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Primary Production: Terrestrial Ecosystems[1]

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The history of growth in understanding of primary productivity and in making estimates of biosphere production is reviewed. Two approaches to estimation of land production are discussed. Production may first be estimated by mean values for ecosystem types and the areas of these. A total production of 100×10^9 tons/year is thus estimated for the continents, making up 29% of the earth's surface. The energy content of net primary production is 426×10^{18} cal for the continents and 261×10^{18} cal for the seas, implying a biosphere energy efficiency of 0.13% relative to incident sunlight of the full spectrum at the earth's surface. As a second approach, the relation of productivity to mean annual temperature and precipitation is analyzed. On the basis of these relationships, a "Miami model" map of primary productivity of the continents is presented.

INTRODUCTION

For man, the primary productivity of the world is of fundamental importance. In primary productivity is captured that portion of solar energy that can support the life of all components of the biosphere. The largest portion of human food is provided by the productivity of plant life on land. From land production also comes our greatest single substance for construction and fabrication—wood—and a host of other products. The productivity of vegetation is one major aspect of the sustained carrying capacity of the earth for man.

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Fossil fuels are accumulated profits from past primary production. The mantle of vegetation protects the earth's surface from destructive erosion. It also provides an important part of the environmental context in relation to which man and his societies have developed and man himself feels most at home. It is by primary productivity, and the growth of plants by the creation of organic matter through photosynthesis, that the life of the vegetational mantle and, thereby, of man is maintained.

The many problems of energy and nutrient flow, and their relation to the structure of communities and potential harvests, make primary productivity of scientific interest. The correlation between the productivity and character of vegetation cover, and the potential for agriculture and the environmental terms set for cultural development, have created additional interest. Many compilations and evaluations of the productivity of the earth and related problems have been made within the last decade. This paper discusses previous and current attempts to assess the productivity of the land surfaces and the earth. Primary productivity is discussed in terms of both dry matter and energy. Quantitative relations of productivity to major environmental determinants are described, and a new way of mapping the earth's productivity patterns by computer is discussed.

HISTORICAL SURVEY

At the American Institute of Biological Sciences Congress, in Miami, Rabinovitch evaluated the history of the discovery of photosynthesis (Rabinovitch, 1971). From the discussion that followed, it seemed evident that many people equate photosynthesis with productivity and identify the raw materials of photosynthesis (water, carbon dioxide, and sunlight energy) as the direct controls of productivity. However, photosynthesis and primary productivity are not so simply equated. To be sure, primary productivity is the realized product of photosynthesis—energy bound into organic matter produced in photosynthesis. Yet primary productivity requires more than photosynthesis, notably the uptake and incorporation of inorganic nutrients into the diverse organic compounds of protoplasm, without which there is no photosynthesizing organism. Temperatures govern annual productivity in various ways that do not result from temperature dependence of the photosynthetic process. On land, productivity is strongly affected by availability of water—not primarily for use in the photosynthetic process itself, but to replace the water lost through the open stomata that make possible carbon dioxide uptake. Before returning to these environmental controls, I shall discuss the history of the understanding of productivity—as distinguished from photosynthesis—and its global amounts.

In this history, one may see at least three major periods: (1) the time before von Liebig, (2) from von Liebig to the International Biological Program, and (3) the IBP and its consequences.

From Aristotle to von Liebig

384-322 B.C.

Aristotle taught that soil—in a manner comparable to that of the intestinal tract of animals—provides predigested food which the plants take up through their roots; he thus emphasized the relationship between plant and soil. This opinion was held generally for 1800 years, until 1450 A.D.

1450 A.D.

Nicolai de Cusa expressed the almost revolutionary idea that "the water thickens within the soil, sucks off soil substances and becomes then condensed to herb by the action of the sun." This was a rather mystic vision, but was apparently the result of his observation. His view emphasized the relationship between plant and water.

About 1600 (1577-1644)

Van Helmont, in the midst of odd attempts to obtain mice from junk and sawdust, made one rather intelligent experiment. He grew a willow twig weighing 5 lb in a large clay pot containing 300 lb of soil and irrigated it with rainwater. After 5 years, he harvested a willow tree of 164 lb, with a loss of only 2 oz of soil. Van Helmont concluded from this that water was condensed to form plants.

1772-1777 or 1779

Priestley, Scheele, and Ingenhousz first discussed the interaction between plants and air. They spoke about melioration and the spoiling of the air by plants in light or darkness.

1804

DeSaussure studied the gas exchange of plants and gave the correct equation for photosynthesis:

Carbon dioxide + water = plant matter + oxygen

From that time on, plant production became a significant field of investigation, though not on the scale of present-day studies. The then newly founded colleges of agriculture and forestry dealt with various aspects of such questions.

From von Liebig to the IBP

1840

As a result of the development of analytical chemistry, von Liebig was able to show the importance of minerals for plant nutrition. He fought intensely against the humus theory, which assumed that plants obtained their substance from organic matter only—the general assumption in agricultural education in those days. While studying the relation between dry matter production and nutrient supply, von Liebig formulated the well-known "law of the minimum."

1862

Von Liebig was also the first to think quantitatively about the impact of vegetation on the atmosphere. He said, in 1862, "If we think of the surface of the earth as being entirely covered with a green meadow yielding annually 5000 kg/ha, the total CO_2 content of the atmosphere would be used up within 21-22 years if the CO_2 were not replaced" (230-240 $\times$ 10^9 metric tons CO_2 consumption/year, according to von Liebig). This sentence was the beginning of geochemical treatment of productivity.

1882

Yield studies were easy to do with agricultural plants in laboratories and in the field. Forests presented special difficulties. The first dry matter productivity figures for forests were not presented until 1882, when Ebermayer made the first comparison of matter productivity between forests (from his own measurements) and field crops (data of Boussingault) in Bavaria. The forests were, of course, more productive. His figures in kilograms per hectare of dry matter (= 10 $\times$ g/m^2) are

Beech:	Wood	3163 kg/ha	Pine:	Wood	3233 kg/ha
	Litter	3334		Litter	3186
	Total	6497		Total	6419
Spruce:	Wood	3435 kg/ha	Potatoes:	4080-4340 kg/ha	
	Litter	3007	Clover:	4200	
	Total	6442	Wheat:	4500	
			Oats:	4250	

These values remained the key figures for about 50 years and were used by geochemists again and again in calculations of chemical elements in the biosphere. It was about 40 years before Boysen Jensen, Burger, Harper (Lieth, 1962), and others began similar measurements.

Eberymayer presented the first calculation of a world total of carbon binding of vegetation based on field measurements, restricting himself to the land areas. From his calculations for Bavaria, he extrapolated that the annual consumption of CO_2 for the entire world was 90 $\times$ 10^9 tons.

1900-1930

More than 60 years after Liebig's "law of the minimum," E. A. Mitscherlich transformed it into the "law of yield." This delay is rather surprising, since the measurement of yield and dry matter production had become very popular during Liebig's time. Mitscherlich's yield law is the first attempt to model productivity (Mitscherlich, 1954).

1908-1913

Figures similar to Ebermayer's (100 $\times$ 10^9 tons) for CO_2 consumption were given by Arrhenius in 1908 and Cimacian in 1913, but neither gave additional biological information (see Noddack and Komor, 1937).

1919

The next major contribution to the knowledge of dry matter production from the land came from Schroeder (1919). He based his calculations primarily on Ebermayer's studies, but by this time there was more reliable information regarding the surface areas of forests, steppes, and cultivated land. Schroeder's calculations gave the following figures for the dry matter production of the total land area of the earth:

Carbon	Carbon dioxide	Dry matter
13 $\times$ 10^9 tons	48 $\times$ 10^9 tons	28 $\times$ 10^9 tons

Schroeder had based his figures on a crude, superficial geographical classification; the next refinement of the production figures would occur when the plant geographers presented their first vegetation maps.

1930

This work probably began with Drude at the end of the nineteenth century and led later to the widely used physiognomic map of Brockmann-Jerosch (1930). From these vegetation maps, production calculations could be made as soon as information became available from the different vegetation units. All later calculations for the production of the world up to the present were based on vegetation units whose areas were physiognomically established (Lieth, 1964; Whittaker and Likens, in Whittaker, 1970; Golley, 1972).

1937

Schroeder's (1919) land production figures were refined by the geochemist

Noddack (1937) (my first chemistry teacher, who is largely responsible for my early interest in this subject matter), and the revised figures were used in reviews and textbooks until 1965. Schroeder was apparently the first to offer some information about the benthic algae, but he did not attempt to say anything about the plankton. The first estimate of total aquatic carbon binding, 28.6 $\times$ 10^9 tons/year, was made by Noddack and Komor (1937). This was more an opinion than a solidly based figure.

1944-1959

Only during the last 30 years has aquatic production received much interest; within this short period of time, figures were presented by Riley (1944), Steemann Nielsen (1954), Steemann Nielsen and Aabye Jensen (1957), Fleming (1957), Fogg (1958), and Ryther (1959), summarized in Gessner (1959) (see also the article by Bunt in this Journal issue).

1960

Müller (1960) summarized estimates of world production up to that time in an extensive review and gave his own estimates of 10.3 $\times$ 10^9 tons of carbon net production on land and 25 $\times$ 10^9 tons for land and sea. From 1960 on, there have been an increasing number of estimates of world production that need not be reviewed in detail. Table I summarizes some of the most significant estimates.

Concluding my discussion of history, I refer again to Rabinovitch's (1971) paper on the discovery of photosynthesis. Following his manner of indicating persons whose work led up to the *primary production equation* (not the photosynthetic equation), I have added the names of those who I think were also instrumental in first evaluating the importance and/or necessity of each of the elements. Entries from Rabinovitch are in parentheses; my entries are in square brackets.

CO_2	+	H_2O	+	light	+	inorganic nutrients
(Senebier)		(de Saussure)		(Ingenhousz)		
[Priestley - Scheele]		[van Helmont]				[von Liebig]

Yield

Oxygen	+	organic matter	+	chemical energy
(Priestley)		(Ingenhousz)		(Mayer)
		[van Helmont]		[Boltzmann]

WORLD PRODUCTION: MAJOR VEGETATION UNITS

Without human interference, major vegetation units of the world are rather stable over long periods of time. Their classification in the literature of the last 20 years, in contrast, has been unstable; there are inescapable reasons why the classification of plant communities remains to some degree subjective. In order to employ a reasonably standard classification system, I have chosen the UNESCO scheme as published by Ellenberg and Mueller-Dombois (1967), in its modification by Olson (1970). This system contains eight formation classes for land vegetation, the classes being subdivided into 28 subclasses and a large number of further divisions. The formation subclasses of this system coincide best with the "biome types" as they are understood by the IBP and the "formation types" of many authors (e.g., Whittaker 1962, 1970). In Table II, production estimates are presented for some 20 such vegetation units. The production values are calculated separately for two different categories: annual dry matter production and annual energy fixation. Carbon content can be estimated as 45% of the dry matter, and CO_2 is estimated as 1.6 times the dry matter.

Table II presents the following data: in column 1, the vegetation unit; in column 2, the area covered by this vegetation type; in columns 3 and 4, the rate of primary productivity; and in column 5, the total annual dry matter production for the vegetation type. The sum total for the earth amounts to 55.2×10^9 tons for the oceans and 100.2×10^9 tons for the continental areas. The values given in Table II coincide reasonably well with the recent estimates of Whittaker and Likens (Whittaker, 1970; Whittaker and Woodwell, 1971) of 164×10^9 tons of dry matter for the world, and of Golley (1972) of 143.8×10^9 tons of dry matter. Among other recent estimates, that of Basilevich *et al.* (1970) differs most from our figures, with 170×10^9 tons of dry matter for land, 55×10^9 tons for the oceans, and a total of 225×10^9 tons.

ENERGY FIXATION

A separate appraisal for the annual energy fixation of the same vegetation units is given in columns 6-8 of Table II. Column 6 gives the averaged figure for the combustion value of the vegetation type, considering actual compositions of vegetation samples as described by Lieth and Pflanz (1968). This is converted into calories fixed per m^2 in column 7 by multiplying the figure of column 6 by the figure of column 4. Column 8 then evaluates the total estimate of energy fixation for the entire vegetation unit. The total for the land surface is 426×10^{18} cal/year. Estimating marine primary productivity as 55×10^9 tons/year; with the caloric equivalents in the footnote to Table II, 261×10^{18} cal/year is obtained for the oceans and a total net primary productivity for the world of 687×10^{18} cal/year is calculated. If 510×10^{18} kcal is accepted as the total annual solar radiation received by the earth, the total energy fixation averages 0.13%, based on 0.07% for the ocean and 0.3% for the land surfaces.

The world total of 687×10^{18} cal/year, calculated on the basis of figures

Table I. Historical Development of Knowledge of Primary Production

A. Matter and energy metabolism of the plants

Years	Authors[a]	Metabolism categories: Soil	Water	Air	Energy
384-322 B.C.	Aristotle	X			•
1450 A.D.	Nicolai de Cusa	X	X		
1577-1644	van Helmont		X		•
1772-1779	Priestley, Scheele, and Ingenhousz			X	•
1804	de Saussure		X	X	X
1840	von Liebig	Mineral cycling	X	X	X
1886	Boltzmann				Radiant energy conversion
Today's problems in the various categories:		Mineral cycling	Water balance	Gaseous metabolism	Energy function

B. Estimates of the annual world primary productivity

Years	Authors	No. vegetation units distinguished	Value for annual production (10^9 tons)	Category assessed
1862	von Liebig	1	230-240	CO_2
1882	Ebermayer	3, on land only	90	CO_2
1919	Schroeder	4, on land only	13	C
			48	CO_2
			28	Dry matter
1937	Noddack	5	64	C
1960	Müller	5	25	C
1969	Whittaker and Likens	15	164	Dry matter
1971	The present study	20	155	Dry matter
			(687×10^{18}	Calories)
			70	C
			257	CO_2

Table I. Continued

C. Mapping of world productivity

Years	Authors	Area mapped	Category mapped
1955	Sverdrup	Ocean	C
1957	Fleming	Ocean	C
1957	FAO team (in Gessner, 1959)	Ocean	C
1956	Patterson (in Lieth, 1962)	Forested areas	Volume of wood
1964	Lieth	1st world map	C (dry matter, calories, CO_2)
1965 (1966)	Rodin and Bazilevich	Land	Mineral cycling, dry matter
1968, 1970	Basilevich, *et al.*	Land	Mineral cycling, dry matter
1971	Lieth, Zaehringer, and Berryhill (in Lieth, 1972)	Land, 1st computer map	C, dry matter, calories

[a] Literature before 1900 is usually quoted from secondary literature and is not included in the literature list.

Table II. Net Primary Productivity and Energy Fixation for the World (Around 1950) [a]

1	2	3	4	5	6	7	8
		Net primary productivity				Annual energy fixation	
Vegetation unit	Area (10^6 km^2)	Range (g $\cdot$ m^{-2} $\cdot$ yr^{-1})	Approximate mean	Total for area (10^9 tons)	Combustion value (kcal/g)	Mean (10^6 cal/m^2)	By area (10^{18} cal)
Forest	50.0		1290	64.5			277.0
Tropical rainforest	17.0	1000-3500	2000	34.0	4.1	8.2	139.4
Raingreen forest	7.5	600-3500	1500	11.3	4.2	6.3	47.2
Summergreen forest	7.0	400-2500	1000	7.0	4.6	4.6	32.2
Chaparral	1.5	250-1500	800	1.2	4.9	3.9	5.9
Warm temperate mixed forest	5.0	600-2500	1000	5.0	4.7	4.7	23.5
Boreal forest	12.0	200-1500	500	6.0	4.8	2.4	28.8
Woodland	7.0	200-1000	600	4.2	4.6	2.8	19.6
Dwarf and open scrub	26.0		90	2.4			10.2
Tundra	8.0	100-400	140	1.1	4.5	0.6	4.8
Desert scrub	18.0	10-250	70	1.3	4.5	0.3	5.4
Grassland	24.0		600	15.0			60.0
Tropical grassland	15.0	200-2000	700	10.5	4.0	2.8	42.0
Temperate grassland	9.0	100-1500	500	4.5	4.0	2.0	18.0
Desert (extreme)	24.0		1	–			0.1
Dry desert	8.5	0-10	3	–	4.5	–	0.1
Ice desert	15.5	0-1	0	–	–	–	–

Table II. Continued

1	2	3	4	5	6	7	8
		Net primary productivity				Annual energy fixation	
Vegetation unit	Area (10^6 km^2)	Range (g·m^{-2}·yr^{-1})	Approximate mean	Total for area (10^9 tons)	Combustion value (kcal/g)	Mean (10^6 cal/m^2)	By area (10^{18} cal)
Cultivated land	14.0	100-4000	650	9.1	4.1	2.7	37.8
Freshwater	4.0		1250	5.0			21.4
Swamp and marsh	2.0	800-4000	2000	4.0	4.2	8.4	16.8
Lake and stream	2.0	100-1500	500	1.0	4.5	2.3	4.6
Total for continents	149.0		669	100.2			426.1

[a]Comments on columns: Column 1, subdivisions are named according to Ellenberg and Mueller-Dombois (1967) and Olson (1970). Column 2, basically result of the effort of three consecutive groups of geobotany students at UNC, Chapel Hill. Adjustments and compromises were made in some cases. Column 3, values were deduced from our own compilations of productivity data, with results very similar to those of Whittaker and Woodwell (1971). Column 4, original, *cf.* Whittaker and Likens (1969) in Whittaker (1970), and Odum (1971). Column 5, product of the positions in columns 2 and 4. All values were rounded off to one decimal point. Column 6, original, *cf.* Jordan (1971[a]) and Odum (1971). Values of 4.5 computed for reefs, estuaries, and inshore waters, 4.9 for open ocean and upwelling areas. Column 7, product of columns 4 and 6. Column 8, product of columns 2 and 7.

in Table II, coincides well with Golley's (1972) figure of 652×10^{18} cal/year. The two assessments reinforce each other, since my estimates are based, for the most part, on a different data pool, with overlap in the two calculations only in the tropical regions. Golley relied heavily on a compilation by Cummins and Wuycheck (1971), which was then available only in mimeographed form, and which was published after I had assembled my Table II. My own listing relied heavily on European data already available and several hundred checks made during the years 1962-1966 (one thesis by Pflanz, 1964, and reports by Velemis, Powell, and Vaasma, mostly unpublished except Lieth, 1965[a], and Lieth and Pflanz, 1968).

Comparison of the energy figures in Table II leads to the observation that among the forest types, caloric contents are correlated with climate and taxonomic group. Caloric values are in general higher in temperate than in tropical forests and higher in gymnosperms than in angiosperms. At the extremes of these two trends, the combustion values in (angiosperm) tropical rainforests are 20-25% lower than in (gymnosperm) boreal forests. This leads to a hypothesis on the success of the angiosperms over the gymnosperms during the last 60 million years (Lieth, 1972; *cf.* Jordan, 1971[b]). One notes how the gymnosperms, in most temperate areas, have been pushed to environments that are marginal (because of aridity, or cold, or soil infertility) for tree growth, while they have been essentially wiped out of the lowland tropics. I suggest as a key adaptive advantage of the angiosperms their ability to construct wood with much less expenditure of energy per unit weight.

OTHER COMMUNITY PROPERTIES

In many papers, productivity is considered also in relation to biomass, assimilatory surface, and chlorophyll content. Ranges of values for these properties have been compiled from the literature and are presented in Table III. They support the data on dry matter productivity and energy binding and provide a basis for the biosphere characterization in the article by Whittaker and Likens in this Journal issue.

Knowledge of biomass (dry organic matter of organisms present at a given time—sometimes referred to as standing crop—as distinguished from productivity as a rate value) is essential for knowledge of nutrient pools in organisms as part of nutrient cycling and biogeochemistry. The higher the productivity of a community, the larger the amount of that productivity that is likely to accumulate as biomass. The correlation is loose, however, and not widely useful for the estimation of productivity itself. Biomass is greatly affected by ages of the dominant plants, and these ages differ much in successional communities. Grasslands and other fire-susceptible communities, even those that are highly productive, tend to have low biomass compared with other communities.

Table III. Biomass of Mature Stands, Leaf Area Indices, and Chlorophyll Contents of Vegetation Units (Source Numbers in Parentheses) [a]

1 Vegetation unit	2 Mature biomass (kg/m^2)	3 Leaf area index or assimilating surface (m^2/m^2)	4 Total chlorophyll (g/m^2)
Tropical rainforest	45 (1, 9)$^+$ 75? (2)	6-10-12-16.6 (1,14)	3-9 (14)
Raingreen forest	42 (1,9)	6-7-10 (1,11)	2-? (11)
Summergreen forest	42-46 (4)	3-12 (4,14)	2-6 (6,14)
Chaparral	26 (8)	4-7-12 (3,8)	?
Warm temperate mixed forest	24 (1)	5-14 (1,14)	3-8 (14)
Boreal forest	20-52 (1)	7-15 (1,2,5)	1.4 (5)
Woodland	2-20 (7,1)	4.2 (14)	?-2 (11)
Tundra	0.1-3 (7)	0.5-1-1.3 (12,13)	0.4-0.6 (12)
Desert scrub	0.1-4 (7)	?	?
Tropical grassland	?-5	1-5 (12,14)	1.7-5 (14)
Temperate grassland	?-3	?-5-9-16 (5,6,17)	0-6-5 (5,6)
Dry desert	0	0	0
Ice desert	0	0	0
Cultivated land (annual crops)	3.5	4-12 (6,15,16)	1-5 (5,6,15,16)
Swamp and marsh	2.5-? (10)	?-11-23.3 (6,14)	0.3-4.3 (5,14)
Lake and stream	?-0.1 (7)$^+$	?	0.005-0.12-1.3 (14)
Algal mass culture (10-cm layer)			(summer) 10-20 (14)
Reefs and estuaries	0.04-4 (7)	?	0.1-1.3-?
Continental shelf	0.001-0.04 (7)	?	0.02-1.33 (14)
Open ocean	?-0.005 (7)	6? (7)	0.03-0.045 (7,14)
Upwelling zones	?	?	0.05-? (14)

[a] Comments on columns: Column 1, corresponds to Table II. Column 2, dry matter, values close to maxima for mature communities of a given type, *cf.* ranges given by Whittaker and Likens (Whittaker, 1970). Column 3, ranges of leaf surface area in m^2 per m^2 of ground surface. Column 4, ranges of chlorophyll content in g per m^2 of ground surface. Sources, as indicated in parentheses: (1) Art and Marks (1971), (2) Rodin and Bazilevich (1966), (3) Martens (1964), (4) Lieth (1962), Lieth *et al.* (1965), (5) Bray, in Lieth (1962), (6) Medina and Lieth (1963, 1964), Medina and San Jose (1970), (7) Whittaker (1970), (8) Lossaint and Rapp (1969), (9) Kira and Ogawa (1971), (10) Reader (1971), (11) Bandhu (1971), (12) Dennis and Tieszen (1971), (13) Vareschi (1953), (14) Aruga and Monsi (1963), (15) Kreh (1965), (16) Schultz (1962), (17) Geyger (1964); secondary literature has been cited here whenever possible because of the very large number of primary sources.

Biomass ranges for terrestrial communities are generally from 0.1 to 5 kg/m^2 in many grasslands, desert scrubs, and tundra communities, 5-20 kg/m^2 in many woodlands (of small trees), shrublands (e.g., chaparral), and young forests, and 20-60 kg/m^2 for many mature forests (Whittaker, 1966, 1970). Additional world biomass data are given by Bowen (1966), Rodin and Bazilevich (1966), Whittaker (1970), Olson (1970), and Bazilevich and Rodin (1971).

Leaf surface is generally expressed as the "leaf area index," as m^2 of leaf surface area over 1 m^2 of ground surface. This, clearly, is an important dimension related to production, for it defines the leaf area through which the gaseous exchange of photosynthesis must occur. Leaf area indices are correlated with productivity, but only roughly so, and not in a way that permits effective prediction of production from the indices. Evergreen communities in general have higher indices than deciduous ones of similar productivity. Most gymnosperm forests have high indices (even after one divides these by 2 to compare them with broadleaf forests, since surface areas are computed for the whole surface of gymnosperm needles but only for one side of broad leaves). Whereas biomass ranges tend to be more in contrast between different communities than are productivity ranges, leaf area ranges tend to be convergent. A wide variety of communities have leaf area indices of 3-6 if they are deciduous, or up to 8 (or, for conifer needles, 16) if they are evergreen. Lower values, of course, occur in dry grasslands, desert scrubs, and tundra, and higher values are reported for managed grassland communities.

Chlorophyll content may seem the community dimension most directly relevant to the prediction of productivity. However, the correlation is, again, loose and the use for prediction insecure. Efficiency of energy capture by chlorophyll differs widely within a community and between communities. Chlorophyll content is rarely, in my experience, at minimum level (see also Gabrielsen, 1960) and may even serve in some cases as a shading pigment that prevents other leaves from being overirradiated. Ranges of chlorophyll content are, like leaf area indices, convergent between communities; the span of 2 to 4 or 6 g chlorophyll/m^2 of ground surface should include a wide range of more productive terrestrial communities, and 0.4-2 should include most others not in extreme environments. Unlike leaf index, chlorophyll can be compared between aquatic and terrestrial communities. Chlorophyll contents of plankton communities are very low (about 1.3 down to 0.05 and even 0.005 g/m^2) compared with terrestrial communities.

Some other community properties have been considered on a worldwide scale but cannot be discussed here; these include gross primary productivity (Golley, 1972) and nutrient pools (Rodin and Bazilevich, 1966; Bazilevich and Rodin, 1971; Young, 1968), litter accumulation (Bray and Gorham, 1964) and decomposition rates (Lieth, 1963), and albedo (Bray, 1962).

PRODUCTION MAPPING

The information summarized in Table II can be utilized for mapping the productivity of the world. In the first such effort (see Table IC), the primary productivity data then available were supplemented with agricultural and forest yield data, using estimated corrections to community productivity, to produce a world productivity map (Lieth, 1964; published also in Duvigneaud, 1967, and Reichle, 1970). Of maps produced since that time, the most recent world productivity map of Basilevich *et al.* (1970) comes much closer to the total value of my 1964 map than did their original map (Rodin and Bazilevich, 1966). The 1964 map, which gives a world production figure in fair agreement with that of Table II, was used to calculate the carbon exchange between atmosphere and biosphere (Junge and Czeplak, 1968).

Such a first effort, as this map is, invites improvement. Not only are more (and in some cases better) productivity measurements available than in 1964, but the use of a computer can be helpful in summarizing, correlating, and interpolating data, and in the printing out of the map itself. Two kinds of productivity maps are then feasible—those based on actual productivity measurements and those based on predictions of productivity from environmental data. The map produced along the first of these lines was essentially an updated version of the terrestrial part of the 1964 map, produced as a student project, mainly by T. Zaehringer and B. Berryhill. The result is entitled "Innsbrucker productivity map," since it was first shown at a 1971 productivity symposium in Innsbruck, Austria (Lieth, 1972), and is given as Fig. 1.

In any landscape, primary productivity varies over short distances. Such differences in productivity are implied by differences in topography and water availability, soil quality, and successional stages. One consequence is that statistical methods must be used to gain regional averages of primary productivity. The first assessment of this nature was made by Filzer (1951) for the agricultural productivity of Central Europe. A second consequence is the need for productivity maps on different scales—from the global and continental to the regional and to the local (on such a scale they will be of aid in land management). Over the last two years, Whigham and I (1971) have prepared a preliminary assessment of regional productivity in North Carolina. The assessment was done by county, based on 11 crops and seven other land use categories. The total primary productivity of each land use category was based on yield figures, when available, on direct spot-check assessments, or on reasonable comparative assumptions. In most cases, it was possible to convert available yield values to total-plant productivity. An average productivity figure, based on all land use categories, was calculated for each county and then put into an outline map of North Carolina. The resulting map is shown in Fig. 2. Maps of this kind are now available for Wisconsin (Stearns *et al.*, 1971),

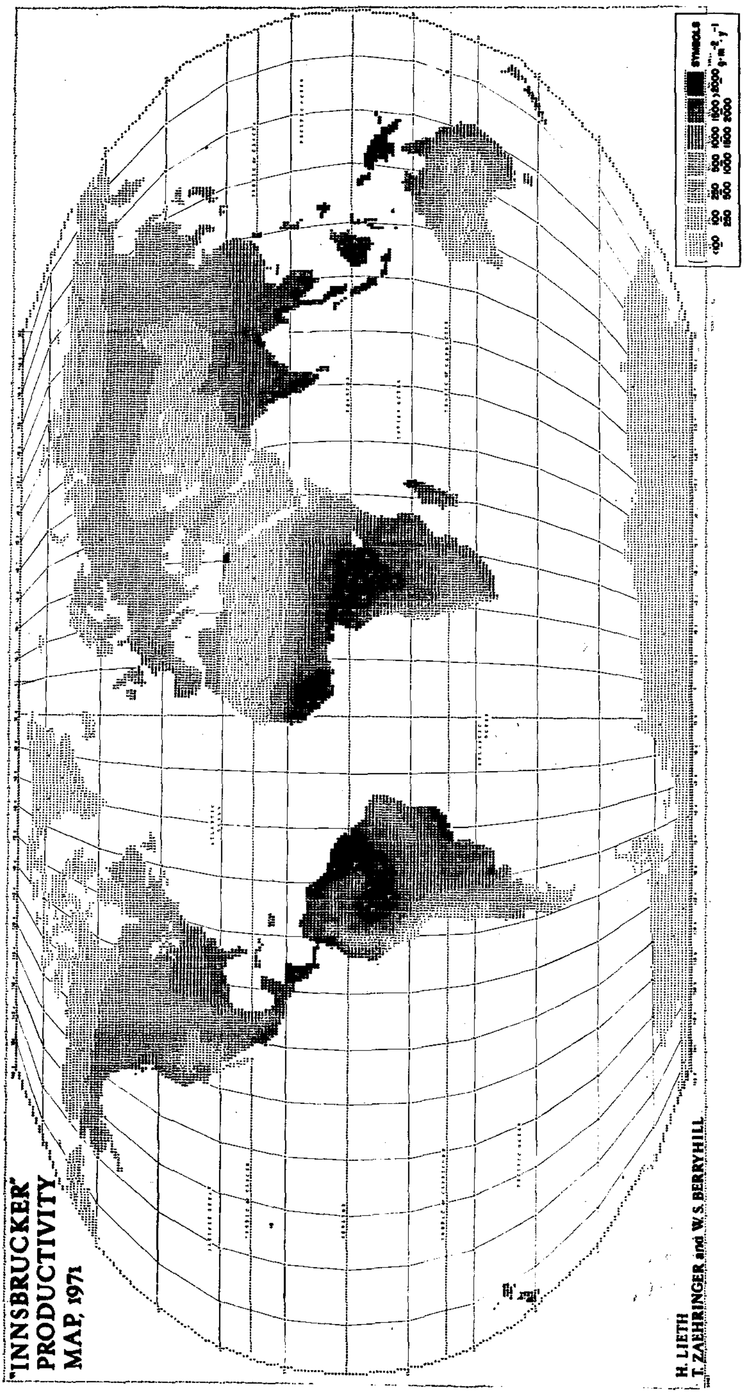


Fig. 1. Innsbrucker productivity map, based on actual measurements of net primary production in natural vegetation.

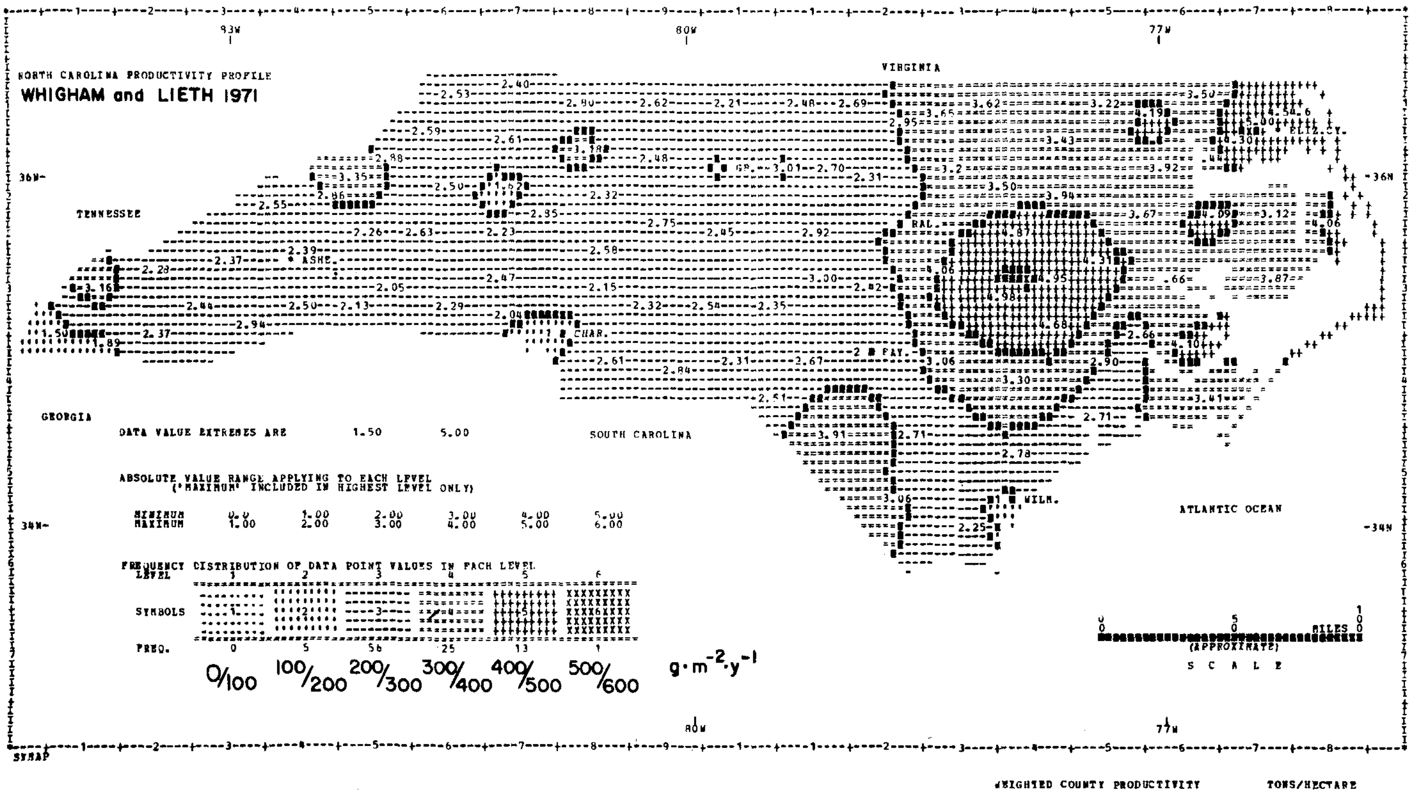


Fig. 2. Weighted county primary productivity averages for the hundred counties of North Carolina. Data values in the body of the map represent hundreds of grams, with the decimal point printed at the county center. The figure legend in the map frame shows the ranges of grams per square meter per year that apply to the level symbols used in the map. The values in the map, which summarize actual net production including agricultural yields corrected to total production, are about *one-fifth to one-half* of what would be expected from natural vegetation and suggest waste of potential resources in current land use practices. The low values of urban counties such as Mecklenberg (City of Charlotte) and Brunswick (City of Wilmington) are particularly striking.

Tennessee (DeSelm, 1971), and New York and Massachusetts (Art *et al.,* 1971); IBP hopes to map the entire United States in this manner.

The local map treating the productivity of particular tracts of land as a guide to their use remains to be developed. It cannot be said that either these local maps or the regional maps will, in the short term, much influence land use in the United States, where many regard land as still abundant. In scarcely any other respect does the United States differ so much from Germany and some other West European nations as in relative quality and control of land use. Perhaps, however, the American "frontier" philosophy of land use will one day change. Knowledge of natural vegetation and the productive potential of land may then offer welcome guidance.

WORLD PRODUCTION: ENVIRONMENTAL DETERMINANTS

As I have said, primary productivity is dependent on a number of environmental conditions, and in the first order among these on land are temperature and available water. If one can establish valid correlation models between these factors and the primary productivity, a worldwide data pool of meterological records can be of value. The relations among precipitation, temperature, and vegetation types were demonstrated several years ago (Lieth, 1956; Lieth and Zauner, 1957). Major vegetation types show different relations to these climatic variables (Fig. 3). The types overlap in relation to annual precipitation and temperature because of the effects of other factors (nutrients and other soil characteristics, fire, continentality, floristic history) that may also affect productivity. Other studies (Lieth, 1961-1968) have established effects of rainfall and temperature on primary productivity, and it seems logical to start modeling with these as principal factors.

My modeling exercises are based on the compilation shown in Table IV, with selected productivity data paired with average annual temperature values and average annual precipitation totals obtained from nearby meteorological stations. The productivity data were taken from recent publications, most of which I had not used for earlier assessments. The meteorological data were taken from the *Climate Diagram World Atlas* (Walter and Lieth, 1960-1967). For my purposes, I grouped the data from the northern hemisphere into four transects, each covering tundra-to-tropics: (1) North and South America, (2) Europe and Africa, (3) Russia and Asia Minor, and (4) East and Southeast Asia. A fifth region, South Africa, was added to test previous assumptions. From Table IV, I attempted a correlation model which could be used to predict the primary productivity from precipitation and temperature values (see Figs. 4 and 5). A first pair of models was developed together with T. Wolaver (Lieth, 1972). These models were refined (with E. Box) by the exclusion of extreme values, to give the results shown in Figs. 4 and 5.

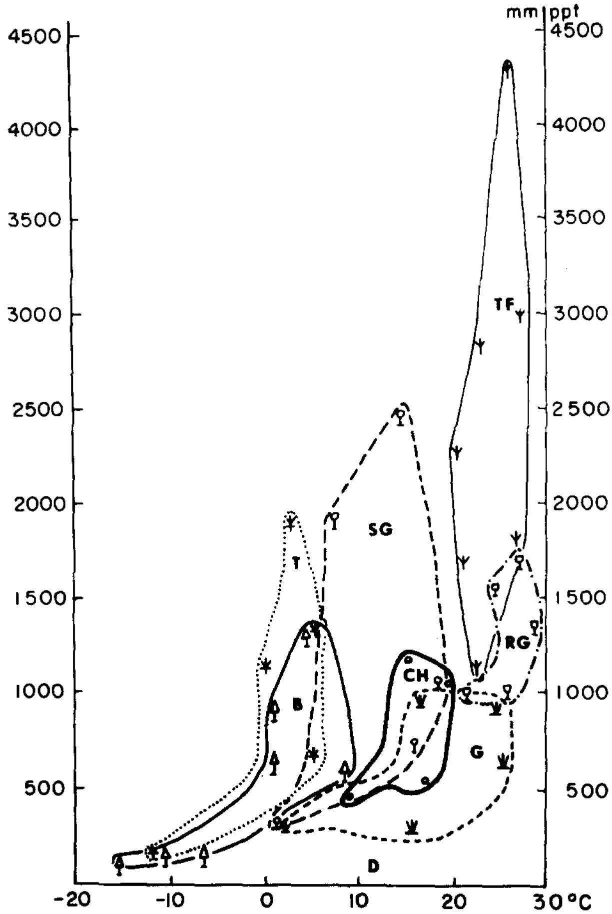


Fig. 3. Graphic model of the relation between temperature, precipitation, and vegetation formation classes, adapted from Lieth (1956). The abscissa is mean annual temperature in °C and the ordinate mean annual precipitation in millimeters. Each line circumscribes meteorological stations corresponding to a given vegetation type. Solid lines enclose evergreen types: B, boreal forest; CH, chaparral; TF, tropical rainforest. Interrupted lines enclose seasonally green vegetation types: T, tundra; SG, summergreen (deciduous) forest; RG, raingreen forest; G, grassland; D, desert and semidesert.

Figure 4 shows the relation between mean annual temperature and productivity. In the upper portion are shown the data used and the curve yielded by calculating the least squares for this data set. In the lower part are two curves and the signatures for the data points from each of the five transects. The upper curve is an optimum curve drawn by "Nyquist" analysis, giving a temperature

Table IV. Selected Productivity Data for Modeling Relations to Climate (Source Numbers in Parentheses) [a]

1 Station name	2 Climate diagram code number	3 Mean annual temperature (°C)	4 Mean annual precipitation (mm)	5 Annual total dry matter productivity (g/m^2)
Region I				
Barrow	Supplement sheet	−12.2	104	100-450 (1)
Kehora	401 030	2.3	641	710 (2)
same	401 030	2.3	641	990 (2)
same	401 030	2.3	641	1629 (2)
Knoxville	401 305	15.2	1156	2408 (3)
New Bern	401 312	17.5	1409	1280 (4)
Raleigh	401 313	15.5	1145	1900 (5)
Coweeta/N.C.	—	12.2	1800	1203 (3)
Iuncos/P.R.	403 007	24.8	1697	1033* (6)
Osa/C.R.	—	25.0	4500	1067* (7)
Darien/R.P.	—	27.0	2000	2106* (8)
Calabozo/V.*	500 075	27.1	1334	1100 (9)
Region II				
Abisco	107 497	−1.0	267	450* (1)
Lund	105 088	7.3	616	1560 (10)
Søøborg	105 102	7.5	585	1350 (1)
Gembloers	103 317	9.2	816	1440 (10)
Heilbronn	106 100	9.7	675	1350 (1)
Heilbronn	106 100	9.7	675	1270 (1)
Murrhardt	106 305	8.2	951	2300 (11)
Lorch	106 475	7.4	823	880 (1)
Nördlingen	106 325	7.9	634	830 (1)
same	106 325	7.9	634	1050 (1)
Wielicka	106 385	7.8	686	1017 (12)
Luzern	107 225	8.6	1121	980 (10)
Bondaye	303 510	26.5	1633	1340 (12)
Region III				
Archangelsk	110 218	0.4	466	560 (13)
Onega	110 217	0.9	497	600 (13)
Vologda	110 239	2.4	288	600 (13)
Velsk	110 255	−1.5	519	790 (13)

Porezkoje	110	178	3.4	508	900	(13)
Briansk	110	082	4.7	469	1100	(13)
Kiev	110	039	6.8	528	840	(13)
Voronesh	110	083	5.6	480	720	(13)
Kursk	110	081	5.2	564	810	(13)
Namangan	111	037	13.4	188	1040	(13)
Roshdestvenskoje	111	078	3.6	135	870	(13)
Kokpetky	111	077	1.5	272	1030	(13)
Verschn. Baskuntschak	111	051	7.7	254	380	(13)
Termez	111	012	17.3	183	430	(13)
Aralskoje More	111	058	6.6	102	120	(13)
Selemiya	201	086	16.7	346	240	(13)
Palmyra	201	065	19.1	131	70	(13)
Region IV						
Kigiljaka Mys	111	403	−14.2	94	100	(13)
Markovo	111	350	− 9.4	200	250	(13)
Kumagaya	206	154	13.3	1335	1540	(10)
same	206	154	13.3	1335	1075	(10)
same	206	154	13.3	1335	3100	(10)
Kyoto	206	132	13.8	1600	1500	(10)
same	206	132	13.8	1600	3530	(10)
same	206	132	13.8	1600	2500	(10)
Chantoburi	205	055	27.2	3235	2850	(14)
Nakorn Sawan	205	116	28.2	1222	2860	(14)
Buitenzorg	207	005	25.0	4117	3275*	(1)

[a]Comments on columns: Column 1, gives the name of the climate record station. Calabozo value used differs from that in the climate diagram. Column 2, gives the climate diagram code number from Walter-Lieth Climate Diagram World Atlas (1960-1967). Dashes indicate that such a diagram was not available and the figures used in columns 3 and 4 were taken either from the authors of column 5 or from the U.S. Weather Service. Column 3, annual mean temperature as given in the diagram. Column 4, annual sum of precipitation as given in the diagram. Column 5, productivity figures as given by the authors, (*) indicates further calculations were necessary. Sources as indicated in parentheses: (1) Lieth (1962), (2) Reader (1971), (3) Whittaker and Woodwell (1971), (4) Nemeth (1971), (5) Wells and Lieth (1970), (6) Jordan (1971*a*), (7) Ewel (1971*a*), (8) Ewel (1971*b*), (9) Medina (1970), (10) Art and Marks (1971), (11) Lieth *et al.* (1965), (12) Walter (1968), (13) Drozdov (1971), (14) Kira and Ogawa (1971). Regions: I, North Alaska to eastern United States to northern South America; II, western Europe and western Africa; III, central Eurasia; IV, eastern Asia and Indonesia.

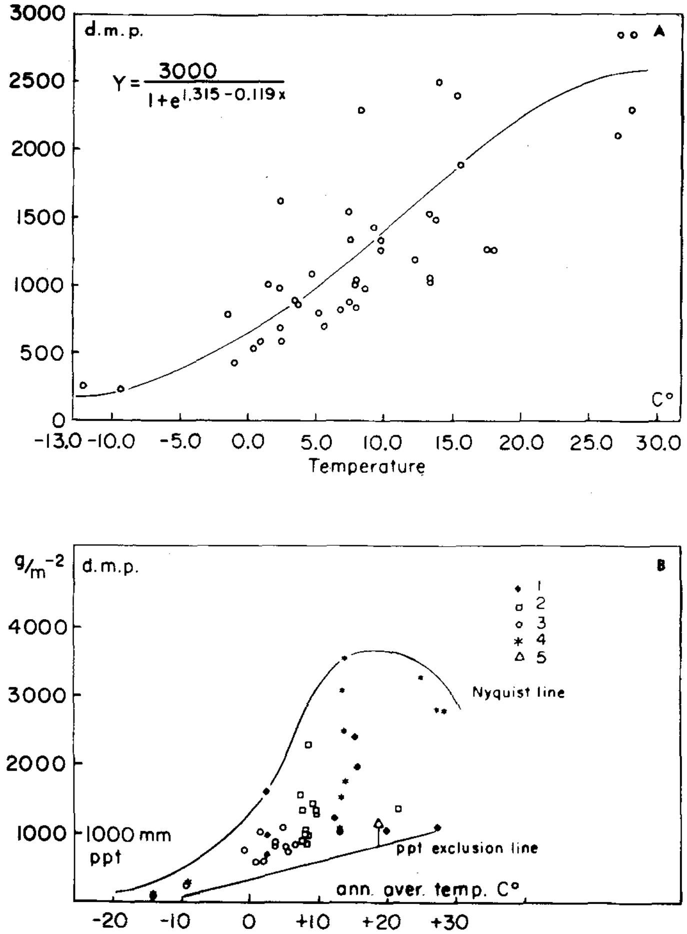


Fig. 4. Productivity *vs.* mean annual temperature. The upper portion (A) of the figure demonstrates the equation calculated from the data in Table IV after excluding extreme values. The lower part (B) depicts the distribution pattern of data points from each region, as listed in Table IV. The abscissa is temperature in °C, the ordinate grams net dry matter produced per square meter per year. In B, the straight line indicates the exclusion line for low precipitation values, and the curve is a "Nyquist" line over the maximum values.

gradient that encompasses the extreme points. The lower curve, a straight line, is an arbitrarily chosen precipitation exclusion line; I eliminated from temperature considerations all values below the line from −10°C and 0 mm ppt to 25°C and 1000 mm ppt. The Nyquist curve seems to indicate (for the existing data) that maximum productivity occurs at about 25°C. (In Fig. 4, the maximum field value appears at about 13°C. This value stems from a young, vigorously growing Japanese plantation and cannot be indicative of the normal growth of climax vegetation in that area. The optimum temperature for productivity, in the range of 15-25°C, agrees with the optimum temperature range for photosynthesis.) We need more data from the humid tropics to define the optimum temperature for primary productivity.

The data enclosed by the two lines were used to calculate the relation between temperature and productivity, assuming that large-area average productivity does not exceed 3 kg/m^2/year and that the curve has a sigmoid shape. The first assumption is derived from our collection of productivity values (see Lieth, 1962-1972). The second argument is deduced from the shape of the Nyquist curve. The predictive formula, as shown in the upper portion of Fig. 4, is

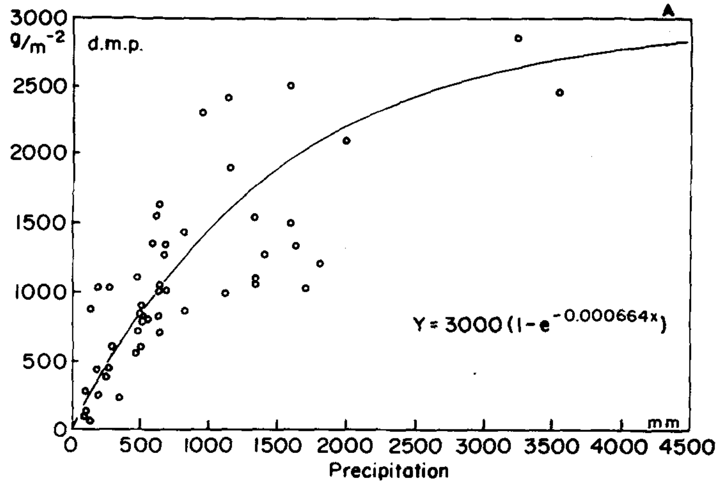
$$y = \frac{3000}{(1 + e^{1.315-0.119x})}$$

where y is the productivity level in g/m^2/year, x is the mean annual temperature in °C, and e is the natural log base. Overall, the relation suggests the van't Hoff rule, with productivity doubling every 10°C between the temperatures of -10 and 20°C. This relation has much to do with lengths of growing seasons and rates of processes other than photosynthesis itself, and the doubling relation does not seem to apply to plankton (see article by Bunt in this Journal issue) or temperate forests (Whittaker, 1966; Whittaker and Woodwell, 1971).

The same approach was taken for productivity *vs.* precipitation (Fig. 5). The lower portion of the figure summarizes the general considerations, containing the data points and three curves. The upper straight slope represents the "Walter ratio," which evaluates the aboveground productivity data collected by Walter (1939, 1964, p. 275; *cf.* Lieth, 1962) in South West Africa, multiplied by 2 for total productivity values. This ratio predicts that in more arid climates 2 g dry matter/m^2 is produced for each millimeter of precipitation; the relation cannot be extended to humid climates. The upper Nyquist line over the maximum data points suggests that the precipitation *vs.* productivity relation follows the usual assumption for yield factors, the saturation curve (Mitscherlich, 1954). The lower straight line marks the exclusion threshold for data pairs where the productivity is clearly limited by low temperatures. This line was set arbitrarily from 0°C and 500 mm ppt to 20°C and 1500 mm ppt. All data that were used to calculate the least squares formula are shown in the upper part of Fig. 5. Assuming that the maximum productivity is 3 kg/m^2/year and saturation-curve form, the relation was calculated as

$$y = 3000\,(1 - e^{-0.000664x})$$

where y is the productivity level in g/m^2/year, x is the precipitation in mm, and e is the natural log base.



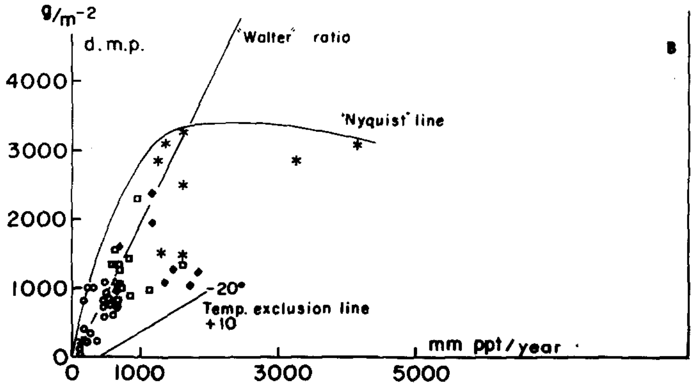


Fig. 5. Productivity *vs.* mean annual precipitation. The upper part (A) demonstrates the equation, and the lower part (B) shows the graphic analysis. The data point symbols are the same as those in Fig. 4. The abscissa is millimeters annual precipitation and the ordinate dry matter net productivity in grams per square meter per year. In B, the lower straight line indicates the exclusion level for low temperature values; the upper straight line is the "Walter ratio" and assumes a production level of 2 g dry matter for each millimeter of annual precipitation; the curve over the maximum values is a Nyquist line suggesting a saturation curve.

I developed a computer program that gave the expected productivity for every combination of total annual precipitation and average annual temperature, between 0 mm and −30°C and 4500 mm and +30°C. The productivity levels were derived by applying von Liebig's principle that the minimum factor controls the production; for each station, the program selected the smaller of the two values computed from temperature and precipitation. Primary productivity

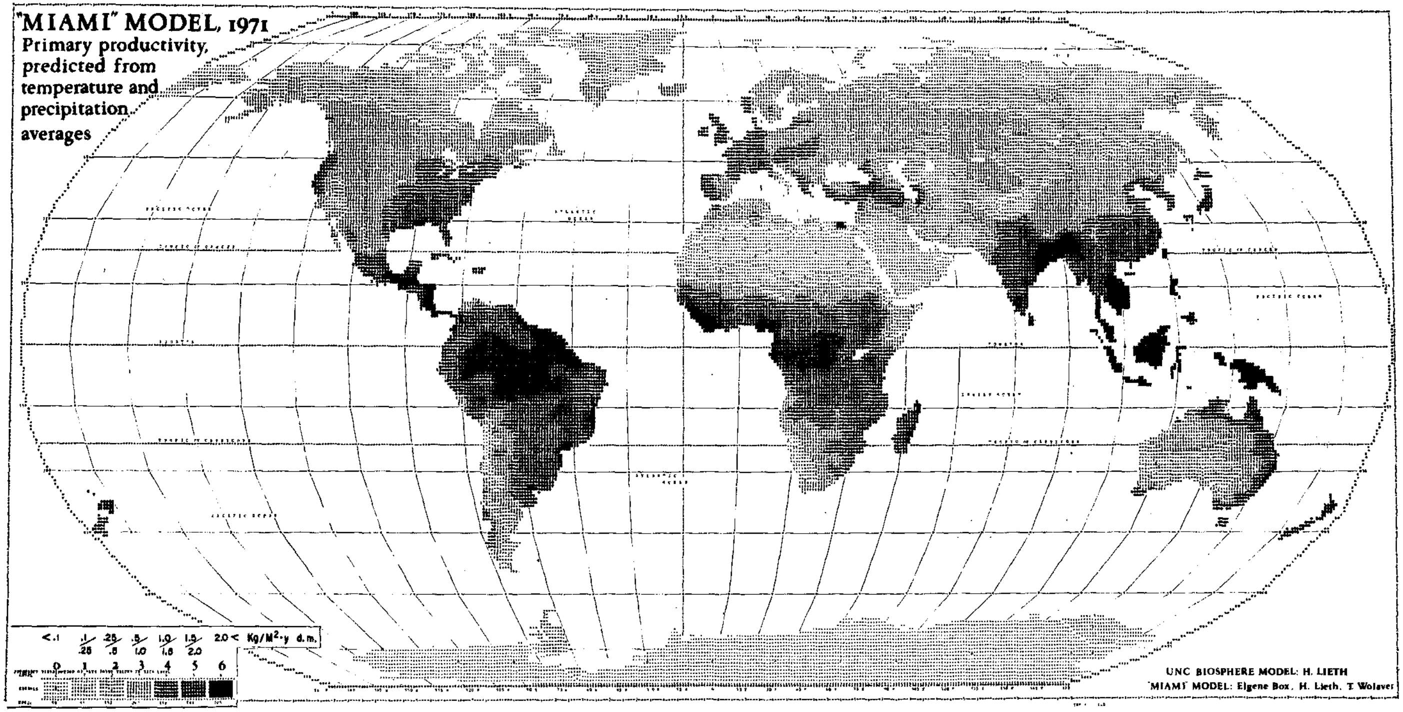


Fig 6. "Miami productivity map." The map gives predictions of the primary productivity on land from annual averages for temperature and precipitation in contrast to the actual measurements used for Fig. 1. The predictions are based on the two equations shown in Fig. 4 and 5 and temperature and precipitation values from Walter and Lieth (1960-1967).

was thus predicted for more than 1000 points (meteorological stations) on the earth's surface selected from the world atlas (Walter and Lieth, 1960-1967). Four to six stations were taken for every area of 10° latitude and 10° longitude. The resulting map is the "Miami model" of world terrestrial primary productivity (Fig. 6).

CONCLUSION

In relation to the history of productivity studies reviewed above, I will emphasize three trends: (1) The development of the understanding of the production equation, its relation to photosynthesis, and the controls on primary productivity. The production equation was completed in the last century, but the factors affecting productivity are still under quantitative investigation today. (2) The increasing refinement and convergence of world production estimates. Von Liebig (1862) extrapolated from a single community assumed to be average for world production. Schroeder (1919) distinguished four land community types, but current estimates are based on 20 or more vegetation types, and there is encouraging agreement among their results. I hope I am not unjustified in suggesting that the major estimates offered here—of 100×10^9 metric tons of dry matter and 425×10^{18} calories of organic energy, net primary production for the land vegetation of the earth—will be subject to refinement in detail but not to major revision. (3) The recent development of new techniques for treating productivity data. Means for analysis, summarization, and mapping of the productivity data are now available by which we may take advantage of the increasing range of information to be expected from the International Biological Program.

All the world estimates I have given are intended to be as of about 1950. I need hardly emphasize to the reader the accelerating rate at which the world is being transformed, and the biosphere affected, by man. The article by Whittaker and Likens in this Journal issue will consider further the prospects of the relation of man and the biosphere.

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