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Geographical Dimensions of Terrestrial Net and Gross Primary Productivity*

Elgene Box

Ecology Curriculum, University of North Carolina,
Chapel Hill, North Carolina 27514, USA

Summary. The paper presents a comparative summary of previous attempts by the author to assess and map global primary productivity using environmental parameters as predictors. The individual components of the productivity process, net production, gross production, dark respiration as well as their regional rates are computed for 10 degree latitudinal belts.

A new version of the Miami Model (Lieth, 1973, 1975) is presented predicting net primary productivity from an increased number of averages of temperature and precipitation. Net primary productivity values in form of dry matter accumulation and caloric energy equivalents are compared.

Introduction

Global maps and tabular global estimates of annual net primary productivity have been presented by several authors during the past two decades, beginning with Lieth (1962, 1964). Most of the estimates are within the ranges 90–130 × 10^9 t/year (dry matter) for the land areas and 50–60 × 10^9 t/year for the oceans (Golley, 1972; Box, 1975b; Cooper, 1975; Lieth, 1975; Lieth and Whittaker, 1975; Utkin et al., 1975; Whittaker, 1975; Whittaker and Likens, 1975). The convergence of these estimates suggests that they may not need major revision, even though higher estimates have also been presented (Bazilevich et al., 1971; Rodin et al., 1975).

Net primary productivity has been related to environmental factors on a global scale by correlation models such as the "Miami Model" (Eq. 4 and 5) of Lieth (1973) and the "Montreal Model" (relating net productivity to actual evapotranspiration) of Lieth and Box (1972). Computer-printed world maps were produced from these models using the SYMAP cartographic program (Laboratory for Computer Graphics and Spatial Analysis) and data-bases gathered by the authors. These environmentally based productivity maps, as well as land ("Innsbruck Model", Lieth,

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* Prof. Dr. H. Walter dedicated to his 80th birthday

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1972) and ocean (Lieth et al., 1972) maps of actual net production, were evaluated by computerized planimetry by Box (1975b) using the planimetry program MAPCOUNT (Box, 1975a, 1978a). The global values obtained are in good agreement with earlier estimates (Box, 1975b).

MAPCOUNT can also be used to estimate regional values and has since been applied to the above-mentioned four productivity maps in order to estimate more precisely certain geographical aspects of net productivity. Estimates of total annual net production of the existing land area and of average annual net productivity per unit area, as depicted by the three terrestrial maps, were obtained for 10⁰ latitudinal belts (Tables 1 and 2) and for individual large land masses (Tables 3 and 4). Estimates of total annual net production and of average annual net productivity per unit area of the oceans, as shown on the single oceans map, were also obtained for 10⁰ latitudinal belts (Table 5). These values are presented here for the first time. The MAPCOUNT values, with four to five significant digits, are presented, but the last digits cannot be considered accurate.

Table 1. Estimates of total annual net primary production (10^9 metric tons of dry matter) of the land areas of 10^0 latitudinal belts

Latitudinal belt	"Innsbruck" map (10^9 t/year)	"Miami Model" (10^9 t/year)	"Montreal Model" (10^9 t/year)
90–80° N	0.036	0.025	–
80–70° N	0.367	0.512	0.196
70–60° N	3.434	4.995	5.473
60–50° N	6.238	9.043	9.479
50–40° N	8.084	12.583	12.924
40–30° N	8.561	13.038	12.249
30–20° N	9.554	10.989	9.397
20–10° N	11.111	10.764	10.416
10–0° N	17.080	17.614	16.530
10–0° S	19.888	20.900	18.249
20–10° S	11.790	13.692	13.513
30–20° S	6.940	8.638	8.726
40–30° S	2.910	3.512	3.413
50–40° S	0.677	0.821	0.834
60–50° S	0.041	0.126	0.151
70–60° S	0.082	0.182	0.011
80–70° S	0.230	0.317	–
90–80° S	0.003	0.023	–
Total land	107.025	127.774	121.561

The values were obtained by MAPCOUNT planimetry (Box, 1975b, 1978a) of the maps indicated: The "Innsbruck" map of estimated actual net productivity (Lieth, 1972), the "Miami Model" map of net productivity predicted from temperature and precipitation (Box et al., 1971), and the "Montreal Model" (C. W. Thornthwaite Memorial Model) of net productivity predicted from actual evapotranspiration (Lieth and Box, 1972). For land areas in each belt, please refer to Table 9

Table 2. Estimates of average annual net primary production (g/m²/year of dry matter) of the land areas of 10° latitudinal belts

Latitudinal belt	"Innsbruck" map (g/m²/year)	"Miami Model" (g/m²/year)	"Montreal Model" (g/m²/year)
90–80° N	139.3	96.4	–
80–70° N	110.9	154.8	59.2
70–60° N	258.3	375.7	411.7
60–50° N	426.7	618.6	648.4
50–40° N	488.7	760.7	781.3
40–30° N	548.0	834.6	784.1
30–20° N	629.2	723.7	618.9
20–10° N	977.9	947.3	916.7
10–0° N	1687.6	1740.4	1633.3
10–0° S	1898.5	1995.1	1742.0
20–10° S	1245.2	1446.0	1427.1
30–20° S	744.0	926.0	935.4
40–30° S	711.8	859.2	834.8
50–40° S	715.9	868.5	882.7
60–50° S	200.1	616.3	736.7
70–60° S	41.8	93.1	5.7
80–70° S	26.4	36.5	–
90–80° S	0.9	5.9	–
Means	716.6	855.5	813.9

The values were obtained by the same operations which produced the values of Table 1. Both total and average thematic values are regularly supplied by MAPCOUNT

Table 3. Estimates of total annual net primary production (10^9 metric tons of dry matter) of individual land masses

Land mass	"Innsbruck" map (10^9 t/year)	"Miami Model" (10^9 t/year)	"Montreal Model" (10^9 t/year)
North America (excl. Greenland)	14.356	17.920	18.263
South America	24.505	28.834	24.432
Eurasia	29.387	40.158	37.960
Africa	29.589	29.438	31.154
Australia	4.236	6.035	5.950
New Zealand	0.336	0.396	0.324

The values were obtained by operations similar to those which produced the values of Table 1. Outlines circumscribing the continents were used, however, in order to delimit the regions to be treated

Table 4. Estimates of average annual net primary productivity (g/m^2/year of dry matter) of individual land masses

Land mass	"Innsbruck" map (g/m^2/year)	"Miami Model" (g/m^2/year)	"Montreal Model" (g/m^2/year)
North America (excl. Greenland)	653.0	815.1	830.7
South America	1377.2	1620.5	1373.1
Eurasia	561.5	767.3	725.3
Africa	977.7	972.7	1029.4
Australia	551.1	785.1	774.1
New Zealand	1250.0	1473.5	1205.4

The values were obtained by the same operations which produced the values of Table 3

Table 5. Estimates of total annual net primary production and average annual net primary productivity of the ocean areas of 10° latitudinal belts

Latitudinal belt	Ocean area (10^6 km^2)	Net production (10^9 t/year)	Mean productivity (g/m^2/year)
90–80° N	3.623	–	–
80–70° N	8.199	0.537	65.5
70–60° N	5.513	0.784	142.3
60–50° N	10.900	2.286	209.7
50–40° N	14.898	3.008	201.9
40–30° N	20.820	1.807	86.8
30–20° N	25.136	1.342	53.4
20–10° N	31.612	1.666	52.7
10–0° N	34.181	2.512	73.5
10–0° S	33.826	2.777	82.1
20–10° S	33.506	2.613	78.0
30–20° S	30.992	2.135	68.9
40–30° S	32.353	3.041	94.0
50–40° S	30.794	6.812	221.2
60–50° S	25.314	8.083	319.3
70–60° S	16.849	2.408	142.9
80–70° S	2.814	0.205	73.0
90–80° S	–	–	–
Total ocean	361.330	42.018	116.3

The values were obtained by MAPCOUNT planimetry of the "Oceans Productivity Map" (Lieth et al., 1972). Area representation of unfrozen ocean in the polar belts was so uncertain that productivity was not counted there

Gross Productivity

As new data have become available, several authors (Golley, 1972; Kira, 1975; Lieth and Box, 1978) have begun attempts to assess the other components of the production-respiration balance of the land vegetation. The available data strongly suggested a correlation between net and gross productivity as the first feasible step. Temperature regimes can probably be estimated to provide the basis for subsequent models relating gross productivity and dark respiration to at least some aspects of annual and diurnal temperature patterns. The data on gross primary production which are available were obtained by adding measured or estimated values of net productivity and dark respiration. Thus, gross productivity, as treated here, must be understood to exclude that temporary production which is lost through photorespiration, which was not measured. The relationship between gross primary production (GPP) and net primary production (NPP), as considered here, is given by the equation

$$\mathrm{NPP} = \mathrm{GPP} - \mathrm{Rd} \tag{1}$$

where Rd represents dark respiration.

Using a small but geographically representative set of measurements collected by Kira (1975), plus some other recent values, Lieth and Box (1978) produced an initial correlation model ($r = 0.91$) relating annual gross production and net production on the land areas. Because of uncertainty about methods of measuring respiration for needle-leaved species, only the available values for broad-leaved species were used. The increase in net production with increasing gross production was seen to follow the pattern of a saturation equation with an upper asymptote around 3000 g/m^2/year (dry matter). The least-squares correlation equation obtained using this functional form is shown as Equation (2):

$$\mathrm{NPP} = 3000\,[1 - \exp(-0.000242\ \mathrm{GPP})]\,. \tag{2}$$

This can be solved easily for gross production:

$$\mathrm{GPP} = -4140 \log e\,[1 - \mathrm{NPP}/3000]\,. \tag{3}$$

All values represent grams of dry matter per square meter per year. This model was presented at the symposium “Advances in Tropical Ecology” held in Panama (March, 1977) and is thus called the “Panama Model”.

In order to construct a world map of annual gross primary productivity using this model, one must have a large set of estimates for the independent variable, net primary productivity. These values can be provided by the Miami Model (Lieth, 1973), which relates annual net primary productivity (NPP) in g/m^2 to mean annual temperature (T) in °C and average annual precipitation (P) in millimeters according to the following equations:

$$\mathrm{NPP(T)} = 3000/[1 + \exp(1.315 - 0.119\ \mathrm{T})]\,, \tag{4}$$

$$\mathrm{NPP(P)} = 3000\,[1 - \exp(-0.000664\ \mathrm{P})]\,. \tag{5}$$

These correlation equations were derived from a geographically representative set of net production measurements (Lieth, 1973), none of which is in the data-base for the

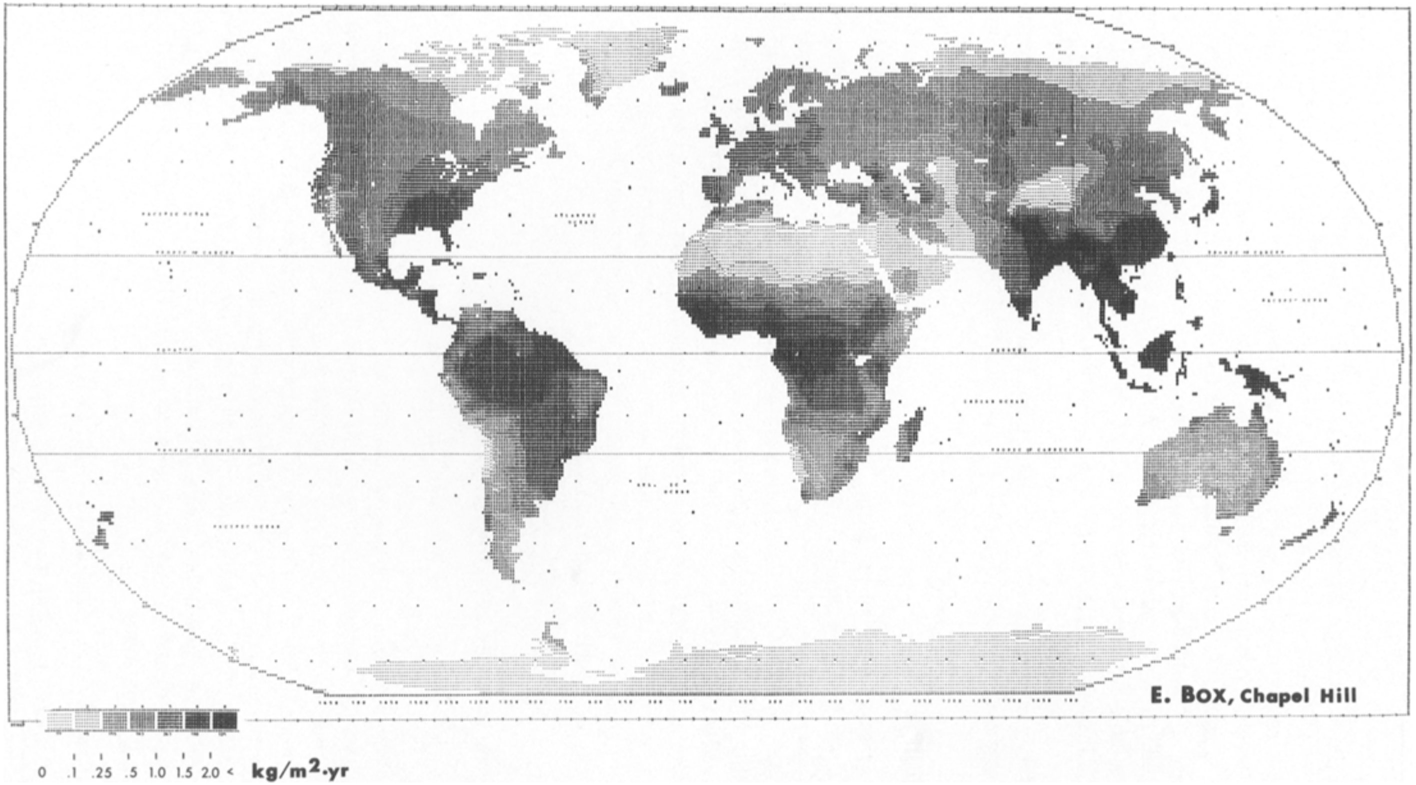

Fig. 1. "Miami Model 1a" *map of estimated annual net primary productivity of the land areas.* The values of net primary productivity are estimated from mean annual temperature and average annual precipitation according to Equations (4) and (5). The original Miami Model productivity map (Box et al., 1971) was developed from 988 data-sites (Lieth, 1973). The improved "Miami Model 1a" is based on the same correlation equations but uses a data-base of 1230 sites, for which more extensive temperature data are available (Lieth and Box, 1978). For Miami Model 1a, net primary productivity is considered to be zero if the highest mean monthly temperature is less than −2° C

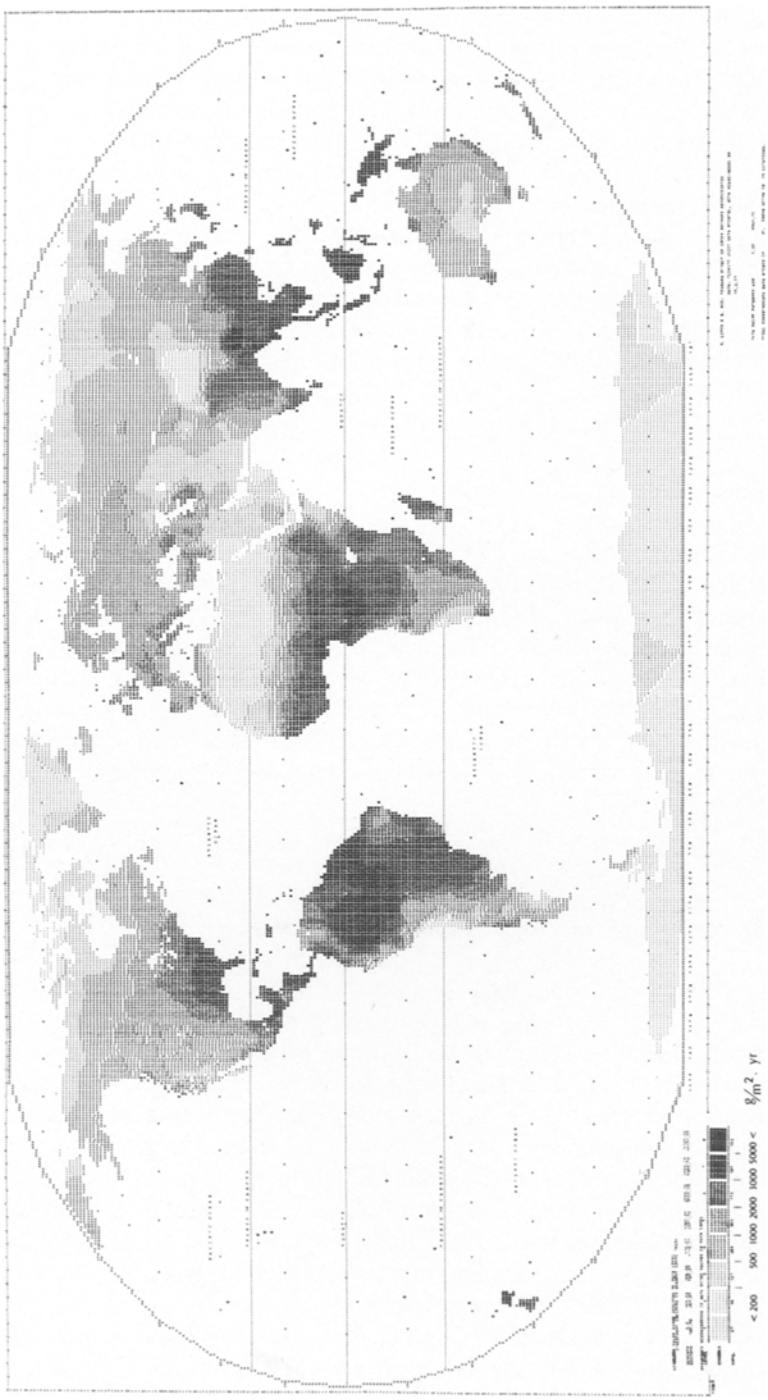

Fig. 2. "Panama Model" map of estimated annual gross primary productivity of the land areas. The estimates of annual gross primary productivity are obtained from Miami-Model estimates of annual net primary productivity using the "Panama Model" (Lieth and Box, 1978), which relates gross productivity to net productivity according to Equation (3). Gross production is understood here to exclude photorespired products (Eq. 1). The spatial interpolation is based on 1230 data-sites

Panama Model. Reflecting Liebig's law of the minimum, the smaller of the two predicted values for NPP is taken as the Miami Model estimate of annual net primary productivity. The global pattern obtained by applying these equations to temperature and precipitation values from 1000 meteorological stations scattered throughout the land areas of the world was called the Miami Model Productivity Map (Box et al., 1971), first presented in Miami in 1971. A newer, improved version of this map (Miami Model 1a), based on data from 1230 meteorological stations, is reproduced here as Figure 1. These 1230 estimates of net productivity were converted by Equation (3) to estimates of gross productivity. The gross productivity estimates were then mapped, using SYMAP and the same cartographic basis as used for the other maps, to produce a world map of estimated annual gross primary productivity (Lieth and Box, 1978). This map is reproduced here as Figure 2.

Dark Respiration

The Miami and Panama models can be used to provide estimates of net and gross productivity for any terrestrial point for which reliable temperature and precipitation data are available and for which other environmental factors are reasonably favorable. Since gross productivity is understood here to represent net productivity plus dark respiration (Eq. 1), the difference between gross and net productivity estimates is an estimate of annual dark respiration. Such estimates of dark respiration were also obtained for the 1230 meterological stations, and the results were mapped to produce probably the first world map of estimated annual dark respiration of terrestrial vegetation (Fig. 3).

Quantitative Assessment of Terrestrial Production-Respiration Patterns

The availability of the three maps (Figs. 1–3) and of MAPCOUNT (Box, 1978a) permits us, for the first time, to assess quantitatively the total amounts and the geographic patterns of all three components of the production-respiration balance of the land vegetation (Eq. 1). Such estimates of regional amounts and spatial variations can perhaps best be presented in the form of a geographic budget, in which the values for the three components are juxtaposed within the selected regions. The size, shape, and number of regions for which estimates can be made by MAPCOUNT are limited not only by computing time and availability of outlines to delimit the regions but also by the degree of resolution of the maps themselves. In order that the major zonal features may be seen, the maps are evaluated by 10° latitudinal belts, as were the net productivity maps in Tables 1 and 2.

The quantification of a map by MAPCOUNT consists of two steps: the determination of the areas of the various contour levels and the conversion of these area values into corresponding thematic (productivity) values. The maps were produced using land-mass outlines (Lieth, 1972) based on the non-equal area Robinson projection (Robinson, 1974). Areas depicted on the maps can be correctly determined by

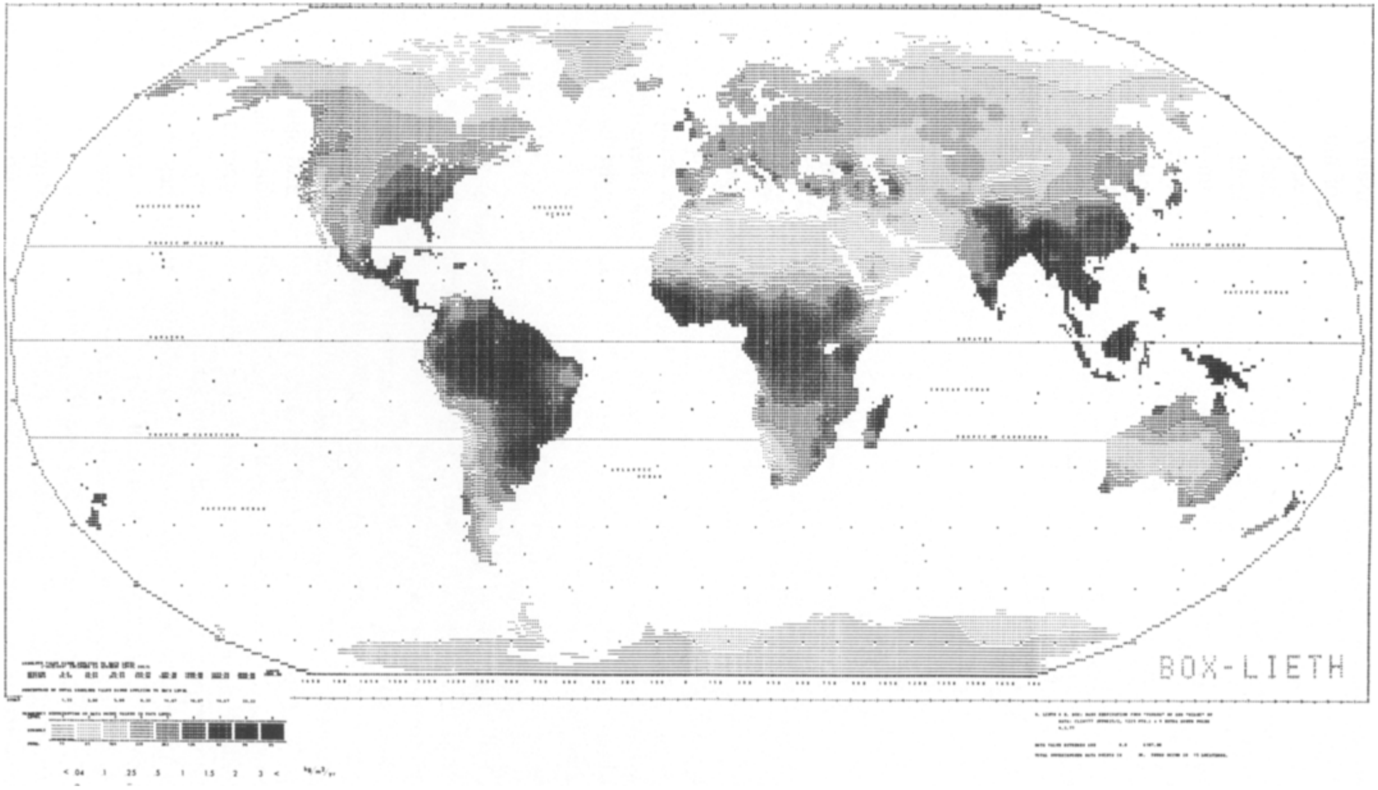

Fig. 3. Estimated annual dark respiration of terrestrial vegetation. The estimates of annual dark respiration are obtained by subtracting Miami-Model estimates of net productivity from Panama-Model estimates of gross productivity (Eq. 1 and Figs. 1 and 2). Gross production is understood here to exclude photorespired products. The spatial interpolation is based on 1230 data-sites

Table 6. Estimates of total annual gross and net primary production and dark respiration (10^9 metric tons of dry matter) of the land areas of 10° latitudinal belts

Latitudinal belt	Gross production (10^9 t/year)	Dark respiration (10^9 t/year)	Net production (10^9 t/year)
90–80° N	0.017	0.0046	0.010
80–70° N	0.603	0.160	0.503
70–60° N	8.067	2.710	5.402
60–50° N	15.401	5.521	9.627
50–40° N	21.048	8.209	12.454
40–30° N	23.260	10.032	12.721
30–20° N	23.245	11.850	11.282
20–10° N	25.646	13.827	12.104
10–0° N	41.958	24.484	18.017
10–0° S	52.360	31.596	20.613
20–10° S	27.408	14.125	13.326
30–20° S	15.730	7.295	8.395
40–30° S	6.485	2.743	3.649
50–40° S	1.324	0.513	0.782
60–50° S	0.270	0.113	0.160
70–60° S	0.325	0.082	0.252
80–70° S	0.131	0.082	0.106
90–80° S	–	–	–
Total land	263.276	133.348	129.404

The values were obtained by MAPCOUNT planimetry (Box, 1975b, 1978a) of the following maps: The "Panama Model" productivity map (Lieth and Box, 1978, see Fig. 2) for gross production, the map of estimated dark respiration shown in Figure 3, and the "Miami Model 1a" (Lieth and Box, 1978, see Fig. 1) for net production. For land areas in each belt, please refer to Table 9

MAPCOUNT, however, by means of a correction procedure based on a mathematical description (subroutine DEFORM) of the area deformation of the projection. The accuracy of this phase of MAPCOUNT evaluations using the combined Lieth-Robinson cartographic basis was evaluated by Box (1975b) and showed a 7% underestimation of total area, occurring mainly in the more distorted polar regions. This general underestimation of area and related total production is eliminated by a second correction procedure, which standardizes results using true area values.

The conversion of areas into productivity amounts is based on characteristic productivity values for the various contour levels. These values were estimated by computing the averages of the individual productivity values in each level. The characteristic values for the lowest contour levels were reduced arbitrarily for those belts in which ice-covered polar regions or extreme arid deserts represent large portions of the total area. Areas counted by MAPCOUNT are multiplied by the corresponding characteristic productivity values to provide the estimates of total productivity.

The estimates of annual production and respiration for the land areas of 10° latitudinal belts, as depicted in Figures 1–3 and quantified by MAPCOUNT, are shown in Table 6 (annual sums) and Table 7 (average annual values, per unit area). A better idea of the relative latitudinal trends is given by the ratios of corresponding production and respiration values, shown in Table 8. Since the values for the three

Table 7. Estimates of average annual gross and net primary productivity and dark respiration (g/m^2/year of dry matter) of the land areas of 10° latitudinal belts

1 Latitudinal belt	2 Gross production (g/m^2/year)	3 Dark respiration (g/m^2/year)	4 Net production (g/m^2/year)	5 Δ Col 2 − [3 + 4]	6 Δ/GPP (%)
90–80° N	67.6	17.9	39.9	9.8	14.5
80–70° N	182.0	48.5	152.2	−18.7	−10.3
70–60° N	606.8	203.9	406.3	− 3.4	− 0.6
60–50° N	1053.5	377.7	658.5	17.3	1.6
50–40° N	1272.4	496.3	752.9	23.2	1.8
40–30° N	1488.9	642.2	814.3	32.4	2.2
30–20° N	1530.9	780.4	743.0	7.5	0.5
20–10° N	2257.0	1216.9	1065.2	−25.1	− 1.1
10–0° N	4145.8	2419.2	1780.3	−53.7	− 1.3
10–0° S	4998.3	3016.2	1967.7	14.4	0.3
20–10° S	2894.5	1491.8	1407.4	− 4.7	− 0.2
30–20° S	1686.2	782.0	900.0	4.2	0.2
40–30° S	1586.3	671.0	892.6	22.7	1.4
50–40° S	1400.4	543.2	827.1	30.1	2.1
60–50° S	1321.4	552.3	783.3	−14.2	− 1.1
70–60° S	165.9	41.7	128.7	− 4.5	− 2.7
80–70° S	15.1	9.5	12.2	− 6.6	−43.7
90–80° S	–	–	–	–	–
Means for land	1762.7	892.8	866.4	3.5	0.2

The values were obtained by the same operations which produced the values of Table 6. Note that the expected additive relation (Eq. 1) across rows is not exact, since values were obtained by planimetry of different maps with different contour intervals. The absolute differences between GPP (column 2) and NPP + Rd (column 3 plus column 4) are shown in column 5 [Δ = GPP − (Rd + NPP)]. These differences are expressed in column 6 as a percentages of GPP

components were obtained by planimetry of different maps with different contour intervals, the production-respiration relations within belts do not balance exactly. The general additive relationship expressed in Equation (1), however, is always clearly evident. Deviation from the relationship of Equation (1) does not exceed 3% except in the polar regions, where values and/or areas are too small to permit accurate assessment by the current method. The error inherent in MAPCOUNT planimetry could be almost eliminated if MAPCOUNT were able to read the actual numerical surface which underlies the printed map. These surfaces can be provided by SYMAP, at greater expense, and MAPCOUNT is being adapted to read them.

Note also that the values for net productivity in Tables 6 and 7 (Miami Model 1a, with 1230 data-points) do not exactly match the Miami Model values in Tables 1 and 2 (based on 1000 data-points). The differences represent a good measure of that portion of the total error in this procedure which is attributable to variation in the number, data values, and location of the data-sites. With possible exception of the polar regions and regions with low land areas, this error is not larger than the error attributable to the underlying measurements and estimates themselves.

Table 8. Ratios of estimated average annual net (NPP) and gross (GPP) primary production and dark respiration (Rd) for the land areas of 10° latitudinal belts

Latitudinal belt	NPP/GPP	Rd/GPP	NPP/Rd
90–80° N	0.590	0.265	2.229
80–70° N	0.836	0.266	3.138
70–60° N	0.670	0.336	1.993
60–50° N	0.625	0.359	1.743
50–40° N	0.592	0.390	1.517
40–30° N	0.547	0.431	1.270
30–20° N	0.485	0.510	0.952
20–10° N	0.472	0.539	0.875
10–0° N	0.429	0.584	0.736
10–0° S	0.394	0.603	0.652
20–10° S	0.486	0.515	0.943
30–20° S	0.534	0.464	1.151
40–30° S	0.563	0.423	1.330
50–40° S	0.591	0.388	1.523
60–50° S	0.593	0.418	1.418
70–60° S	0.776	0.251	3.086
80–70° S	0.808	0.629	1.284
90–80° S	–	–	–
Means	0.492	0.506	0.970

The ratios are computed from the values in Table 7. The divergence from the normal trend of the ratios for the northern polar and southern polar and subpolar belts is, to some extent, an artifact caused by the division of small numbers

Annual Energy Fixation by the Land Vegetation

The energy content of the land vegetation is a product of net productivity and the energy content (combustion values) of the plants concerned. Highly lignified plants, such as boreal and mediterranean evergreen trees, have the highest combustion values (around 4.8–4.9 kcal/g), while herbaceous plants generally have the lowest values (around 4.0 kcal/g). Estimates of mean energy fixation have been presented by Lieth (1975) for about 20 biome types.

Using these energy-fixation estimates and the geographic distributions (including ecotones) of these biome types, one can produce a world map of estimated average annual energy fixation by the natural vegetation cover. Such a map was produced by Box (1976) and is known as the "Berlin Model", since it was first presented in Berlin (Lieth, 1978). This map is reproduced here as Figure 4[1].

The quantification by MAPCOUNT of the Berlin Model energy-fixation pattern was performed by 10° latitudinal belts in the same manner as was done for the other maps. Both total energy fixed annually by the respective land areas and mean energy fixation rate per unit area were estimated. The results are shown in Table 9.

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[1] A world map of estimated annual photosynthetic efficiency was also produced but is awaiting refinements before being published. It was produced, using the program MAPMATH (Box, 1978b), by dividing the Berlin Model cartographic surface by a surface representing the estimated annual solar radiation at the earth's surface

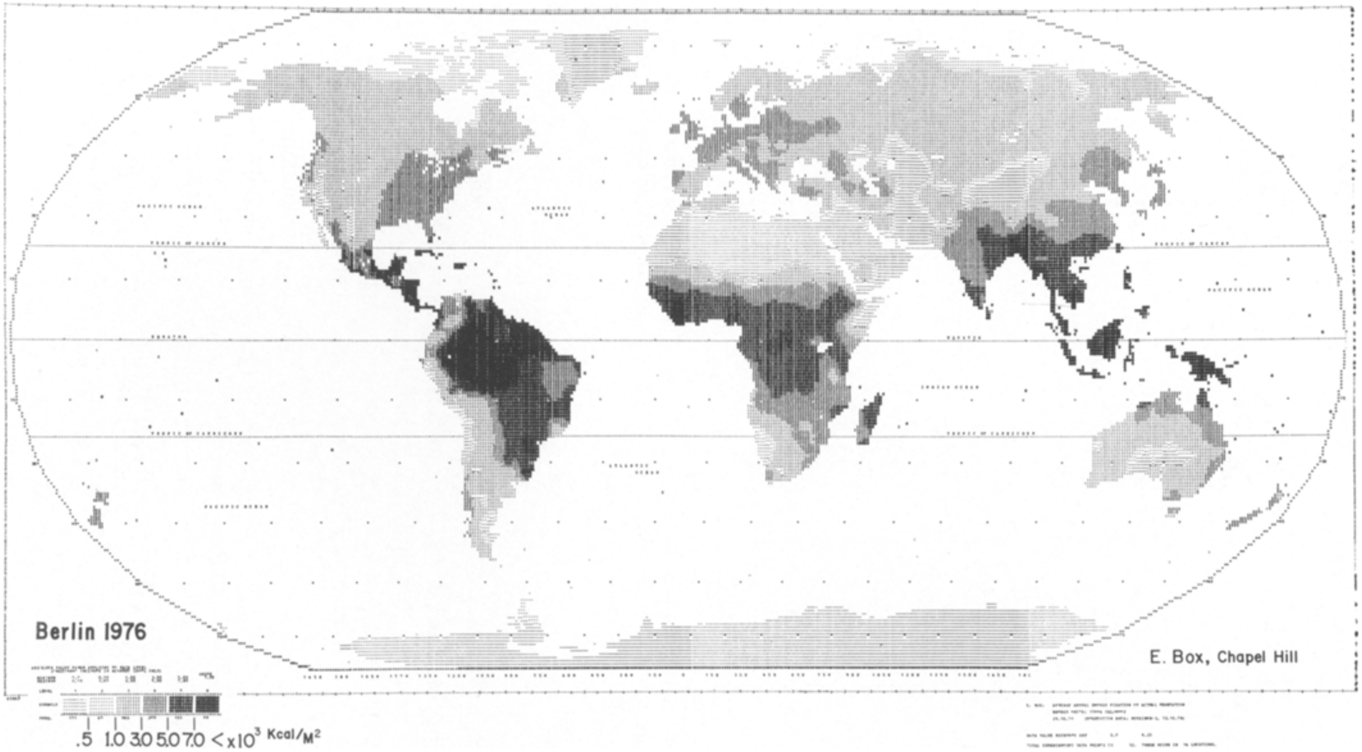

Fig. 4. "Berlin Model" map of estimated annual energy fixation of terrestrial vegetation (Box, 1976). The estimates of annual energy fixation were obtained from average energy fixation rates for 13 terrestrial vegetation types (Lieth, 1975) and a computer-generated map of the distributions (including overlaps) of *these vegetation* types (Box, in preparation). The spatial interpolation is based on about *1200 data-sites*

Table 9. Estimates of total energy fixed annually by terrestrial vegetation and of mean energy fixation per unit area, by 10° latitudinal belts

Latitudinal belt	Land area (10^6 km^2)	Total energy fixed (10^{15} kcal/year)	Mean energy fixation (10^3 kcal/m^2/year)
90–80° N	0.256	0.123	0.481
80–70° N	3.310	2.003	0.605
70–60° N	13.295	26.149	1.967
60–50° N	14.619	37.776	2.584
50–40° N	16.541	40.763	2.464
40–30° N	15.622	36.545	2.339
30–20° N	15.184	33.189	2.186
20–10° N	11.362	40.323	3.549
10–0° N	10.121	57.860	5.717
10–0° S	10.476	65.200	6.224
20–10° S	9.469	43.819	4.628
30–20° S	9.328	27.492	2.947
40–30° S	4.088	10.178	2.490
50–40° S	0.945	2.077	2.197
60–50° S	0.204	0.428	2.092
70–60° S	1.958	0.269	0.137
80–70° S	8.696	0.892	0.102
90–80° S	3.884	–	–
Total land	149.358	425.085	2.846

The values were obtained by MAPCOUNT planimetry of the "Berlin Model" map of average annual energy fixation by the natural vegetation (Box, 1976)

Observations

1. The estimates of annual totals for the earth's land areas (Table 6) are 263 × 10^9 t of gross production, 133 × 10^9 t of dark respiration, and 129 × 10^9 t of net production (dry matter). For the land areas as a whole, total annual net production seems to be about 50% of total annual gross production, nearly balancing total dark respiration.

2. The general trend on all the terrestrial maps is one of high values in the warmer belts near the equator decreasing monotonically to low values in the colder belts near the poles. Slight inversions in the subtropical belts can be seen for net productivity (Tables 2 and 7) and for average energy fixation (Table 9). The tropical region from 20° N to 20° S contains roughly 50% of the total terrestrial potential for net production (Table 6), and half of the energy fixed by the terrestrial vegetation is bound within this zone (Table 9).

3. Net productivity in the oceans (Table 5), on the other hand, has its highest values in the subpolar belts of both hemispheres, where water temperatures remain most nearly constant all year. Low values occur everywhere else, with a slight secondary high near the equator. The two southern subpolar belts spanning 50–70° S yield one-third of the oceans' total net production (nearly 15 × 10^9 g/year), an amount equal to the production of the entire Northern Hemisphere. The total annual production of the oceans, as depicted on the Oceans Productivity Map, is estimated as 42 × 10^9 t per year, a value which is considered to be about 20% too low, especially in the southern subpolar region (Box, 1975b; Lieth, 1975; Whittaker and Likens, 1975).

4. Estimated terrestrial gross production is, of course, always significantly greater than either estimated net production or estimated dark respiration alone (Table 7). Latitudinal means of terrestrial net production are seen to exceed those of dark respiration poleward of 30° N and 20° S, while the opposite is seen to hold in the tropics. This is entirely consistent with other observations and is due to the higher temperatures in the tropics, which cause dark respiration to increase at a faster rate than does gross production.

5. South America shows the highest estimated mean net productivity (Table 4) of the large land masses (ignoring New Zealand), while mostly temperate Eurasia and arid-subtropical Australia show the lowest mean productivity estimates. Relatively small Australia also has the lowest estimated total net production, while large Eurasia has the highest.

6. The highest average metabolic values for a single belt are found in the belt 0—10° S on all maps (Tables 2, 7, and 9), although the belt 0—10° N has the world's highest average values of both temperature and rainfall (Sellers, 1965).

7. The ratio of latitudinal means of net and gross productivity (Table 8, column 1) is seen to vary, almost linearly, from a minimum of about 40% in the equatorial belts to over 60% in the polar and subpolar belts. This suggests that the ratio of net to gross productivity decreases in general, due to the rapid increase of respiration with temperature, as gross productivity increases. The relation between latitudinal means of dark respiration and of net production is seen even more clearly in the ratio NPP/Rd (Table 8, column 3). (The total range of actual local values is probably somewhat larger. The divergence from the general trend in the northern polar and southern subpolar belts is, to some extent, an artifact due to the low land area and absolute values of these belts.)

8. For the three models of net productivity (Table 2), the Miami and Montreal Models of potential net productivity give consistently higher estimates than does the Innsbruck Model of estimated actual production. The differences between estimated potential and actual net production are greatest in the temperate zones, around 300 g/m^2/year in the zone 30—60° N and around 150—200 g/m^2/year in the zone 10—50° S. The differences generally do not exceed 100 g/m^2/year in the tropics, except for the belt 10—20° S. (The large discrepancy in the belt 50—60° S is probably an artifact caused by the small land area there.) One can readily assume that these discrepancies represent a measure of man's reduction of the productive capacity of the landscape which he occupies.

9. The estimate of the total annual energy fixation by the land vegetation (Table 9) is 425.5 × 10^{15} kcal per year. This value is somewhat higher than Golley's (1972) estimate of 378 × 10^{15} kcal, which was obtained by summing estimated totals for estimated areas of the major vegetation types. Half of the total in Table 9 is fixed by the tropical region from 20° N to 20° S. The total annual energy fixation of the Northern Hemisphere (about 275 × 10^{15} kcal, or 65% of the total) is almost twice that of the Southern Hemisphere (about 150 × 10^{15} kcal). The latitudinal trend is generally the same as that for production and respiration but is complicated by the occurrence of a broad zone in each hemisphere (20–60°) in which latitudinal mean energy-fixation values change only slightly, all falling between 2.0 and 3.0 × 10^3 kcal/m^2/year. These plateaus spanning the temperate zones of both hemispheres are mainly the result of the greater ecoclimatic and physiognomic diversity of these regions. The energy-fixation trend in the Northern Hemisphere is inverted across the entire temperate zone, though values differ only slightly.

10. Although net production could be increased, theoretically, by the elimination or reduction of photorespiration, it seems that the sharp increase in dark respiration in the tropical regions necessarily limits the yields which can be expected there. Expressed in average net productivity (Table 7), the productive potential of the extrapolar world seems to be divided into three distinct zones (each with considerable internal variation): the tropical (1000–2000 g/m^2/year), the Northern Hemisphere temperate (500–800 g/m^2/year), and the Southern Hemisphere subtropical (800–1000 g/m^2/year).

Conclusion

The above results are to be treated as initial estimates. The estimates of gross productivity and dark respiration represent the first such quantitative attempts on a global and regional scale. It is hoped that they and the regional results for net productivity and energy fixation will encourage more attempts to assess quantitatively both local and world-scale ecological energetics.

The values for gross productivity and dark respiration also provide quantitative guidelines for further work on production-respiration balances of entire ecosystems and on annual and diurnal courses of production and respiration in plants and plant stands. These are problems of central importance to ecosystems and physiological ecology.

Additional measurements of dark respiration (gross production) are needed in order to refine the respiration and gross productivity models. Net productivity and more basic environmental factors should also be measured concurrently, so that models relating respiration and gross productivity to environmental variables can be refined or newly developed. The author would be grateful to have such data sent to him.

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