Geo-Eco-Trop, 1977, 1 (2), 95-102

RATES OF PRIMARY PRODUCTIVITY IN TROPICAL GRASSLAND, SAVANNA AND FOREST

Peter G. MURPHY *

RÉSUMÉ.

Estimation de la productivité primaire de prairies, savanes et forêts tropicales. L'auteur passe en revue les données disponibles relatives aux estimations de la productivité primaire pour quatre biomes tropicaux essentiels : la prairie (13 stations), la savane (19 stations), la forêt tropicale (4 stations) et la forêt sempervirente ombrophile (10 stations). Les valeurs moyennes de la productivité primaire nette, exprimée en T/ha/an, sont respectivement de 10,8 ; 8,9 ; 16,2 et 24,0. Les priorités pour les futures recherches écologiques de la productivité en régions tropicales sont données.

ABSTRACT.

The author reviews the available data on rates of primary productivity in four major tropical terrestrial biomes : grassland (13 sites), savanna (19 sites, seasonal forest (4 sites) and evergreen rain forest (10 sites). Average values of net primary productivity in mt/ha/yr are respectively of 10.8, 8.9, 16.2 and 24.0. Recommendations for future research in tropical production ecology are given.

INTRODUCTION

The objective of this paper is to review the available data on rates of primary productivity in four major categories of tropical terrestrial ecosystems : grassland, savanna, seasonal forest and evergreen rain forest. This brief review is based upon two other more comprehensive papers on this topic (MURPHY 1975,1977).

Definitions are in order. Gross primary productivity (GPP) is the total solar energy photosynthetically fixed as organic matter by an ecosystem in a given period of time. GPP includes the fraction of energy that is utilized in autotrophic respiration (R.) The fraction of energy (or organic matter) that remains following respiration loss is net primary productivity (NPP). The equation : GPP = NPP + autotrophic R summarizes this relationship.

Methods most commonly used to estimate NPP include the harvest method, involving the periodic measurement of biomass accrual, most commonly used for herbaceous vegetation, and allometric methods, utilizing dimensional relationships that allow difficult to measure parameters, such as biomass, to be estimated from easily measured parameters, such as stem diameter in trees. In some cases

* Department of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan, 48824, U.S.A.

total forest NPP has been estimated from the productivity of just a portion of the vegetation, for example foliage, a factor then being used to convert to total NPP. In steady state ecosystems, total annual litter production has been used to estimate annual NPP, as rate of soil (with litter) respiration, total heterotrophic R being assumed equal to NPP.

The estimation of GPP involves measurement of autotrophic R, most easily accomplished by measuring rates of CO^2 exchange. Very few data on GPP for tropical ecosystems are available.

Most of the existing data on productivity are for temperate and boreal ecosystems. The data for tropical ecostems are relatively scarce, especially considering that tropical ecosystems occupy such a large area of the earth. In the tables of net productivity values that follow, many of the values are only estimates based on the limited data actually published by the authors cited. Assumptions made in making the estimates are described in the footnotes.

RATES OF NET PRIMARY PRODUCTIVITY (NPP)

Grassland. Table 1 shows annual rates of NPP for 13 grassland sites in India, South Africa, and Australia. NPP ranges from 0.4 metric tons per hectare per

Table 1. Annual NPP in tropical grassland.

Location	Approximate growing season (days)	Annual rainfall (mm)	Total annual NPP (mt/ba)	Reference
Varanasi, India 25°18'N 83°1'E	120	725	14.2	Ambasht et al., 1972
Varanasi, India 25°18'N 83°1'E	120	725	10.6	Choudhary, 1972
Varanasi, India 28°18'N 83°1'E	120	725	6.5**	Choudhary, 1972
Varanasi, India 28°18'N 83°1'E	120	725	7.9*	Singq, 1968
Chakia, Varanasi, India 25°18'N 83°1'E	150	1000	38.1	Ambasht et al., 1972
Kurukshetra, India 29°58'N 76°50'E	120	770	29,8	Singh and Yadava, 1972
Jodhpur, India 26°15'N 73°3'E	90	289	1.8*	Gupta et al., 1972
Delhi, India 28°54'N 77°13'E	120	800	13.3*	Varshney, 1972
Udaipur, Iqdia 24°32'N 73°25'E	90	627	3.0*	Vyas et al., 1972
South West Africa	—	360	5.2*	Walter, 1964
Pretoria, South Africa 25°43'S 28°16'E	—	607	1.5*	Bourlière and Hadley, 1970
Springbok Flats, South Africa 29°35'S 17°55'E	—	162	1.7*	Louw, 1968
Katherine, Australia 14°15'S 132°20'E	110	660	2.5*	Norman, 1963

* Includes an estimated 40 % for unmeasured below ground parts (based on the data of Varshney, 1972).

** Includes an estimated 52 % for unmeasured below ground parts (based on the data of Choudhary, 1972).

year (mt/ha/yr) to 38.1 mt/ha/yr. The low values occur in areas that receive less than 700 mm of annual precipitation. The high value of 38.1 represents a moist, successional Indian grassland, dominated by the C-4 species *Heteropogon contortus*. On sites that receive between 700 and 1000 mm of rain annually, NPP ranges above 6.5 mt/ha/yr. Average NPP, based on 11 representative sites, is 10.8 mt/ha/yr. All of the available estimates were obtained using the harvest method. In most cases root production was merely estimated, as indicated in the footnotes.

Savanna. Table 2 shows annual rates of NPP for 19 savanna sites in India, Nigeria, Ghana, Ivory Coast, Senegal, Chad, Rhodesia, Tanzania, Zaïre, Vene-

Table 2. Annual NPP in tropical savanna.

Location	Approximate growing season (days)	Annual rainfall (mm)	Total annual NPP (mt/ha)	Reference
Jodhpur, India 26°15'N 73°3'E	90	361	14.5	Bazilevich and Rodin, 1966
Rajastan, India 31°20'N 72°00'	—	610	7.3	Rodin and Bazilevich, 1965
Gir Forest, India	120	820	6.8*	Bourlière and Hadley, 1970 (data of Hodd)
Gir Forest, India	120	820	4.8*	Bourlière and Hadley, 1970 (data of Hodd)
Olokemeji, Nigeria 8°57'N 6° 30'E	270	1168	11.3*	Hopkins, 1965 and 1968
Shika, Nigeria 8°57'N 6°30'E	200	1118	5.7*	Rains, 1963
Eruja, Ghana 8°N 2°W (Approx.)	—	1500	14.5*	Nye and Greenland, 1960
Lamto, Ivory Coast 7° 43'N 6°30'W	270	1370	16.6*,OD	Roland, 1967
Richard-Toll, Senegal 14°53'—14°58'W	60	300	0.7*	Morel and Bourlière, 1962
Lidney, Chad 17°N 19°E (approx.)	40	320	0.7*	Gillet, 1967
Mohi, Chad 17°N 19°E (approx.)	40	320	2.0*	Gillet, 1967
Rimé, Chad 17°N 19°E (approx.)	40	320	2.3*	Gillet, 1961
Tebede, Chad 17°N 19°E (approx.)	40	320	5.3*	Gillet, 1967
Matopos, Rhodesia 17°50'S 29°30'E	—	650	2.3*	Bourlière and, Badley, 1970 (data of West)
Serengeti, Tanzania 6°48'S 33°58'E	—	700	8.7*	Bourlière and Hadley 1970 (data of Verschuren)
Kivu, Albert Park, Zaïre	—	860	8.0*	Bourlière and Hadley, 1970 (data of Verschuren)
Kivu, Albert Park, Zaïre	—	860	29.2*	Bourlière and Hadley, 1970 (data of Verschuren)
Llanos of Venezuela	130	1300	5.3*	Blydenstein, 1962
Costa Rica	—	2044	23.2*	Daubenmire, 1972

* Includes an estimated 40 % for unmeasured below ground parts (based on the data of Varshney, 1972).
OD Oven-dry weight estimated as 50 % of fresh weight.

zuela and Costa Rica. Rates of NPP range from 0.7 mt/ha/yr to 29.2 mt/ha/yr and average 8.9 mt/ha/yr. In general, NPP increases with increasing annual precipitation. Many of these estimates were derived by the authors from measurements of biomass at the end of the growing season ; these values may, therefore, underestimate true productivity by as much as 30 to 75 % because of turnover during the growing season (MATHEWS and WESTLAKE, 1969).

Seasonal forest. Table 3 shows annual rates of NPP for four seasonal forest sites in India, Ivory Coast, Nigeria and Venezuela. Rates of NPP range from 11.4 mt/ha/yr to 24.6 mt/ha/yr and average 16.2 mt/ha/yr. As indicated by the footnote, two of these estimates were obtained from measurements of litter production.

Table 3. Annual NPP in tropical seasonal forest.

Location	Approximate growing season (days)	Annual rainfall (mm)	Total annual NPP (mt/ha)	Reference
Varanasi, India 25°18'N 83°1'E	120	1040	15.5	Bandhu, 1971
Ivory Coast 5° N 5°W (approx.)	—	1500	13.4	Muller and Nielsen, 1965
Ihadan, Nigeria 7°26'N 3°48'E	—	1230	11.4*	Madge, 1965
Calabozo Plains, Venezuela 8°48'N 67°27'W	—	1200	24.6*	Medina and Zelwer, 1972

Evergreen rain forest. Table 4 shows annual rates of NPP for 10 evergreen rain forest sites in Thailand, Indonesia (Java), Sarawak, Ivory Coast, Ghana, Zaïre, Brazil, Venezuela and Puerto Rico. Rates of NPP range from 10.3 mt/ha/yr for a lower montane forest in Puerto Rico to 32.1 mt/ha/yr for lowland forest in Sarawak. Average NPP for nine representative sites is 24 mt/ha/yr.

Average annual rates of autotrophic R have been determined in only a few tropical ecosystems. Consequently, there are few estimates of GPP in the literature. F.B. GOLLEY (personal communication) recently summarized the available estimates of GPP for tropical forests and found that GPP for nine tropical forest ecosystems, ranging from seasonal forest to mangrove swamp, ranged from 32 mt/ha/yr to 144 mt/ha/yr and averaged 86 mt/ha/yr. Since average NPP for tropical forest, wet and dry, is about 21.6 mt/ha/yr, autotrophic respiration must, on the average, account for about 75 % of GPP. The dryer, seasonal forests seem to have lower rates of R relative to GPP, about 69 %, than the moister, evegreen forests which average about 81 %, although at this time the scarcity of the data dictate against accepting this pattern as a generalization.

* Estimated by multiplyng annual leaf litter production or annual leaf litter respiration by three (based on data presented by BRAY and GORHAM, 1964). Some of these estimates may be hight because in some cases litter samples included small branches.

Table 4. Annual NPP in tropical evergreen rain forest

Location	Approximate growing season (days)	Annual rainfall (mm)	Total Annual NPP (mt/ha)	Reference
Thailand 7°35'N 99°00E	365	2000	28.6	Kira et al., 1967
Tjibodas, Java 7°S 107°E (approx.)	365	2000	24.3 +	Wanner, 1970
Sarawak 3°N 112°E (approx.)	365	3800	32.1 +	Wanner, 1970
Ivory Coast 5°N 5°W (approx.)	365	—	24.6 +	Bernhard-Reversat et al., 1972
Ghana 8°N 2°W (approx.)	365	—	24.3	Nye, 1961
Congo 3°S 13°48'E	365	—	31.5	Bartholomew et al., 1953
Manaus, Brazil 3°01'S 60°00'W	365	1800	16.8+	Klinge, 1968
Rancho Grande, Venezuela 5°N 65°W (approx.)	365	1750	23.4+	Medina and Zelwer, 1972
El Verde, Puerto Rico 18°N 66°W (approx.)	365	3800	10.3	Jordan, 1971
El Verde, Puerto Rico 18°N 66°W (approx.)	365	3800	12.3 ‖	Odum and Jordan, 1970, & Odum, 1970

RATES AND EFFICIENCIES OF NPP ACROSS LATITUDE

Table 5 shows average rates of annual NPP in tropical, temperate, and borea grassland and forest. Tropical rain forests are 1.8 times more productive than temperate forests and 3 times more productive than boreal forests. If the NPP of

Table 5. Comparison of NPP in temperate[1] and tropical forest and grassland

	Latitude	Growing Season (Days)	Mean Annual NPP (g/m2)	Total Radiation[2] (kcal/m2/G.S.)[4]	NPP (g/1000kcal)	NPP Efficiency[3] (cal NPP/cal rad) × 100
Boreal Forest	50°N	100	800	717,020	1.1	0.4 %
Temperate Forest	40°N	180	1300	1,289,890	1.0	0.4
Tropic. Rain Forest	0°	365	2400	2,452,160	1.0	0.4
Temperate Grassland	40°N	180	500	1,289,890	0.4	0.2
Tropical Grassland	15°N	116	1080	828,500	1.3	0.5

‖ Based on rates of CO_2 exchange.
\+ Estimated by multiplying annual leaf litter production or annual leaf litter respiration by three (based on data presented by BRAY and GORHAM, 1964). Some of these estimates may be high because in some cases litter samples included small branches.
1 Average rates of NPP for temperate ecosystems were obtained from WHITTAKER (1970).
2 Solar radiation input was estimated from a table of total possible radiation, by month and latitude, presented by KONDRATYEV (1969).
3 It was assumed that the caloric content of one gram of oven dried plant tissue is four kilocalories.
4 G.S. = growing season.

forests at different latitudes is compared on the basis of solar radiation available during the growing season, however, the amount of NPP per unit of solar radiation (NPP efficiency) is similar, 0.4 %, across latitude. The actual efficiencies are probably higher than shown because the calculations were based on total, unintercepted radiation rather than that actually available at the earth's surface. The clear implication is that efficiency of NPP is independent of latitude in climatic areas suitable for the occurrence of forest vegetation. Solar radiation available during the growing season is the primary determinant of annual forest NPP.

Tropical grasslands are 2.2 times more productive, annually, than temperate grasslands, even though their growing seasons, on the average, are about 35 % shorter because of moisture constraints. Tropical grassland have an estimated NPP energy efficiency of 0.5 % whereas temperate grasslands average only 0.2 %. These data suggest that tropical grasslands, in addition to being more efficient than temperate grasslands, are more efficient than temperate or tropical forests as well. The reason for this is not known but it may well be due to the fact that tropical grasslands have a high percentage of plant species with the C-4 (efficient) pathway of photosynthesis. The C-4 pathway allows utilization of high light intensities and is well adapted to dry conditions. Temperate grasslands have fewer C-4 species, and woody forest vegetation, at all latitudes, is largely or exclusively C-3 in physiology. Certainly the reasons for these differences in efficiency of NPP among ecosystems need to be explored more thoroughly. In many respects a comparison of efficiencies of GPP would be more meaningful than a comparison of efficiencies of NPP. At present, however, there are insufficient data to accomplish such a comparison.

CONCLUSION

I will conclude with several recommendations for future research in tropical production ecology. More data on both NPP and GPP are needed for all types of ecosystems. The wide variation in values reported here is partially due to the lumping of different ecosystems into over-simplified categories. Additional data will allow a more detailed analysis. A full description of biotic and abiotic ecosystem characteristics is essential for meaningful interpretation of productivity data and for comparison with other studies. The proportions of C-3 and C-4 plants should be indicated whenever the information is available. Additionally, more detail on the components of productivity, i.e. root, stem, foliage, etc., is badly needed. Such data will allow relationships to be derived that will make possible the rapid estimation of total productivity at additional sites, even if only limited data are available. Data on components of NPP are also needed to help in determining possible heterotrophic utilization of the organic production. Finally, there is great need for long term studies. Information on year to year variation in NPP, as it relates to climatic and other environmental fluctuations, is extremely scanty even though this information is essential for development of long term management strategies.

REFERENCES

AMBASHT (R.S.), MAURYA (A.N.), and SINGH (U.N.), 1972. Primary production and turnover in certain protected grasslands of Varanasi, India, p. 43-50. In P.M. Golley and F.B. Golley (eds.) Tropical ecology with an emphasis on organic production. Univ. Georgia, Athens.

BANDHU (D.), 1971. A study of the productive structure of tropical dry deciduous forest at Varanasi. Ph.D. Thesis. Banaras Hindu Univ.

BARTHOLOMEW (W.V.), MEYER (J.) and LAUDELOT (H.), 1953. Mineral nutrient immobilization under forest and grass fallow in the Yangambi (Belgian Congo) region. *Publ. INEAC, Ser.* Sci., 57, 27 p.

BAZILECH (N.I.), and RODIN (L.E.), 1966. The biological cycle of nitrogen and ash elements in plant communities of the tropical and sub-tropical zones. *For. Abst. Leading Serv.*, 38.

BERNHARD-REVERSAT (F.), HUTTEL (C.), and LEMÉE (G.), 1972. Some aspects of the seasonal ecologic periodicity and plant activity in an evergreen rain forest of the Ivory Coast, (in French with English summary) p. 217-218, 219-234. In P.M. Golley and F.B. Golley (eds.) Tropical ecology with an emphasis on organic production. Univ. Georgia, Athens.

BLYDENSTEIN (J.), 1962. The *Trachypogon* savanna in the high plains. Ecological study of the area surrounding Calatgo, Guarico State, Venezuela. *Bol. Soc. Ven. Cienc. Nat.*, 23 : 139-206.

BOURLIÈRE (F.), and HADLEY (M.), 1970. The ecology of tropical savannas, p. 125-152. In R.F. Johnson (ed.) Annual review of ecology and systematics, Vol. 1. Annual Reviews Inc.

BRAY (R.), and GORHAM, 1964. Litter production in forests of the world, p. 101-157. In J.B. Cragg (ed.) Adv. Ecol. Res. Vol. 2. Academic Press.

CHOUDHARY (V.B.), 1972. Seasonal variation in standing crop and net above-ground production in *Dichanthium annulatum* grassland at Varanasi, p. 51-57. In P.M. Golley and F.B. Golley (ed.) Tropical ecology with an emphasis on organic prodlction. Univ. Georgia, Athens.

DAUBENMIRE (R.), 1972. standing crops and primary production in savanna derived from semideciduous forest in Costa Rica. *Bot. Gaz.*, 133 (4) : (4) : 395-401.

GILLET (H.), 1961. Pâturages sahéliens du Ranch de l'ouadi rimé. *J. Agr. Trop. Bot. Appl.*, 8 : N° 10-11, p. 465-536.

GILLET (H.), 1967. Essai d'évaluation de la biomasse végétale en zone sahélienne (végétation annuelle). *J. Agr. Trop. Bot. App.*, 14 : 123-258.

GUPTA (R.K.), SAXENA and SHARM., (S.K.) 1972. Above-ground productivity of grasslands at Jodhpur, India, p. 75-93. In P.M. Golley and F.B. Golley (eds.) Tropical ecology with an emphasis on organic production. Univ. Georgia, Athens.

HOPKINS (B.), 1965. Observations on savanna burning in the Olokemeji Forest Reserve, Nigeria. *J. Appl. Ecol.*, 2 : 367-381.

HOPKINS (B.), 1968. Vegetation of the Olokemeji Forest Reserve, Nigeria : V. The vegetation of the savanna site with special reference to its seasonal changes. *J. Ecol.*, 56 : 97-115.

JORDAN (C.F.), 1971. Productivity of a tropical rain forest and its relation to a world pattern of energy storage. *J. Ecol.*, 59 : 127-142.

KIRA (T.), OGAWA (H.), YODA (K.), and OGINO (K.), 1967. Comparative ecological studies in three main types of forest vegetation in Thailand. IV. Dry-matter production, with special reference to the Khao Chong rain forest. *Nature Life Southeast Asia*, 5 : 149-174.

KLINGE (H.), 1968. Litter production in an area of Amazoniam terra firma forest. Part I. Litter-fall, organic carbon and total nitrogen contents of litter. *Amazonia*, I (4) : 287-301.

KONDRATYEV (K. Ya.), 1969. Radiation in the atmosphere. Academic Press. 912 pp.

LOUW (A.J.), 1968. Fertilizing natural veld on red loam soil of the Springbok flats : 2· Effect of sulphate of ammonia and superphosphate on air-dry yield and mineral content. *S. Afr. J. Agr. Sci.*, 11 : 629-636.

MADGE (D.S.), 1965. Leaf fall and litter disappearance in a tropical forest. *Pedobiologia*, 5 (4) : 273-288.

MATHEWS (C.P.), and WESTLAKE (D.F.), 1969. Estimation of production by populations of higher plants subject to high mortality. *Oikos*, 20 : 156-160.

MEDINA (E.), and ZELWER (M.), 1972. Soil respiration in tropical plant communities, p. 245-267. In P.M. Golley and F.B. Golley (eds.) Tropical ecology with an emphasis on organic production. Univ. Georgia, Athens.

MOREL (G.), and BOURLIÈRE (F.), 1962. *Terre et Vie*, 16 : 371-393.

MULLER (D.), and NIELSEN (J.), 1965. Production brute, pertes par respiration et production nette dans la fôret ombrophile tropicale. *Forstl. Forsogsv. Danm.*, 29 : 69-160.

MURPHY (P.G.), 1975. Net primary productivity in tropical terrestrial ecosystems. In :H. Lieth and R.H. Whittaker (eds.) Primary productivity of the biosphere. Springer-Verlag, 352 pp.

MURPHY (P.G.), 1977. Producciôn de materia orgânica. In : E. Medina and H. Klinge (eds.) Fundamentos de la ecologia de los tropicos (in prep.).

NORMAN (M.J.T.), 1963. The pattern of dry matter and nutrient content changes in native pastures at Katherine, N.T. Aust. *J. Exp. Agr. Anim. Husb.*, 3 : 119-124.

NYE (P.H.), 1961. Organic matter and nutrient cycles under moist tropical forest. *Plant Soil*, 8 : 333-346.

NYE (P.H.), and GREENLAND (D.J.), 1960. The soil under shifting cultivation. *Tech. Commun. Commonw. Bur. Soils*, 51 : 1-156.

ODUM (E.P.), and ODUM (H.T.), 1959. Fundamentals of ecology, Chapter 3. W.B. Saunders, Co. 546 pp.

ODUM (H.T.), 1970. Summary : An emerging view of the ecological system at El Verde, p. I-191 to I-289. In H.T. Odum and R.F. Pigeon (eds.) A tropical rain forest. Division of Technical Inf., USAEC.

ODUM (H.T.), and JORDAN (C.F.), 1970. Metabolism and evapotranspiration of the lower forest in a giant plastic cylinder, p. I-165 to I-189. In H.T. Odum and R.F. Pigeon (eds.) A tropical rain forest. Division of Technical Inf. USAEC

RAINS (A.B.), 1963. Grassland research in northern Nigeria 1952-1962. *Misc. Pap. Inst. Agr. Res., Samaru*, 1 : 1-67.

RODIN (L.E.), and BAZILEVICH (N.I.), 1965. Prodlction and mineral cycling in terrestrial vegetation. Oliver and Boyd, London. 288 pp.

SINGH (J.S.), 1968. Net above-ground community productivity in the grasslands at Varanasi, p. 631-653. In R. Misra and B. Gopal (eds.) Proc. Symp. Recent Adv. Trop. Ecol. 2. Int. Soc. Trop. Ecol., Varanasi.

SINGH (J.S.), and YADAVA (P.S.), 1972. Biomass structure and net primary productivity in the grassland ecosystem at Kurukshetra, p. 59-74. In P.M. Golley and F.B. Golley (eds.) Tropical ecology with an emphasis on organic production. Univ. Georgia, Athens.

VARSHNEY (C.K.), 1972. Productivity of Delhi grasslands, p. 27-42. In P.M. Golley and F.B. Golley (eds.) Tropical ecology with an emphasis on organic production. Univ. Georgia, Athens.

VYAS (L.N.), GARG (R.K.), and AGARWAL (S.K.), 1972. Net above-ground production in the monsoon vegetation at Udaipur, p. 95-99. In P.M. Golley and F.B. Golley (eds.) Tropical ecology with an emphasis on organic production. Univ. Georgia, Athens.

WALTER (H.), 1954. Le facteur eau dans les régions arides et sa signification pour l'organisation de la végétation dans les contrées sub-tropicales, p. 27-39. In colloques Internationaux du Centre National de la Recherche Scientifique, Vol. 59. Les Divisions Ecologiques du Monde. Centre National de la Recherche Scientifique, Paris.

WANNER (H.), 1970. Soil respiration, litter fall and productivity of tropical rain forest. *J. Ecol.*, 58 : 543-547.

WHITTAKER (R.H.), 1970. Communities and ecosystems. Macmillan Co. 162 pp.