dm^{-3}$	Carbon content, $\times 10^9$ tons	Increase, %	Source
1850	268	567	0.0	Keeling and Stuiver (1978)
1900	290	613	8.0	Stuiver (1978)
1958	314	664	17.0	Stuiver (1978)
1982	340	720	27.0	Tolbert (1984)

due to combustion of fossil fuels of photosynthetic origin and the production of cement, approximately 5×10^5 tons of carbon are released yearly into the atmosphere and that this amount will rise along with the increasing needs of the earth's population for technical energy and cement. Presently about 95% of technical energy comes from combustion of photosynthesis products and the remaining amount from nuclear energy plants and hydroelectric power plants. It has been calculated that if the rate of releasing carbon into the atmosphere is maintained at the present level, then by the year 2035, the CO_2 concentration in the atmosphere will equal 600 $mm^3\ dm^{-3}$ (Kimball and Idso 1983). Such a high concentration of CO_2 in the atmosphere will cause the so-called "greenhouse effect", because the infrared radiation emitted from the earth's surface will be absorbed by the atmospheric CO_2. This in turn may cause the temperature of the globe to rise by about 2-3°C, and in the polar regions, by 7-9°C. A rise in the globe's temperature will release huge amounts of water from glaciers, bringing up the levels of oceans and seas, submerging low-laying areas and cause a change in climatic regions (Reck 1975, Kimball and Idso 1983).

However, the problem seems to be more complicated. Combustion of fossil fuels is accompanied by increasing pollution of the atmosphere with SO_2, gaseous hydrocarbons and industrial particulates. Together, these pollutants speed up cloud formation. Increased cloudiness, due to reflection of the sun's rays from the earth, decreases the amount of energy reaching the surface of the globe, thus limiting not only the greenhouse effect, but also photosynthesis (McCormick and Ludwig 1967, Fennelly 1976, Stuiver 1978).

This briefly described effect of increased atmospheric concentrations has greatly interested not only biologists, but members of the general public as well. From the point of view of interest here, that is increasing food production, increased CO_2 concentrations in the air seem to be favorable because, as has been shown in numerous studies, in air containing 1000 $mm^3\ dm^{-3}$ CO_2, photosynthesis and growth in C_3 plants increases about two-fold, while in C_4 type plants, by about 15-20% (Tolbert 1984). This quantitatively different effect of CO_2 on C_3 and C_4 type plants is due to the occurrence of photorespiration in C_3 plants and its lack in C_4 type plants.

In C_3 type plants, the enzyme initiating reactions in the C_3 cycle and C_2 cycle, that is photosynthesis and photorespiration, respectively, is the bifunctional enzyme — carboxylase/oxygenase (Lorimer 1981). Competition between both cycles for the substrates, that is CO_2 and O_2, determines the ratio between cycle C_3 carboxylation and cycle C_2 oxygenation. At low atmospheric CO_2 concentrations, a compensation point is established at which net photosynthesis equals zero. Increasing the O_2 concentration to about 35% brings about the same effect, the compensation point is raised and net photosynthesis equals zero. In this way the competition between carboxylase/oxygenase for CO_2 and O_2 guarantees a balance of CO_2 in the atmosphere. In other words, the properties of this enzyme are the reason that increased photosynthesis is always accompanied by increased photorespiration in C_3 type plants (Poskuta and Nelson 1986a, b). Data from literature to date show that the cofactors for both opposing reactions are still unknown, as are the hormonal growth factors of plants which could modulate their kinetic properties. Studies on *Arabidopsis* mutants have shown that elimination of photorespiration was lethal for the plants (Somerville and Ogren 1982). Great hopes are held for genetic engineering, whose aim is to identify and change specific amino acids in the active centers of carboxylase/oxygenase and bring about changes in the kinetic properties of the enzyme favoring carboxylation and reducing oxygenation.

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REFERENCES

Alsudery A., 1985. The world food problems: Assessement and solutions. In: Crop productivity — Research imperatives revisited. An Intern. Conference held at Boyne Highlands Inn, October 13-18, 1985, and Airlie House, December 11-13, 1985, Gibbs M., Carlson C. (eds.), pp. 71-80.

Anderson J. H., 1985. The politics of agricultural research. In: Crop productivity — Research imperatives revisited. An Intern. Conference held at Boyne Highlands Inn, October 13-18, 1985 and Airlie House, December 11-13, 1985, Gibbs M., Carlson C. (eds.), pp. 48-56.

Austin R. B., 1981. A combined genetic and chemical approach to increasing and stabilizing wheat yields. In: Opportunities for manipulation of cereal productivity. Hawkins A. F., Jeffcoat N. B. (ed.), Monograph 7, British plant growth regular group. Oxford. pp. 46-57.

Austin R. B., Ford A. M., Morgan C. L., Kaminski A., Miller T. E., 1984. In: Advances in photosynthesis research. Proc. VI. Intern. Congr. Photosynthesis. Vol. IV. Sybesma C. (ed.). Brussels, Belgium. W. Junk Publ., The Hague. pp. 103-110.

Barker R. 1985. The changing world of research opportunities. In: Crop productivity — Research imperatives revisited. An Intern. Conference held at Boyne Highlands Inn, October 13-18, 1985 and Airlie House December 11-13, 1985, Gibbs M., Carlson C. (eds.), pp. 103-110.

Coombs J., 1984. Prospects of improving photosynthesis for increased crop productivity. In: Advances in photosynthesis research. VI Intern. Congress Photosynthesis, Brussels, Belgium. Vol. IV. Sybesma C. (ed.), W. Junk Publ., The Hague. pp. 111-120.

Coombs J., Hall D. O., 1982. Technigues in bioproductivity and photosynthesis. Coombs J., Hall D. O. (eds.). Pergamon Press, Oxford-New York-Toronto-Sydney-Paris-Frankfurt. pp. 159-166.

Day P. R., 1985. The impact of biotechnology on agricultural research. In: Crop productivity — Research imperatives revisited. An Intern. Conference held at Boyne Highlands Inn, October 13-18, 1985 and Airlie House, December 11-13, 1985, Gibbs M., Carlson C. (eds.), pp. 94-102.

Fennelly P. F., 1976. The origin and influence of airborne particulates. Amer. Sci. 64: 46-56.

Gates D. M., Strain B. R., Weber J. A., 1983. Ecophysiological effects of changing atmospheric CO_2 concentration. In: Encyclopedia of Plant Physiol. NS. Vol. 12D. Lange O. L., Nobel P. S., Osmond S. B., Ziegler H. (eds.), Springer-Verlag, Berlin-Heidelberg--New York. pp. 503-526.

Hess C. E., 1985. Past, present and future of agricultural research. In: Crop productivity — Research imperatives revisited. An Intern. Conference held at Boyne Highlands Inn, October 13-18, 1985 and Airlie House, December 11-13, 1985. Gibbs M., Carlson C. (eds.) pp. 81-93.

Johnson G. L., 1985. Agricultural surpluses — research on agricultural technologies, institutions, people and capital growth. In: Crop productivity — Research imperatives revisited. An Intern. Confereance held at Boyne Highlands Inn, October 13-18, 1985 and Airlie House, December 11-13, 1985. Gibbs M., Carlson C. (eds.) pp. 57-70.

Keeling C. D., Stuiver M., 1978. Atmospheric carbon dioxide in the 19th century. Science 202: 1109.

Kimball B. A., Idso S. B., 1983. Increasing atmospheric CO_2: effects on crop yield, water use and climate. Agric. Water Manage. 7: 55-72.

Lorimer G. H., 1981. The carboxylation and oxygenation of ribulose 1,5 bisphosphate: the primary events in photosynthesis and photorespiration. Ann. Rev. Plant Physiol. 32: 345-383.

Ludlow M. M., 1985. Photosynthesis and dry matter production in C_3 and C_4 pasture plants with special emphasis on tropical C_3 legumes and C_4 grasses. Austr. J. Plant Physiol. 12: 557-572.

McCormick R. A., Ludwig J. H., 1967. Climate modification by atmospheric aerosols. Science 156: 1358-1359.

Poskuta J. W., 1983. Photosynthesis and food problem. In: Photosynthetic solar energy conversion and storages. Poskuta J. W. (ed.), Wyd. UW, Warszawa, pp. 267–278.

Poskuta J. W., 1984. Fotosynteza a problem wyżywienia. In: 10 lat Olimpiady Biologicznej. Wyd. Szkol. Pedag., Warszawa. pp. 93-110.

Poskuta J. W., Nelson C. J., 1986a. Oxygen and radiation effects on CO_2 exchange in light and in darkness of decaploid and hexaploid tall fescue (*Festuca arundinacea* Schreb.). Acta Soc. Bota. Pol. 55: 35-43.

Poskuta J. W., Nelson C. J., 1986b. Role of photosynthesis and photorespiration and of leaf area in determining yield of tall fescue genotypes. Photosynthetica 20: 94-101.

Reck R. A., 1975. Aerosols and polar temperature changes. Science 188: 728-730.

Somerville C. R., Ogren W. L., 1982. Genetic modification of photorespiration. Trends Biochem. Sci. 7: 171-174.

Stuiver M., 1978. Atmospheric carbon dioxide and carbon reservoir changes. Science 199: 253-258.

Tolbert N. E., 1984. Effect of increasing atmospheric CO_2 on photosynthesis. In: Advances in photosynthesis research. Proc. VI Intern. Photosynthesis Congr. Vol. IV. Sybesma C. (ed.), Brussels, Belgium. W. Junk Publ., The Hague, pp. 181-191.

Wittwer S. H., 1985. Food production: Technology and the resource base. Science 188: 579-584.

Wittwer S. H., 1985. Research imperatives: A decade of change. In: Crop productivity — Research imperatives revisited. An Intern. Conference held at Boyne Highlands Inn, October 13-18, 1986 and Airlie House, December 11-13, 1985. Gibbs M., Carlson C. (eds.), pp. 1-6.

Fotosynteza a problem wyżywienia

Streszczenie

Badania w dziedzinie fotosyntezy są szczególnie predysponowane do rozwiązywania naczelnego problemu współczesności, tj. wyżywienia wzrastającej liczby ludności na świecie. W artykule przedstawione są dane dotyczące tempa przyrostu ludności świata, rozmiarów produkcji i wysokości plonów najważniejszych roślin rolniczych. Dyskutowane są zależności między wydajnością fotosyntetyczną roślin C_3 i C_4 a ich plonowaniem. Prezentowane jest zagadnienie zwiększającego się stężenia CO_2 w atmosferze Ziemi i jego wpływ na fotosyntezę, fotooddychanie i akumulację biomasy przez rośliny.